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FISH COMMUNITIES OF SUBTROPICAL SEAGRASS MEADOWS AND ASSOCIATED HABITATS IN SHARK BAY, WESTERN AUSTRALIA

Michael R. Heithaus

ABSTRACT

Seagrass habitats support some of the most productive marine communities and provide critical habitat for many fish species. Previous studies have shown that fish communities of seagrass meadows are usually more diverse than those of adjacent habitats. However, most studies have been conducted in very shallow waters and generally have used seining methods to collect fish, which tend to select for slower species as well as small species and size classes. Antillean–Z style fish traps were used to study the fish communities of seagrass and associated habitats in both deep and shallow waters of Shark Bay, Western Australia. While more individuals were caught per trap in vegetated than in unvegetated habitats, the number of species and biomass was influenced by an interaction of depth and seagrass cover. The structure of fish communities was influenced by an interaction among season, seagrass cover, and depth. Unlike previous studies, a small number of species dominated fish trap catches, most notably, striped trumpeters, *Pelates sexlineatus* Quoy and Gaimard, 1925 and western butterfish, *Pentapodus vitta* Quoy and Gaimard, 1824. The factors that influenced the abundance of common species, including season, depth, and seagrass cover, often interacted and varied among species. This study suggests that future research on fish communities of seagrass ecosystems would benefit from using several sampling techniques and considering multiple environmental factors simultaneously.

Seagrass meadows are among the most productive ecosystems in the world and provide critical habitat for many species of fish by providing protection from predators as well as abundant food resources (Bell and Pollard, 1989; Connolly 1994a). Seagrass ecosystems are under increasing pressure and many seagrass habitats are being destroyed rapidly (Shepherd et al., 1989). In order to understand and protect these critical habitats, it is important to document the communities supported by undisturbed seagrass ecosystems and understand the factors that naturally influence the distribution and abundance of associated species. The seagrass beds of Shark Bay, Western Australia, are not under threat of human destruction, owing largely to Shark Bay's remote nature, relatively low commercial fishing pressure, and its listing as a United Nations World Heritage area in 1991. Thus, Shark Bay provides an opportunity to investigate the fish communities of seagrass beds in a relatively undisturbed ecosystem.

Fish communities in seagrass habitats are usually both more diverse and contain more individuals than adjacent unvegetated areas (Black et al., 1990; Ferrell and Bell, 1991; Connolly, 1994b; Gray et al., 1996), but this pattern is not universal (Hanekom and Baird, 1984). Most studies on fishes in seagrass habitats have been carried out in very shallow waters (e.g., <1.5 m, Ferrell and Bell, 1991; Gray et al., 1996), and although differences in species composition and abundance have been found between deep and shallow seagrass beds (Bell et al., 1992; Travers and Potter, 2002), the generality of these results is unclear. In addition, sampling techniques have been limited largely to seining or trawling, which tend to be selective for smaller species and size classes (Ferrell and Bell, 1991; Gray et al., 1996; de Troch et al., 1996), and are likely to be more efficient at catching slow-moving species than large mobile ones (Travers and Potter, 2002). Fish

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traps have been used successfully to sample fish communities in tropical estuaries (e.g., Sheaves, 1992, 1995) and may provide insights into the fish communities of seagrass habitats different from those obtained by seining and trawling methods because they capture larger individuals, are able to sample fast-swimming species, and can readily be used in a variety of water depths.

In this study, I used Antillean-Z fish traps to investigate the structure and diversity of fish communities as well as the distribution and abundance of particular fish species in seagrass habitats and associated unvegetated areas of both shallow and deep habitats. The goals of this study were to 1) describe the fish communities of the Eastern Gulf of Shark Bay using fish traps; 2) determine the patterns of species richness and diversity among different habitats and seasons; 3) determine the factors that influence the distribution and abundance of common fish species; and 4) investigate seasonal changes in the size distribution of common species.

Methods

Study Site.—The study was conducted from June–December 1997, March–July 1998, and February–July 1999 in the Eastern Gulf of Shark Bay, Western Australia (~25°45′S, 113°44′E; Fig. 1). Shark Bay is a large, semi-enclosed bay with extensive shallow seagrass beds (< 4 m depth), surrounded by deeper waters (embayment planes, 6–15 m). The boundaries between habitats are generally distinct. To minimize edge effects, areas 4–6 m deep were not included in analyses. Shallow habitats are predominantly covered by seagrasses (~85–90% cover; primarily monospecific stands of *Amphibolis antarctica* Sonder and Ascherson, 1867 and occasionally *Posidonia australis* Hooker, 1858), but also contain patches of sand. In contrast, deep habitats (generally > 7.5 m) are covered largely by sand or silt with some isolated seagrass patches (~2–10% seagrass cover). The habitats in this study were classified by two factors: depth (shallow, deep) and cover (seagrass, no seagrass).

Shark Bay is situated at the boundary between tropical and temperate waters and both warm- and cold-water fish species are present (Hutchins, 1990). Seasonal fluctuations in water temperatures are found in the study site, which correspond to dramatic changes in the abundance of several species of large vertebrates (Heithaus, 2001). During warm months surface water temperatures are generally above 20°C but they drop to a minimum of 14°C in the winter months. Due to the mixed species composition of the bay, these seasonal fluctuations in water temperature may influence the abundance of some species. For the purposes of this paper, seasons are defined as "warm" (September–May) or "cold" (June–August), based on both water temperature and the timing of seasonal shifts in the community of large vertebrates present in the bay (see Heithaus, 2001).

Field Methods.—Fish were captured with Antillean-Z fish traps. Traps were ~1.1 m long, 0.6 m tall, and 0.6 m wide and had straight, conical entrances that were tapered from ~40 × 25 cm to 25 × 15 cm at the opening into the trap (see Sheaves, 1992 for a detailed description of trap design). Traps were covered with a small (12 mm) square wire mesh or a larger (35 mm) hexagonal mesh. Traps were baited with ~250 g of cut pilchards *Sardinops neopilchardus* (Steindachner, 1879) placed in a bait capsule hung from the ceiling of the trap. The bait capsules were made of PVC pipe that was capped at both ends and had numerous 10 mm holes to allow water to flow easily through the capsule while preventing bait removal by fish in the trap.

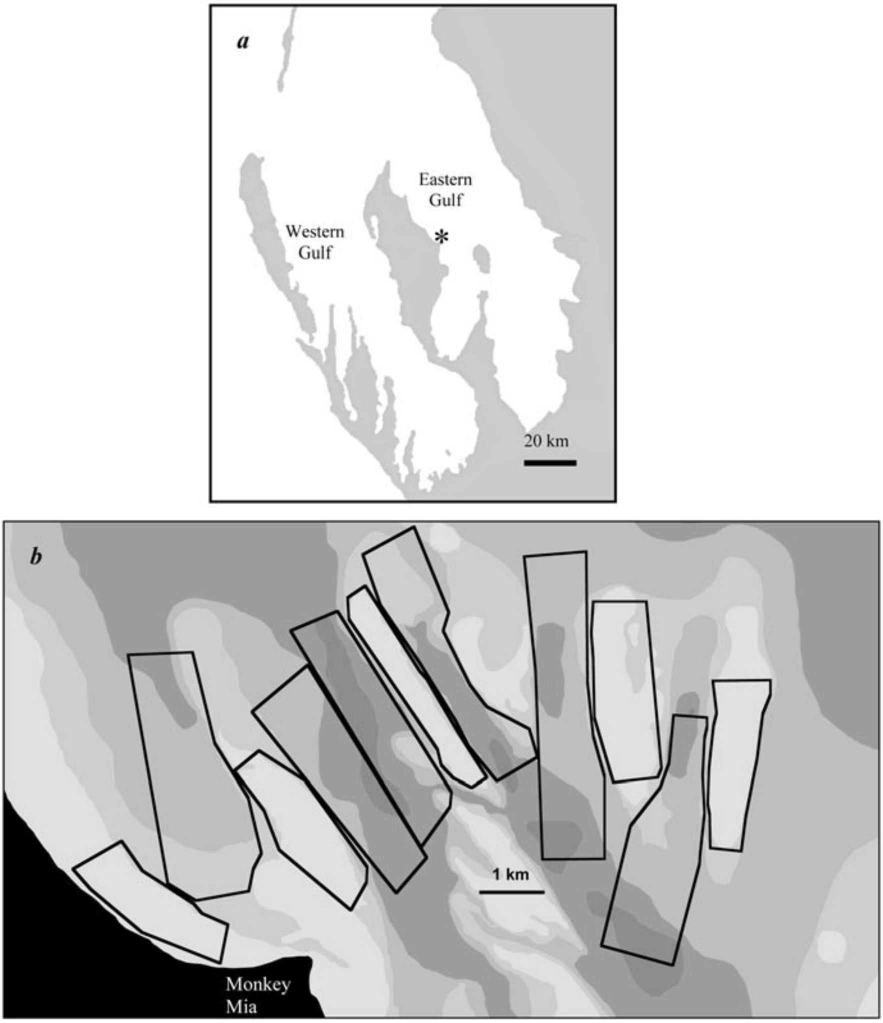


Figure 1. A) Shark Bay, Western Australia. The study site was located in the Eastern Gulf and is indicated with an asterisk. B) The study area was divided into eleven sampling zones for fish trapping, indicated with polygons. The lightest color represents shallow water (< 2 m at MSLW) and successively darker colors represent waters 2–5 m, 5–7 m, 7–9 m, and > 9 m. Land is black.

