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Interactions between mangrove and seagrass habitats mediated by estuarine nekton assemblages: coupling of primary and secondary production*

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Abstract

In Terminos Lagoon, México, more than 80 fish species use the mangrove and seagrass habitats. We studied nekton dynamics in an inlet seagrass system and a more sheltered seagrass/mangrove system located behind a barrier island. Seasonal community biomass ranges from 0.6 to 5.2 g wet wt m^{-2}. For the two habitats together, there are 28 dominant species. Eleven species were common to both areas: *Sphoeroides testudineus* (Linnaeus, 1758), *Archosargus rhomboidalis* Linnaeus, 1758, *A. probatocephalus* (Walbaum, 1792), *Arius felis* (Linnaeus, 1766), *A. melanopus* (Gunther, 1864), *Eucinostomus gula* (Cuvier & Valenciennes, 1830), *Bairdiella chrysoura* (Lacépède, 1803), *Orthopristis chrysoptera* (Linnaeus, 1766), *Chilomycterus schoepfi* (Walbaum, 1792), *Opsanus beta* (Goode & Bean, 1879) and *Lutjanus griseus* (Linnaeus, 1758). Ten species used exclusively the inlet seagrass system: *Urolophus jamaicensis* (Cuvier, 1817), *Haemulon aurolineatum* (Cuvier, 1829), *H. bonariense* (Cuvier, 1830), *H. plumieri* (Lacépède, 1802), *Anisotremus virginicus* (Linnaeus, 1758), *Odontoscion dentex* (Cuvier, 1830), *Corvula sanctae-luciae* (Jordan, 1890), *Nicholsina usta* (Valenciennes, 1839), *Stephanolepis hispidus* (Linnaeus, 1766) and *Diodon hystrix* Linnaeus, 1758. Seven species were dominant only in the seagrass/mangrove system: *Anchoa mitchilli* (Cuvier & Valenciennes, 1848), *Scorpaena plumieri* Bloch, 1789, *Cynoscion nebulosus* (Cuvier & Valenciennes, 1830), *Diapterus rhombeus* (Cuvier & Valenciennes, 1830), *Bairdiella ronchus* (Cuvier & Valenciennes, 1830), *Cichlasoma urophtalmus* (Günther, 1862) and *Acanthostracion quadricornis* (Linnaeus, 1758). Comparative analysis showed that periodic variation in biomass and diversity of fish assemblages in seagrass and seagrass/mangrove habitats were synchronized with sizes and densities of population, season of the year (dry, wet, 'nortes'), circulation pattern, and patterns of primary production (phytoplankton, *Thalassia testudinum* Konig, 1805; and *Rhizophora mangle* Linnaeus). This analysis allowed the definition of 3 life-cycle patterns with a clear nektonic 'seasonal programming' following the timing of primary production in these critical habitats: (1) marine species which spawn in or near the inlet with eggs and larvae transported into and distributed throughout the lagoon by the predominant

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currents; (2) estuarine-marine species which spawn in different habitats of the lagoon and use the seagrass/mangrove system as a nursery area, and (3) species which complete their life history in the inlet seagrass and/or seagrass/mangrove systems.

Introduction

The ecological value of mangrove and seagrass habitats for refuge, reproduction, feeding, recruitment, nursery and growth areas for a number of tropical coastal fishes is well documented (e.g., Zieman *et al.*, 1984; Lewis *et al.*, 1985; Yáñez-Arancibia, 1985; Thayer *et al.*, 1987; Robertson & Duke, 1987; Bell & Pollar, 1989).

Nevertheless, there is little information on the use of seagrass habitats alone as compared with seagrass/mangrove habitats. Fish populations may be restricted to one specific habitat or distributed in both of them. Although fish diversity and biomass are appreciable in all habitats, there are clear seasonal patterns related to such factors as river discharge, water circulation, primary production, and other biotic and abiotic factors (e.g., Blaber & Blaber, 1980; Pinto, 1987; Yáñez-Arancibia *et al.*, 1988). The latter two papers are among the very few recent references presenting evidence of coupling between estuarine nekton and primary production of mangroves.

The purpose of this work was to assess: (1) the synchrony of fish habitat utilization with the water circulation pattern, season of the year, and primary productivity, and (2) the importance of the relationship between different habitats which are strongly coupled.

The study site

Terminos Lagoon is located in the Southern Gulf of Mexico (18 °N, 91 °W). It covers *ca* 2500 km^2 including wetlands, and has an average depth of 3.5 m. This system has a high diversity of habitats and species. We consider two seagrass habitats (Fig. 1): seagrass beds in Puerto Real inlet without adjacent mangroves (S), and seagrass beds adjacent to mangrove swamps (S–M) behind Isla del Carmen, the barrier island separating Terminos Lagoon from the Gulf of Mexico. S is a clear-water, marine habitat with a strong tidal current and a net flow from the Gulf to the lagoon, sandy sediments, a salinity range from 30 (December) to 37‰ (June), a temperature range from 24 (December) to 31 °C (June). The dominant plants are *Thalassia testudinum*. The S–M is a more turbid, marine-estuarine habitat with moderate tidal currents, mixed sandy-clay-silt sediments, a salinity range from 15 (November) to 36‰ (May), and a temperature range from 22 (February) to 30 °C (September). The dominant plant communities are intermingled *Rhizophora mangle* fringing mangrove swamps and *T. testudinum* beds. Based on precipitation, river discharge, winds, and temperature, three seasons have been identified. The dry season from February to May, a tropical rainy season with thunder-showers from June to October, and the 'nortes' season with periodic rains and strong winds associated with frontal passages from October to February (Yáñez-Arancibia & Day 1982, 1988).

Material and methods

Fish collection and data base

Fish were collected with a 5 m shrimp otter trawl (mouth opening while fishing was 2.5 m, 19 mm mesh) with tows of 10 to 12 min at 2 to 2.5 knots; individual trawls covered an area of 1500 to 2000 m^2. Depths sampled varied but never exceeded 3.0 m. Ninety trawl tows were made in bimonthly collections from February 1981 to January 1982 in the S–M zone (seagrass meadows and adjacent to mangrove borders). During each sampling period, tows were made every two hours over a 24-h period. In the S zone a total of 168 trawl tows were made over 24-h periods in bimonthly collections from August 1980 to July 1981. Specimens were fixed in neutralized 10% formalin.