Up to ten traps were set concurrently from an 11 m catamaran. In most cases, traps were set simultaneously in both deep and shallow habitats to avoid biases caused by tidal or diel movements of fishes. In addition, an equal proportion of small- and large-mesh traps were placed in each habitat to remove potential biases of mesh size on catches (Sheaves, 1995). The location of the initial trap in a habitat was haphazard but further traps were placed along a line, spaced at least 80 m apart (usually over 150 m) to avoid overlap in catch radii, which was generally < 40 m (Sheaves, 1992). Traps were "soaked" for ~2 hrs to maximize catch rate and minimize trap saturation (Sheaves, 1995). When traps were recovered, the fork length (FL) of every fish was measured and a sample of individuals of each species was weighed using an Ohaus electric balance (Model LS2000, 2000 g capacity, 1.0 g accuracy). All individuals were returned to the water alive. For those species in which many individuals were occasionally caught in a single trap, length-weight relationships (Table 1) were used to determine biomass without weighing all individuals. Sharks were omitted from biomass analyses due to their disproportionately large size. However, inclusion of sharks in biomass estimates does not change general results.

STATISTICAL METHODS.—Patterns of species composition and abundance within fish communities were described with principal components analysis. To improve the quality of this analysis, only species with more than 90 individuals were included and all data were log (x + 1) transformed prior to analysis (Clarke and Green, 1988). Only principal components with eigenvalues > 1.0 were included in subsequent analyses (Tabachnick and Fidell, 1983). Species were considered an important factor of a principal component if their loading value was > 0.55 or < –0.55 (Tabachnick and Fidell, 1983).

The influences of season, depth, and seagrass cover on the number of species and individuals captured per trap, biomass per trap, and catch rates of each of the ten most common species were investigated using a three-way factorial general linear model design with all analyses conducted in JMP IN 4.0.3 (SAS Institute Inc.). Season, depth, and cover were all treated as class variables and fixed effects. Count data were square root transformed and biomass data were log (x + 1) transformed and checked for homogeneity of variances using Bartlett's test (Zar, 1984). Non-significant interactions with P > 0.10 were removed from analyses. If two factors showed a significant interaction, the factors involved were not considered as main effects regardless of significance level. Similarly, if the three-way interaction was significant, I did not further consider the two-way interactions and main effects. Tukey's test, which corrects for multiple comparisons, was used to determine significant differences among means in the case of interactions.

The influences of season, depth, and cover on community structure were determined with MANOVA on principal component scores for each trap set that captured fish. Factors were considered fixed effects and non-significant interaction terms were removed from the analysis. I used contrasts in JMP IN 4.0.3 (SAS Institute, Inc.) to determine significant differences among means in the case of interactions, and F-tests to determine which factors had significant effects on individual principle components. All P-values from both contrasts and F-tests were Bonferroni corrected for multiple comparisons.

Table 1. Length (mm) – weight (g) relationships of 11 species used to generate biomass estimates.

Species	N	Equation	R^2
Amniataba caudavittata	18	$Y = 2.9659e^{0.0195x}$	0.91
Apogon rueppellii	16	$Y = 0.2259e^{0.0452x}$	0.92
Choerodon rubescens	6	$Y = 2.9889e^{0.0182x}$	0.91
Pagrus auratus	68	$Y = 6.6011e^{0.0164x}$	0.96
Lethrinus laticaudis	23	$Y = 1.7954x – 20.715$	0.92
Monacanthus chinensis	12	$Y = 0.3691x – 20.215$	0.94
Pelates sexlineatus	252	$Y = 3.3898e^{0.0167x}$	0.93
Pentapodus vitta	168	$Y = 1.5230e^{0.0221x}$	0.95
Psammoperca waigiensis	30	$Y = 4.2952e^{0.0160x}$	0.97
Rhabdosargus sarba	28	$Y = 1.2605x – 113.160$	0.95
Saurida undosquamis	12	$Y = 3.8252e^{0.0128x}$	0.94

RESULTS

COMMUNITY STRUCTURE.—Overall, 648 traps were set for ~1296 hrs. Traps were set in vegetated shallow (n = 198), unvegetated shallow (n = 40), vegetated deep (n = 37), and unvegetated deep (n = 373) habitats. Of these sets, 294 were during warm months and 354 during cold months. In total, 13,734 individuals representing 31 fish species from 23 families were captured (Table 2). Additionally, five bar-bellied sea snakes (*Hydropis elegans* Grey, 1842) were caught. *Pelates sexlineatus* numerically dominated the catch (76.8%) followed by *P. vitta* (13.0%). *Pagrus auratus* Forster, 1801 (1.7%), *Amniataba caudavittata* Richardson, 1845 (1.4%), and *Rhabdosargus sarba* Forskaal, 1775 (1.2%) were the only other species to contribute over 150 individuals to the catch (Table 2). Together these five species accounted for over 93% of the individuals captured.

There were both qualitative and quantitative differences in community composition among habitats. Although *P. sexlineatus* and *P. vitta* dominated all habitats, the relative abundance of *P. sexlineatus* was far greater in seagrass habitats of both deep and shallow areas while in unvegetated habitats, *P. vitta* was dominant (Fig. 2).

Four principal components (each defining a group of species that tend to covary) had eigenvalues > 1.0. Together, they explained 59% of the variation in fish communities (Table 3). Only nine species were identified as significant factors in principal components. In all cases, loading factors were positive, indicating that principle components were influenced by the presence of these species. PC1 was characterized by the presence of *R. sarba*, *P. vitta*, and *Pelates quadrilineatus* Bloch, 1770 and PC2 was driven primarily by *P. sexlineatus* and *A. caudavittata*. *Lethrinus laricaudis* Alleyne and Macleay, 1877 and *P. auratus* were the significant species in PC3 while PC4 was characterized by *Psammoperca waigiensis* Cuvier, 1829 and *Apogon rueppellii* Günther, 1859.

A three-way interaction (Table 4) among seagrass cover, depth, and season influenced community structure (i.e., principal component scores), but community components responded to different factors. Both PC1 and PC4 were influenced by the three-way interaction (Table 5). The abundance of species associated with PC1 was high during cold months in both types of shallow habitat and deep vegetated ones and lowest during warm months and in unvegetated habitats (Fig. 3). PC4 was highest in shallow habitats during warm months, but abundances of *P. waigiensis* and *A. rueppellii* were low in cold months, especially in unvegetated areas (Fig. 4). The *P. sexlineatus* and *A. caudavittata* species group (PC2) was more abundant in shallow habitats and in seagrass covered areas than in deep habitats and unvegetated ones, while the species that constitute PC3 were more abundant in deep habitats (Table 5). However, *L. laricaudis* and *P. auratus* (PC 3) were also relatively abundant in seagrass areas during warm months (Fig. 5).

COMMUNITY DIVERSITY AND FISH ABUNDANCE.—Overall, a similar number of species was caught in shallow and deep areas, but more species were caught in areas covered by seagrass than in unvegetated areas (Table 2). Eight of 23 species (34.8%) represented by more than a single individual were restricted to one depth range with five in deep waters and three in shallow waters. Most notably, *P. auratus* was found only in deep habitats and *A. caudavittata* only in shallow waters. Five species were found only over seagrass, including *A. caudavittata* and *P. quadrilineatus*, and three species were found only over unvegetated areas.