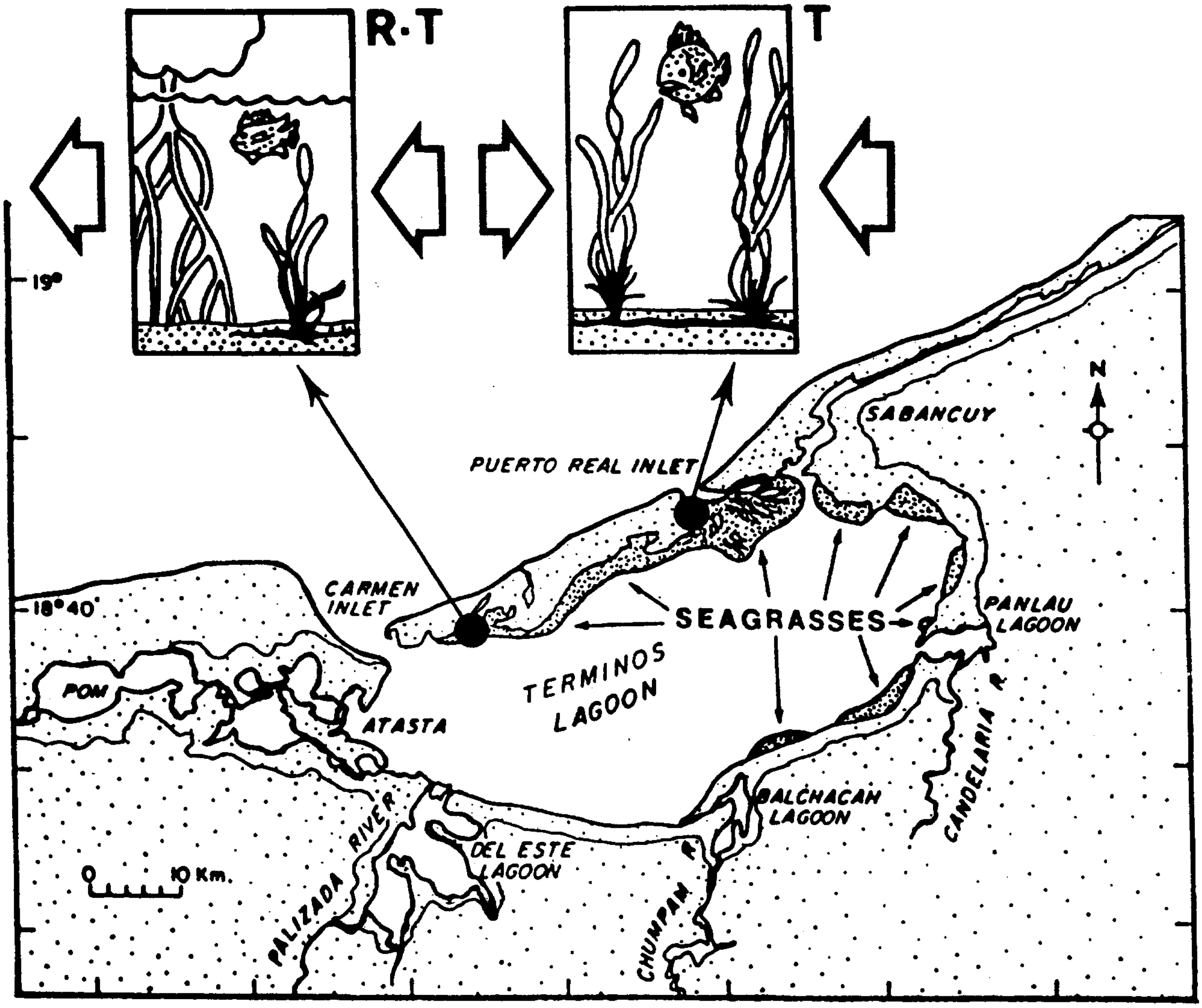

Fig. 1. Terminos lagoon. The locations of the experiments are shown: the seagrass system in Puerto Real Inlet (S or T), and the seagrass/mangrove system (S–M or R–T) in Estero Pargo Inlet. The net waterflow is in the S to S–M pathway.

In the laboratory, fish were identified, counted, weighed and measured. The information function (H′) of Shannon & Weaver (1963) was calculated. The Wilhm (1968) function (H′w) was used to evaluate weight heterogeneity by species. All calculations of indices were based on use of natural logs. The abundance of fish was calculated by biomass (wet weight per area g m^2). An index of seasonal abundance (Roger & Herke, 1985; Yáñez-Arancibia *et al.*, 1988) was used to follow changes in dominant fish species. The monthly index of each species was calculated as the average catch per month divided by the highest monthly average catch of the species multiplied by 100. Thus the highest monthly catch for each species had an index of 100. Dominant fish populations were defined on the basis of frequency (percentage of occurrence), broad distribution, weight and numerical abundance (Yáñez-Arancibia *et al.*, 1985, 1988). For additional methodological analysis see Claridge *et al.* (1986).

Primary production data

Aquatic primary productivity data were obtained from Day *et al.* (1982, 1988a). Seagrass productivity data were obtained from Day *et al.* (1982), Moore & Wetzel (1988), and Soberón-Chávez *et al.* (1988). Mangrove productivity data were obtained from Day *et al.* (1982, 1987, 1988b). See Table 1. Specific methodologies are indicated in those papers.

Habitat characteristics

Temperature, salinity, dissolved oxygen, depth and transparency with a Secchi disk were measured during each field trip. Observations of the submerged and surrounding vegetation, benthic macrofauna, tide, currents and climatic conditions were made.

Results

In the S-M system the total catch of fish was 14200 individuals belonging to 77 species, while in S system the catch was 7700 individuals from 83 species. The seasonality of the ecological parameters of diversity, species composition, and biomass of the fish community at the two sites

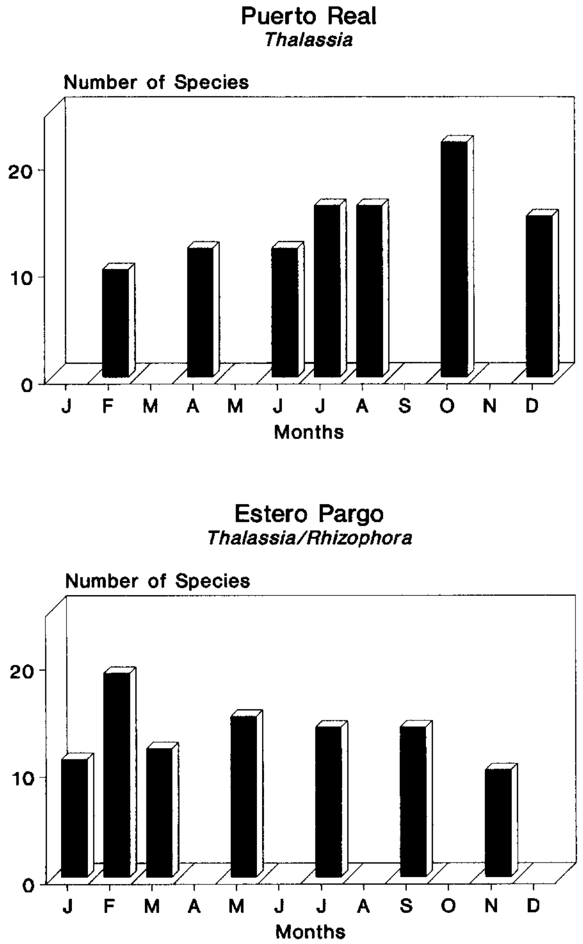

Fig. 2. Number of fish species in seagrass system (*Thalassia*) and seagrass/mangrove system (*Rhizophora*/*Thalassia*) in each month.