The number of species caught per trap set was influenced by an interaction between depth and cover and an interaction between season and depth (Table 6). More species were caught per trap in deep seagrass-covered areas than any other habitat and the few-

Table 2. Overall catches and occurrences of fish species caught in fish traps. D = deep, S = shallow, Y = seagrass present, N = seagrass absent. Habitat and cover type in bold represent the most common occurrence.

Scientific name	Common name	N	Habitat	Cover
Apogonidae				
Apogon rueppellii	Gobbleguts	100	D, **S**	**Y**, N
Carangidae				
Selaroides leptolepis	Smooth tailed trevelly	41	**D**	**N**
Carcharhinidae				
Carcharhinus amblyrhychos	Grey reef shark	1	**S**	**Y**
Centropomidae				
Psammoperca waigiensis	Sand bass	91	D, **S**	**Y**, N
Chaetodontidae				
Chelmon marginalis	Marginated coralfish	1	**D**	**N**
Congridae				
Unidentified		1	**S**	**Y**
Gerreidae				
Gerres subfasciatus	Roach	1	**S**	**Y**
Harpadontidae				
Saurida undosquamis	Large-scaled grinner	8	**D**	**N**
Hemiscyllidae				
Chilioscyllium punctatum	Grey carpet shark	7	**S**	**Y**
Labridae				
Choerodon cauteroma	Bluespotted tuskfish	16	**S**	**Y**
Choerodon cyanodus	Blue tuskfish	10	D, **S**	**Y**
Halichoeres brownfieldi	Brownfield’s wrasse	1	**S**	**Y**
Lethrinidae				
Lethrinus laticaudis	Black emperor	92	D, **S**	**Y**, N
Lutjanidae				
Lutjanus carponotatus	Stripey seaperch	6	**D**	**N**
Monacanthidae				
Monacanthus chinensis	Fan-bellied leatherjacket	102	D, **S**	**Y**, N
Scobinichthys granulatus	Rough leatherjacket	16	D, **S**	**Y**, N
Mugiloididae				
Parapercis nebulosa	Red barred grubfish	9	**D**	**N**
Mullidae				
Upeneus tragula	Bartailed goatfish	6	**D**, S	Y, **N**
Nemipteridae				
Pentapodus vitta	Western butterfish	1,782	**D**, S	Y, **N**
Orectolobidae				
Orectolobus ornatus	Banded wobbegong	1	**S**	**Y**
Pseudochromidae				
Labracinus lineatus	Lined dottyback	34	D, **S**	**Y**, N
Platycephalidae				
Cymbacephalus nematophthalmus	Fringe-eyed flathead	1	**S**	**Y**
Scorpaenidae				
Apistops sp.	Waspfish	1	**D**	**N**
Sparidae				
Rhabdosargus sarba	Tarwhine	161	D, **S**	**Y**, N
Pagrus auratus	Pink snapper	240	**D**	Y, **N**
Teraponidae				
Amniataba caudavittata	Yellowtail trumpeter	198	**S**	**Y**
Pelates sexlineatus	Striped trumpeter	10,548	D, **S**	**Y**, N
Pelates quadrilineatus	Trumpeter	144	D, **S**	**Y**
Tetraodontidae				
Torquigener pleurogramma	Banded toadfish	73	**D**, S	Y, **N**
Torquigener pallimaculatus	Orange-spotted toadfish	40	**D**, S	Y, **N**
Lagocephalus sceleratus	Silver toadfish	2	D, S	Y, N

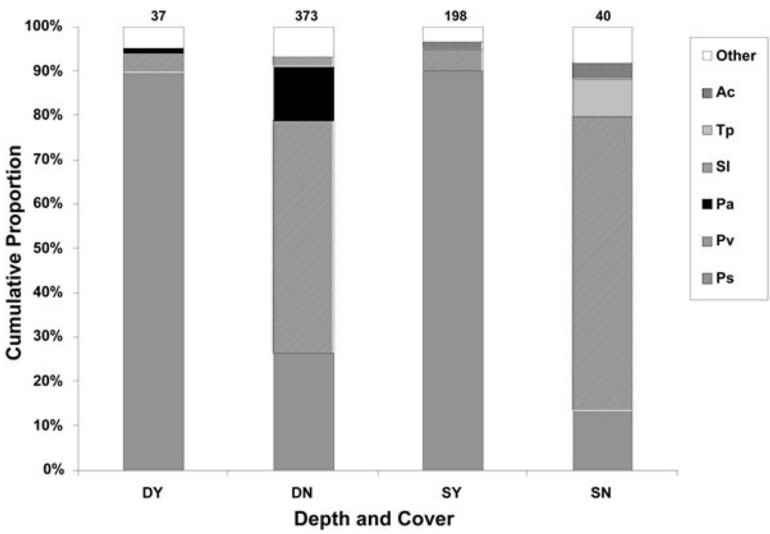


Figure 2. Variation in community composition among depths and cover types. Communities are more similar among locations with similar cover rather than similar depths. D = deep, S = shallow, Y = seagrass present, N = seagrass absent, TP = *Torquigener pleurogramma* Regan, 1903, Sl = *Selaroides leptolepis,* Pv = *Pentapodus vitta,* Pa = *Pagrus auratus,* Ac = *Amniataba caudavittata,* Ps = *Pelates sexlineatus.*

est species per trap were caught in deep unvegetated habitats (Fig. 6A). Also, more species per trap were caught in shallow habitats during warm months than deep habitats during warm months and both shallow and deep areas during cold months (Fig. 6B).

The number of individuals caught in each trap was only influenced by cover with significantly more individuals captured in seagrass beds (mean = 39.2 ind set^{-1}, s = 83.5, n = 250 trap sets) than in areas without seagrass (mean = 5.8 ind set^{-1}, s = 11.6, n = 398 trap sets; Table 6). Biomass per trap was significantly influenced by an interaction between depth and cover (Table 6). The average biomass captured per trap was highest in seagrass habitats, especially deep ones and lowest in deep unvegetated areas (Fig. 7). There was no influence of season on biomass per trap (Table 6), but there was a non-significant trend towards higher biomass during cold months.

Table 3. Factor loadings (with varimax rotation) of principal components with eigenvalues greater than 1.0.

	PC1	PC2	PC3	PC4
Proportion of total variance	0.17	0.15	0.14	0.13
Eigenvalue	2.1	1.3	1.2	1.2
Species				
Pelates quadrilineatus	0.76			
Pentapodus vitta	0.66			
Rhabdosargus sarba	0.57			
Pelates sexlineatus		0.81		
Amniataba caudavittata		0.80		
Lethrinus laticaudis			0.79	
Pagrus auratus			0.72	
Psammoperca waigiensis				0.87
Apogon rueppellii				0.73

Table 4. MANOVA table showing the influence of season, depth, and seagrass cover on community structure described by four principal components.

Factor	Approximate F	$df_{num,demom}$	P
Season	16.4	3,647	< 0.001
Depth	6.5	3,647	< 0.001
Cover	1.4	3,647	0.23
Season:Depth	7.1	3,647	< 0.001
Season:Cover	2.7	3,647	< 0.05
Cover:Depth	1.1	3,647	0.36
Season:Depth:Cover	5.1	3,647	< 0.002

SPECIES-SPECIFIC ABUNDANCE.—The catch rates (ind/2-h trap set) of the ten most common species in the sample varied with different factors (Table 7). The number of individuals captured per trap of *A. caudavittata*, *A. rupelli*, *R. sarba*, *Monacanthus chinensis* Osbeck, 1765 and *P. sexlineatus* was higher in seagrass covered areas than unvegetated ones while more *P. auratus* were captured per trap in unvegetated habitats (Fig. 8). Additionally, *A. caudavittata* and *P. sexlineatus* were also found primarily in shallow areas and *P. auratus* were captured exclusively in deep habitats (Fig. 9). *Monacanthus chinensis* abundance was also influenced by an interaction between depth and season with the highest catch rates in shallow areas during warm months (Fig. 10). *Lethrinus laticaudis* catch rates differed according to an interaction between season and cover (Fig. 11). Catches were highest in seagrass habitats during warm months. *Pentapodus vitta* catches were influenced by a three-way interaction (Fig. 12). Catches tended to be high in deep vegetated habitats during both seasons and in shallow unvegetated habitats during cold months. The lowest catches were during warm months outside of deep vegetated areas. *Psammoperca waigiensis* capture rates were also influenced by the three-way interaction with the highest abundance in shallow habitats during warm months (Fig. 13).

SEASONAL CHANGES IN SIZE DISTRIBUTION.—The size distributions of the ten most common species are shown in Figure 14. Seven of the ten most common species showed significant seasonal changes in mean size (Table 8). *Amniataba caudavittata*, *A. rueppellii*, *L. laticaudis*, *M. chinensis*, and *R. sarba* were all larger, on average, in warm months. In contrast, the mean size of *P. auratus* and *P. sexlineatus* was greater in cold months. There were no seasonal changes in the size of *P. quadrilineatus*, *P. vitta*, and *P. waigiensis*. However, due to the very low catches of *P. waigiensis* in cold months it is unlikely that a difference in mean size would be detected.

Table 5. ANOVA table showing the influence of season, depth, and seagrass cover on principle component scores. Dashes indicate that an interaction was eliminated from the final ANOVA model (i.e., P > 0.10).

	PC 1		PC 2		PC 3		PC 4	
Factor	$F_{1,647}$	P	$F_{1,647}$	P	$F_{1,647}$	P	$F_{1,647}$	P
Season	18.8	< 0.001	0.04	0.51	8.2	0.004	23.1	<0.001
Depth	0.1	0.80	8.0	0.005	4.2	0.04	15.6	<0.001
Cover	3.1	0.07	7.6	0.006	8.0	0.004	0.03	0.85
Season:Depth	1.4	0.24	-	-	-	-	19.3	<0.001
Season:Cover	0.6	0.44	-	-	17.8	<0.001	3.2	0.06+
Cover:Depth	0.2	0.58	-	-	-	-	1.2	0.25
Season:Depth:Cover	9.8	< 0.002	-	-	-	-	3.8	0.04

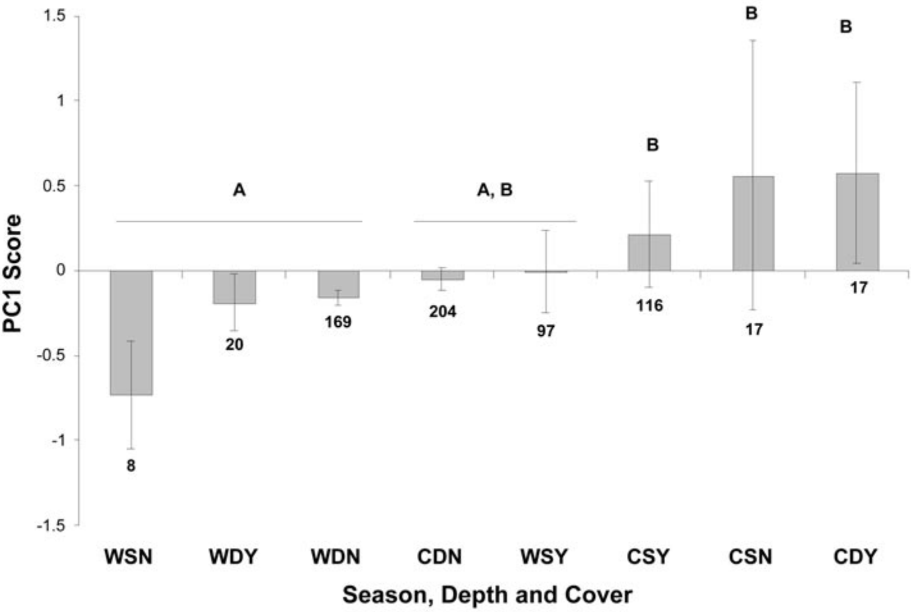


Figure 3. Differences in principal component scores for all combinations of season, depth and cover for PC1. W = warm, C = cold, D = deep, S = shallow, Y = seagrass present, N = seagrass absent. Bars labeled with the same letter are not significantly different from each other at P < 0.05 after Bonferroni correction. Sample sizes are given below bars. Error bars represent 95% confidence intervals.

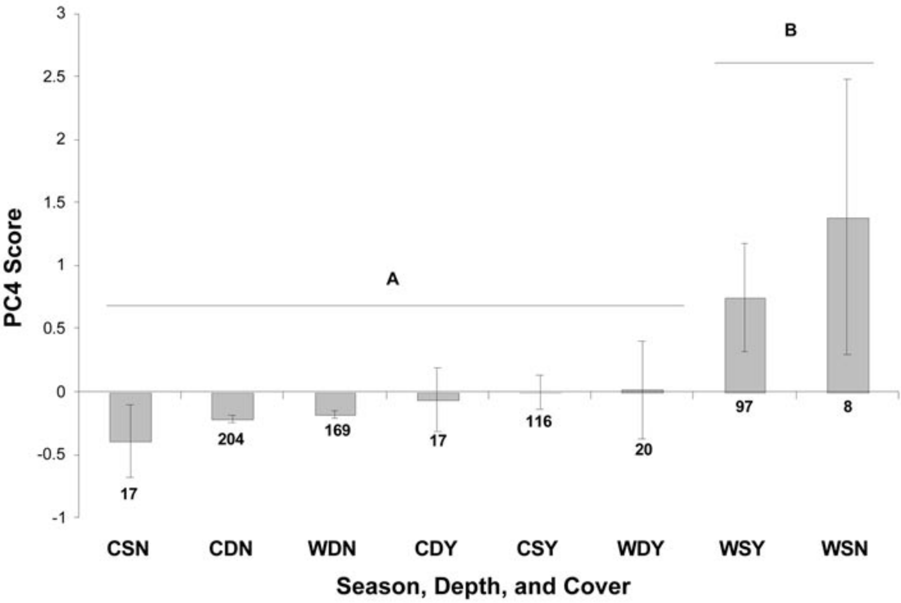


Figure 4. Differences in principal component scores for all combinations of season, depth and cover for PC4. W = warm, C = cold, D = deep, S = shallow, Y = seagrass present, N = seagrass absent. Bars labeled with the same letter are not significantly different from each other at P < 0.05 after Bonferroni correction. Sample sizes are given below bars. Error bars represent 95% confidence intervals.

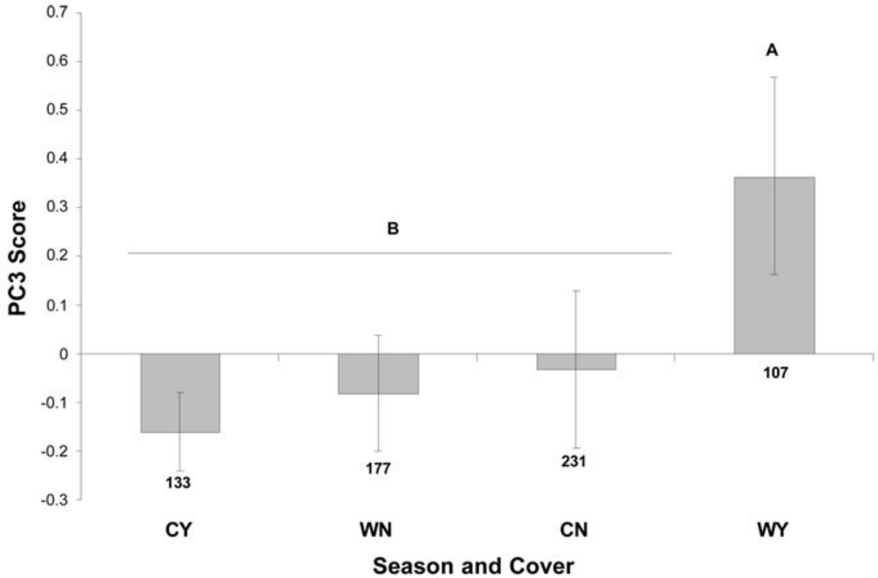


Figure 5. Differences in principal component scores for all combinations of season and cover for PC3. W = warm, C = cold, Y = seagrass present, N = seagrass absent. Bars labeled with the same letter are not significantly different from each other at $P < 0.05$ after Bonferroni correction. Sample sizes are given below bars. Error bars represent 95% confidence intervals.

Discussion

The seagrass habitats of Shark Bay tend to support fish communities with more species and individuals caught per trap than adjacent unvegetated areas. This is consistent with many other studies of fish communities in seagrass habitats (Bell and Pollard, 1989; Ferrell and Bell, 1991; Gray et al., 1996). However, I found that seagrass habitats, especially in shallow water, were dominated by a single species. This result contrasts with previous studies, including others in Shark Bay, which found that fish communities of shallow seagrass meadows were more diverse than those in adjacent unvegetated regions, but that these communities were not dominated by a single species (Hanekom and Baird, 1984; Black et al., 1990; Connolly, 1994b; Travers and Potter, 2002). Other studies have found that relatively few species comprise over 90% of the captures in seagrass ecosystems of southeastern Australia, but the most common species are often found in

Table 6. ANOVA table showing the influence of season, depth, and seagrass cover on the number of individuals, number of species, and biomass (g) captured per 2 h trap set. Dashes indicate that an interaction was eliminated from the final ANOVA model (i.e., $P > 0.10$).

	No. individuals		No. species		Biomass (g)	
Factor	$F_{1,647}$	P	$F_{1,647}$	P	$F_{1,647}$	P
Season	2.0	0.15	15.1	< 0.001	2.8	0.09
Depth	0.4	0.51	0.3	0.59	0.04	0.84
Cover	35.6	< 0.001	36.5	< 0.001	24.0	< 0.001
Season:Depth	-	-	12.1	< 0.001	-	-
Cover:Depth	-	-	18.9	<0.001	10.0	0.002

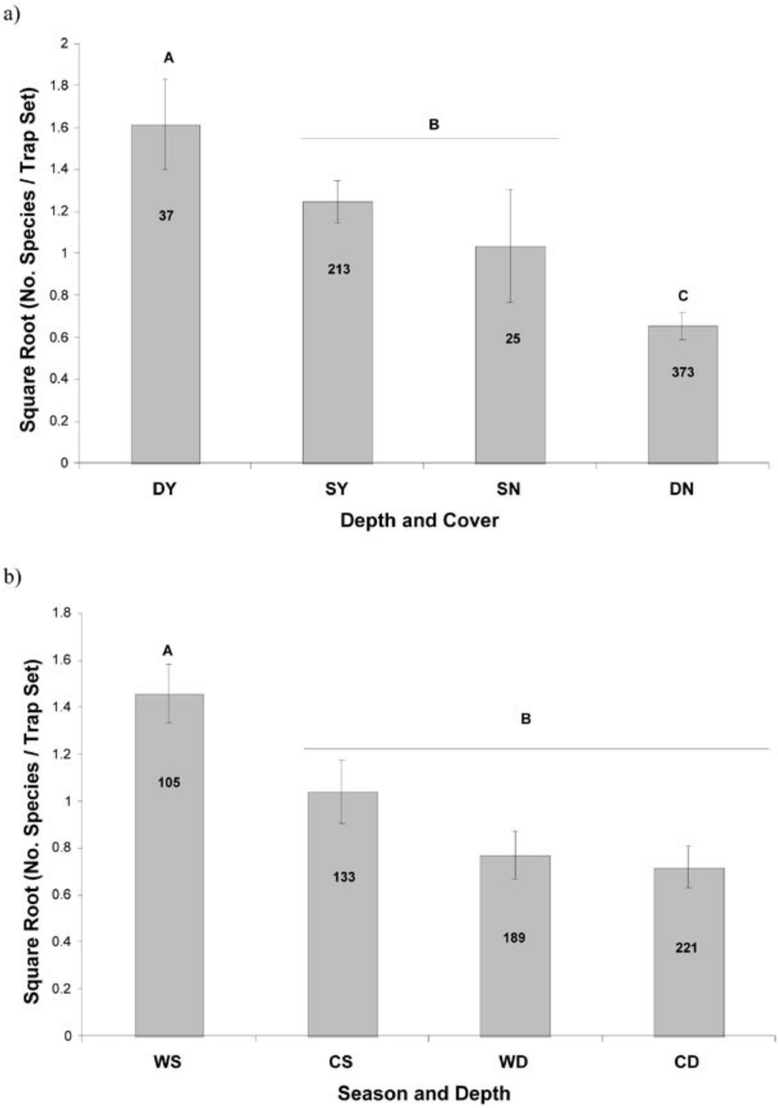


Figure 6. Influence of A) depth and cover and B) season and depth on the number of species caught in each trap set. Bars labeled with the same letter are not significantly different at $P < 0.05$. Y = seagrass present, N = seagrass absent, D = deep, S = shallow, W = warm, C = cold. Sample sizes are given inside bars. Error bars represent 95% confidence intervals.

roughly equal abundance (Robertson, 1980; Bell et al., 1992; Gray et al., 1996). The difference in the patterns of species abundance found in this and previous studies may be due to variation in sampling methods.

Comparisons among studies of fish communities in Shark Bay suggest that sampling methodology has a major impact on the fish community described. Previous studies in Shark Bay have used hand-pulled seines (Black et al., 1990) and otter trawls (Travers and Potter, 2002). Both of these methods are less likely than fish traps to capture large, fast-moving individuals, and species with high long-term mobility (e.g., Robichaud et al.,

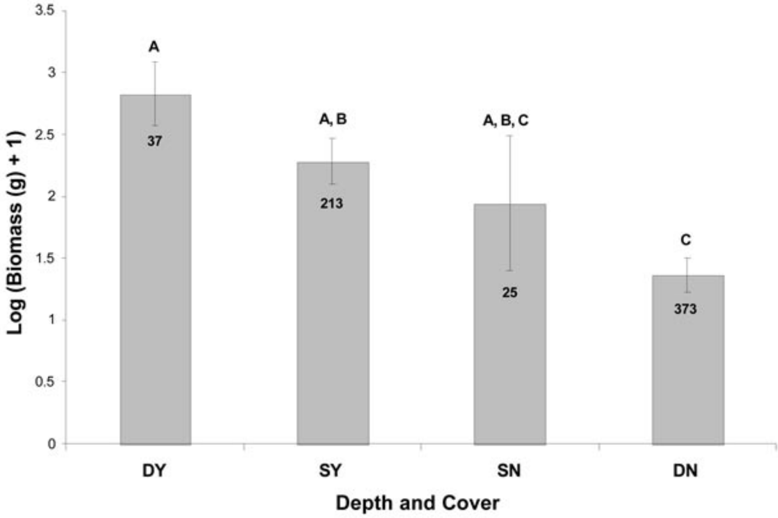


Figure 7. Influence of depth and cover on the biomass (g) captured per trap. Bars labeled with the same letter are not significantly different at $P < 0.05$. D = deep, S= shallow, Y = seagrass present, N = seagrass absent. Error bars represent 95% confidence intervals.

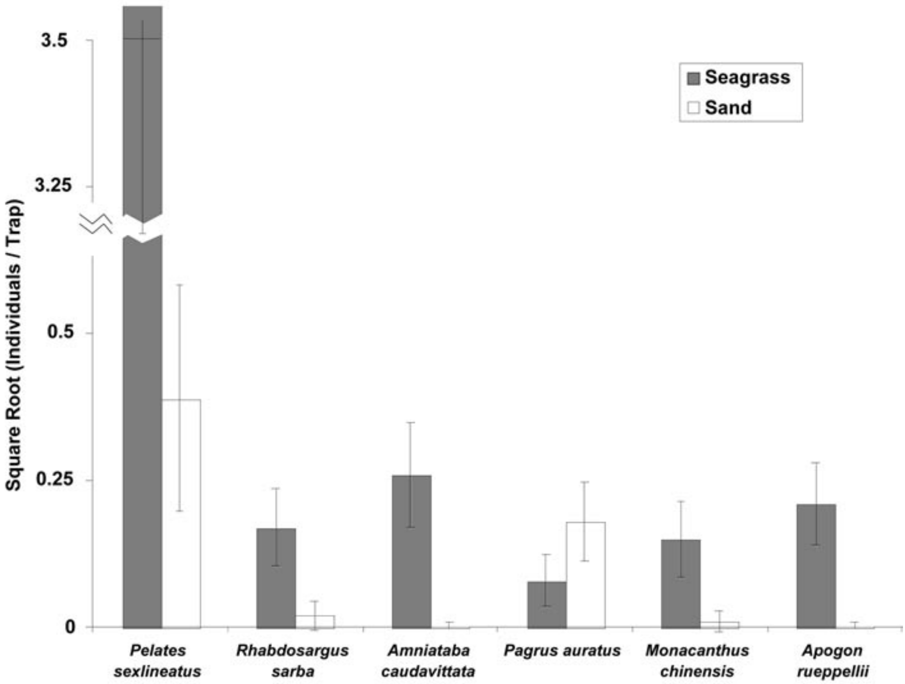


Figure 8. Influence of seagrass cover on the catch rate (ind set^{-1}) of common species in Shark Bay. Error bars represent 95% confidence intervals.

Table 7. ANOVA table showing the influence of season, depth, and seagrass cover on number of individuals captured per 2 h trap set for the ten most commonly captured species. Species are arranged in order of relative abundance. Figures 8–13 illustrate the nature of significant results.

	Pelates sexlineatus		*Pentapodus vitta*		*Pagrus auratus*	
Factor	$F_{1,647}$	P	$F_{1,647}$	P	$F_{1,647}$	P
Season	3.6	0.06	14.6	<0.001	0.04	0.83
Depth	7.1	0.008	3.2	0.07	21.4	<0.001
Cover	36.2	<0.001	2.6	0.11	4.9	0.027
Season:Depth	-	-	0.6	0.42	-	-
Season:Cover	-	-	2.0	0.16	-	-
Cover:Depth	-	-	3.5	0.06	-	-
Season:Depth:Cover	-	-	6.8	0.009	-	-

	Pelates quadrilineatus		*Monbacanthus chinensis*		*Apogon rueppellii*	
Factor	$F_{1,647}$	P	$F_{1,647}$	P	$F_{1,647}$	P
Season	0.02	0.89	14.4	<0.001	0.2	0.66
Depth	1.3	0.25	4.6	0.32	0.9	0.34
Cover	2.3	0.13	10.4	0.001	14.8	<0.001
Season:Depth	-	-	10.0	0.002	-	-
Season:Cover	-	-	-	-	-	-
Cover:Depth	-	-	-	-	-	-
Season:Depth:Cover	-	-	-	-	-	-

	Amniataba caudavittata		*Rhabdosargus sarba*	
Factor	$F_{1,647}$	P	$F_{1,647}$	P
Season	0.03	0.85	1.6	0.20
Depth	6.8	0.009	0.4	0.51
Cover	6.0	0.01	6.0	0.01
Season:Depth	-	-	-	-
Season:Cover	-	-	-	-
Cover:Depth	3.8	0.05	-	-
Season:Depth:Cover	-	-	-	-

	Lethrinus laticaudis		*Psammoperca waigiensis*	
Factor	$F_{1,647}$	P	$F_{1,647}$	P
Season	28.7	<0.001	73.8	< 0.001
Depth	2.0	0.15	57.8	< 0.001
Cover	17.2	<0.001	9.2	0.003
Season:Depth	-	-	54.4	< 0.001
Season:Cover	23.1	<0.001	18.6	< 0.001
Cover:Depth	-	-	16.7	< 0.001
Season:Depth:Cover	-	-	10.6	0.001

2000). However, fish traps are less efficient at capturing smaller individuals and species with lower long-term mobility. Thus, the relatively high catches of *P. sexlineatus*, *P. vitta*, and *P. auratus* in the fish trapping study relative to previous studies in Shark Bay, especially that of Travers and Potter (2002), are likely due to their ability to avoid being captured in seines and otter trawls. Similarly, while fish traps caught *M. chinensis* (abundance rank 8, n = 100) and *A. rueppellii* (abundance rank 7, n = 102), these slow-swimming species were the most abundant species in otter trawls within Shark Bay (abundance rank 1, n = 1695 and abundance rank 2, n = 867, respectively; Travers and Potter, 2002).

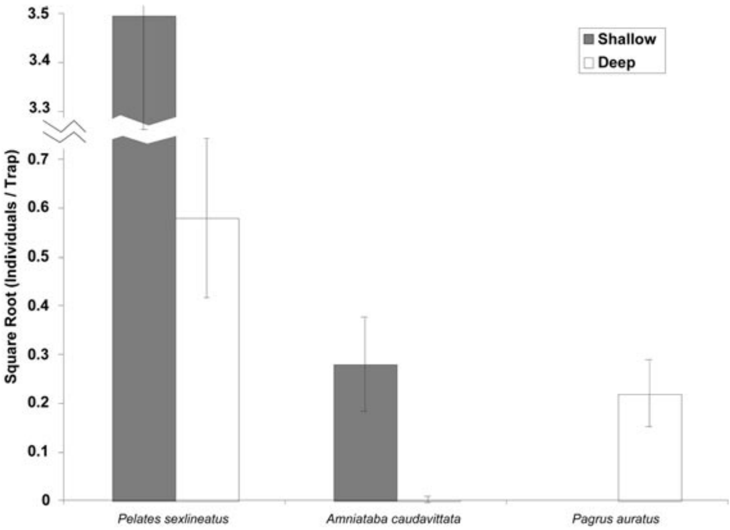


Figure 9. Influence of water depth on the catch rate (ind set^{-1}) of common species in Shark Bay. Error bars represent 95% confidence intervals.

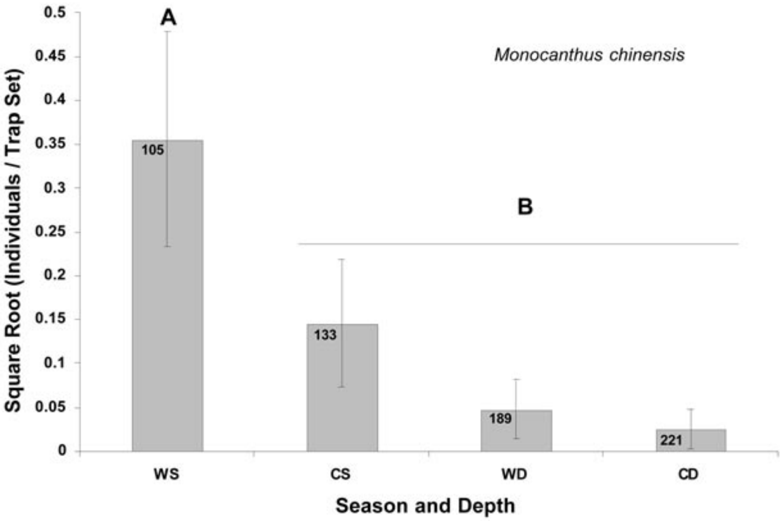


Figure 10. Influence of the interaction between season and depth on catch rates (ind set^{-1}) of *Monocanthus chinensis*. Bars labeled with the same letter are not significantly different at $P < 0.05$. W = warm, C = cold, D = deep, S = shallow. Sample sizes are given inside bars. Error bars represent 95% confidence intervals.

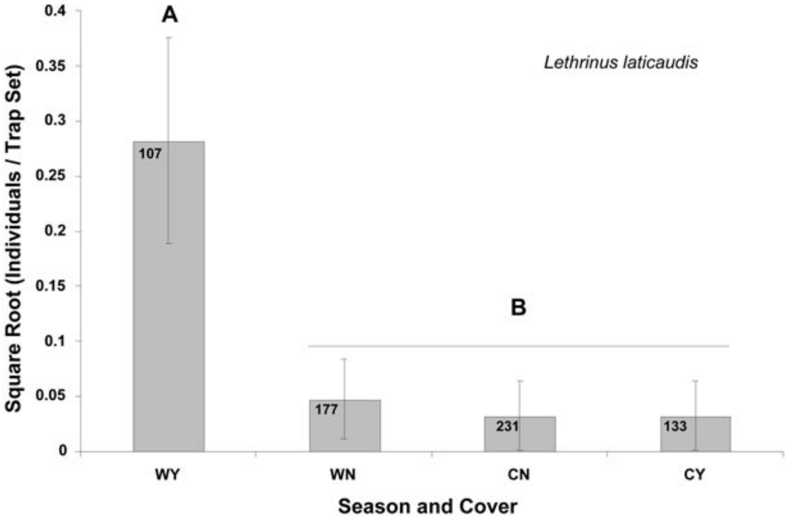


Figure 11. Influence of the interaction between season and cover on catch rates (ind set^{-1}) of *Lethrinus laticaudis*. Bars labeled with the same letter are not significantly different at $P < 0.05$. W = warm, C = cold, Y = seagrass present, N = seagrass absent. Sample sizes are given inside bars. Error bars represent 95% confidence intervals.

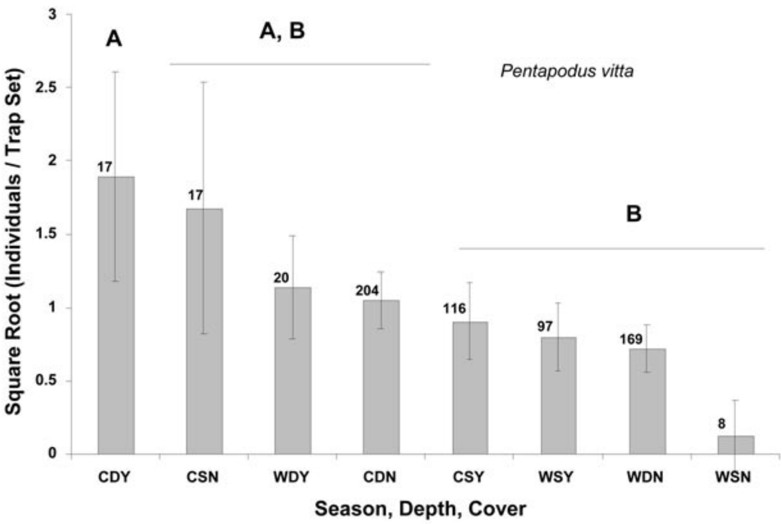


Figure 12. Influence of the interaction between season, depth, and cover on catch rates (ind set^{-1}) of *Pentapodus vitta*. Bars labeled with the same letter are not significantly different at $P < 0.05$. D = deep, S = shallow, Y = seagrass present, N = seagrass absent. Sample sizes are given above bars. Error bars represent 95% confidence intervals.

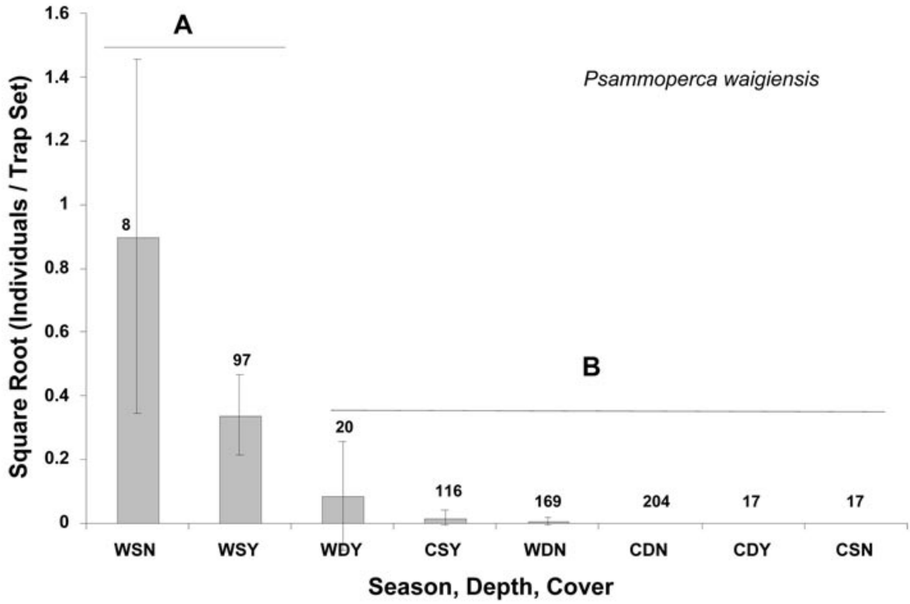


Figure 13. Influence of the interaction between season, depth, and cover on catch rates (ind set^{-1}) of *Psammoperca waigiensis*. Bars labeled with the same letter are not significantly different at P < 0.05. W = warm, C = cold, Y = seagrass present, N = seagrass absent, D = deep, S = shallow. Sample sizes are given above bars. Error bars represent 95% confidence intervals.

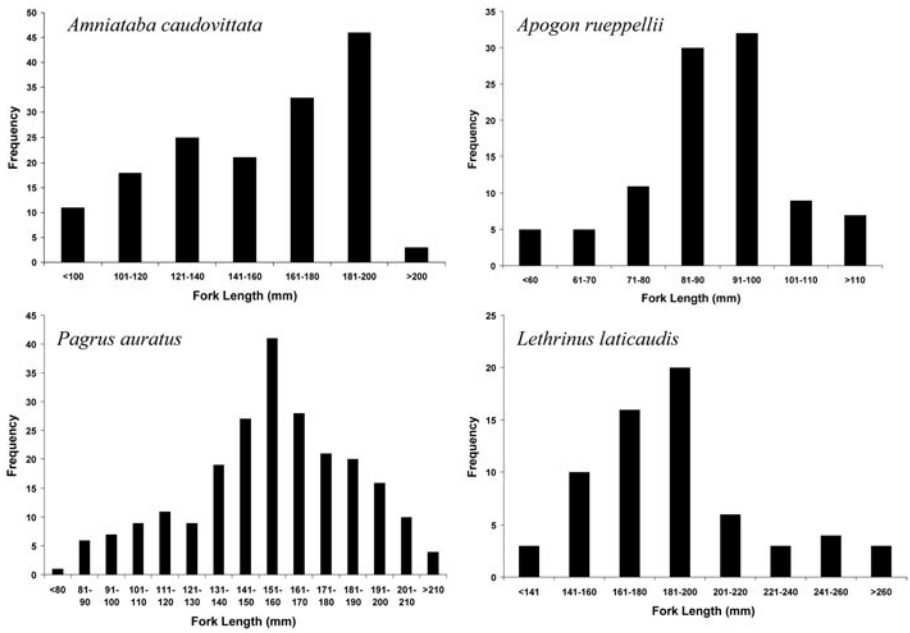
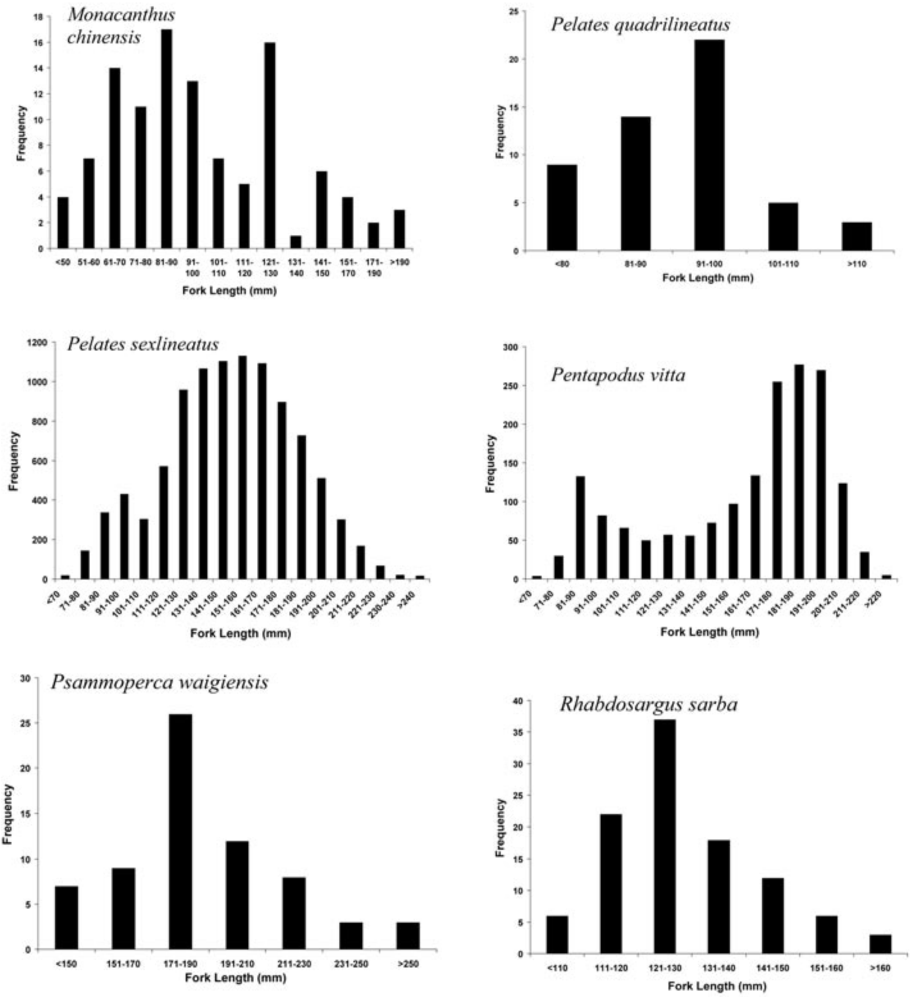


Figure 14. *(this and opposite page)* Size distributions of the ten most common fish species collected by fish traps in Shark Bay, Austalia.



Another difference between fish trapping and more commonly used methods for sampling seagrass fishes is that fish traps are less likely to capture very small individuals that are readily captured in seine hauls and trawls. This difference probably explains why fish traps caught only 31 species compared to 58 species captured by seines (Black et al., (1990), even though Black et al. (1990) captured far fewer individuals (n = 4357 compared to n = 13,734). Despite the overlapping sampling areas, only 15 species were caught by both sampling gears. Likewise, Travers and Potter (2002) collected 83 species with a relatively small sample of individuals (n = 4907). Qualitative underwater visual observations (Bohnsack and Bannerot, 1986) support the observed pattern of *P. sexlineatus* and *P. vitta* dominating fish communities of the study area (pers. obs.). Therefore, while fish traps underestimate the number of species inhabiting seagrass habitats relative to seining and trawling, it is possible that fish traps provide a more accurate assessment of the dominance of a small number of highly mobile species in terms of both biomass and the number of individuals. Future studies which employ multiple techniques simultaneously (e.g., fish traps, seining, trawls, visual censuses) within the same study

Table 8. Average FL (mm) during cold and warm months of the ten most commonly caught species. NS = not significant. Bold typeface indicates seasons with significantly greater mean FL.

Species	Warm (n)	Cold (n)	t (df)	P
Amniataba caudavittata	**171.5 (74)**	144.3 (83)	5.9 (155)	< 0.0001
Apogon rueppellii	**94.6 (48)**	86.4 (51)	2.4 (97)	< 0.05
Lethrinus laticaudis	**190.3 (51)**	167.8 (12)	2.1 (61)	< 0.05
Monacanthus chinensis	**104.6 (79)**	88.6 (31)	2.0 (108)	< 0.05
Pagrus auratus	145.4 (96)	**164.1 (133)**	4.5 (227)	< 0.0001
Pelates quadrilineatus	92.8 (14)	90.0 (39)	0.8 (51)	NS
Pelates sexlineatus	150.3 (5,410)	**157.3 (1,789)**	7.5 (7,196)	< 0.0001
Pentapodus vitta	160.8 (529)	160.4 (1,219)	0.2 (1,746)	NS
Psammoperca waigiensis	189.5 (67)	206.0 (2)	0.8 (66)	NS
Rhabdosargus sarba	**138.0 (33)**	126.6 (71)	3.2 (102)	< 0.01

location are required to fully understand the particular biases of each method and to determine the best protocol for accurately describing fish communities of seagrass and associated habitats.

One interesting result of this study was the finding that deep seagrass areas had significantly more species and a marginally higher biomass of fish captured per trap set than did shallow seagrass areas. This result is consistent with Bell et al. (1992) who found that deep (6–7 m) *P. australis* beds in New South Wales, Australia tend to support fish communities with more individuals and more species than do shallow seagrass beds. This suggests that although deep seagrass beds may be relatively uncommon habitats they may be important to fish communities in seagrass ecosystems. In contrast, Travers and Potter (2002) found that in the Western Gulf of Shark Bay, nearshore (shallow) seagrass beds had a greater density and diversity of fishes than offshore (deeper) seagrass beds. The differences in results may be due to variation in sampling methods and the diversity and density of small species in nearshore shallow areas that are less likely to be captured by fish traps.

Despite seagrass covered areas having higher fish species richness, individual abundance, and biomass, unvegetated habitats also supported relatively diverse communities. Over 70% of the species represented by more than ten individuals were found in both vegetated and unvegetated areas and ten species were found most often in unvegetated areas. This suggests that unvegetated habitats, especially in shallow waters, are also important to populations of fishes in Shark Bay. Furthermore, seagrass cover was not the only factor that influenced the number of species and biomass captured in each trap. Water depth interacted with seagrass cover to influence the biomass of fish captured and this same interaction as well as an interaction between season and depth influenced the number of species that were captured. Therefore, studies that only consider one factor in isolation (e.g., seagrass vs no seagrass or deep seagrass vs shallow seagrass) may not fully describe patterns of species abundance.

Differences in the structure of fish communities have been found between seagrass habitats and adjacent bare sand areas (e.g., Black et al., 1990; Ferrell and Bell, 1991; Travers and Potter, 2002), between deep and shallow seagrass habitats (Bell et al., 1992; Travers and Potter, 2002), and among months (Ferrell et al., 1993). This study simultaneously investigated the influences of seagrass cover, depth, and season on the structure of fish communities. I found that all three of these factors interacted to influence overall community structure. However, while several components of the community were affected by this three-way interaction, others responded to different combinations of factors. This shows that it is important to consider a variety of factors simultaneously to gain insights into the factors influencing the structure of fish communities in seagrass ecosystems. This finding is particularly important to conservation efforts for fish communities of seagrass ecosystems and associated habitats. To understand possible anthropogenic effects on these marine communities, it is important to consider the many factors that may naturally influence community structure and how different community components are likely to respond to changes in various factors (e.g., destruction of seagrass).

The abundances of the ten most commonly caught species were correlated with different factors. For most species, the presence of seagrass was correlated with higher catch rates regardless of depth or season, and similar affinities for seagrass and unvegetated habitats were found in this study and previous ones in Shark Bay with the exception of *P. vitta*. A complex suite of factors influenced the abundance of *P. vitta* with relatively low catches in shallow seagrass areas relative to deep seagrass and shallow sand habitats during some months. In contrast, Black et al. (1990) found that *P. vitta* was more common over shallow seagrass habitats than shallow unvegetated areas, and Travers and Potter (2002) found over three times as many *P. vitta* over bare sand. These differences are likely due to differences in the size classes of fish sampled and possibly the seasons in which sampling occurred. The size classes of *P. vitta* captured by fish traps show a bimodal distribution. While large size classes made up most of the catch and were found predominantly over sand, small size classes were most often captured in seagrass covered habitats. Thus, the differences in habitat use identified in this study and those of Black et al. (1990) and Travers and Potter (2002) probably reflect an ontogenetic shift in habitat use by *P. vitta*. Season and depth were also main effects on the catch rates of some species. In general, when there was a seasonal change in abundance, catch rates were higher during warm months. One particularly interesting result is that the species that made up specific principal components in the community analysis did not necessarily respond to the same factors when analyzed separately (e.g., PC4). Therefore, future studies may benefit from considering not only community-level patterns, but also interspecific variation in the factors influencing spatial distributions and abundance.

Pagrus auratus, the pink snapper, is a species of both commercial and recreational importance in Shark Bay. There is a distinct breeding stock of *P. auratus* in the Eastern Gulf of Shark Bay (Johnson et al., 1986), which had been severely depleted by 1997, largely by recreational fishers outside of the current study area (G. Jackson, Western Australia Marine Research Laboratories, North Beach, pers. comm.). This drop in biomass resulted in a closure of the fishery in June 1998, which lasted until March 2003. In order to facilitate the recovery of this species, protecting juvenile habitats is critical. Results of this study demonstrate that, unlike many other commercially important species which are found in shallow seagrass habitats (Bell and Pollard, 1989), *P. auratus* juveniles are found predominantly in deep habitats. Although catch rates were higher in areas where seagrass was absent, the smallest size classes were often caught in sets over deep seagrass beds. Thus, protection of the sparse patches of seagrass in deep habitats may be important for conservation and management of *P. auratus* stocks.

This study shows that fish traps can provide valuable data on the fish communities of seagrass habitats and complement data derived from seining and trawling methods. However, more work is needed to understand the exact bias of each sampling technique, and to determine optimal methods for accurately describing fish communities of seagrass and adjacent unvegetated areas. Although seagrass habitats supported the most species, individuals, and biomass, these habitats were dominated by a single species. This study also shows that it is important to consider the influences of a variety of habitat characteristics and environmental factors, and the interactions among them, as catch rates of some species can be influenced by a suite of factors.

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Addresses: *Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, BC, Canada* and *Marine Program, Department of Biological Sciences, Florida International University, Biscayne Bay Campus, 3000 NE 151 St, North Miami, Florida 33181. Telephone: (305) 919-5234. E-mail: <heithaus@fiu.edu>.*