was related to the environmental characteristics of each study site. Only 50% of the fish species captured were common to both sites *i.e.*, *Harengula jaguana* Goode & Bean, 1879, *Anchoa hepsetus* (Linnaeus, 1758), *Cetengraulis edentulus* (Cuvier, 1829), *Synodus foetens* (Linnaeus, 1766), *Hippocampus hudsonius* (De Kay, 1824), *Prionotus carolinus* (Linnaeus, 1766), *P. scitulus* Jordan & Gilbert, 1882, *Chloroscombrus chrysurus* (Linnaeus, 1766), *Selene vomer* (Linnaeus, 1758), *Lutjanus synagris* (Linnaeus, 1758), *Eucinostomus argenteus* (Bleeker, 1863), *Pareques acuminatus* (Bloch & Schneider, 1801), *Chaetodipterus faber* (Brussonet, 1782), *Chaetodon ocellatus* Bloch &

Table 1. Annual aquatic primary productivity (APP; gC m^2 yr^{-1}) and litterfall values (g m^2 yr^{-1}) in seagrass and seagrass mangrove systems.

Location	Date	Reference
Terminos Lagoon APP	219	Day *et al.*, 1982
Terminos Lagoon		
Central grassbed APP	240	Day *et al.*, 1988a
Grassbed edge APP	222	Day *et al.*, 1988a
Central lagoon APP	197	Day *et al.*, 1988a
Estero Pargo		
APP	333	Day *et al.*, 1988a
Primary production of mangrove species		
Litterfall, leaves	594	Day *et al.*, 1982
Litterfall, flowers & fruit	192	Day *et al.*, 1982
Litterfall, wood	48	Day *et al.*, 1982

Table 2. Ecological parameters of fish community in seagrass (S) system (Puerto Real Inlet, Terminos Lagoon).

Months	No. of species	No. of indiv.	Weight (g)	H'n	H'w	D	J'	Biomass g m^{-2}	Density ind. m^{-2}	Popu. size g ind^{-1}
Feb	10	45	2034.6	1.73	1.68	2.43	0.77	0.7	0.02	51
Apr	12	44	5471.6	2.07	1.55	3.04	0.86	1.91	0.02	111
Jun	12	78	4160.4	1.75	1.84	2.65	0.72	1.39	0.03	44
Jul	16	119	4362.7	1.93	1.86	3.12	0.72	1.75	0.05	35
Aug	16	141	5035.1	1.91	1.88	3.21	0.72	1.72	0.05	38
Oct	22	167	9012.2	2.32	1.92	4.13	0.73	3	0.06	53
Dec	15	83	4987.5	2.13	2	3.25	0.8	1.71	0.03	62

Naturgesch, 1787, *Citharichthys spilopterus* Gunther, 1862, *Etropus crossotus* Jordan & Gilbert, 1882, *Aluterus schoepfi* (Linnaeus, 1766), *Sphoeroides greeleyi* (Gilbert, 1900), *S. spengleri* (Bloch, 1782). This low similarity is because the fish community at the inlet seagrass site was composed mainly of marine species, while that at the seagrass/mangrove area was drawn from several ecological subsystems of Terminos Lagoon. Thus the species composition at the S–M site is more heterogeneous given the co-existence of freshwater, estuarine and marine species.

There were distinct seasonal patterns for the ecological parameters as depicted in Figs 2 through 5. The number of species (Fig. 2) was higher for S from July through December, with a peak of 22 species in October (Table 2). For S–M, the number of species was relatively constant over the year with the exception of a single peak (19 species) in February (Table 3).

Biomass and density of fishes were generally higher at S during the wet and 'nortes' seasons and at S–M during the dry season (Table 2, Figs 3 and 4). In general, however, the density was much higher at S–M. The average weight of individual fish was higher at S reflecting the predominance of juvenile and preadult fish at S–M (Fig. 5). With the exception of a peak in February, there was little seasonality in individual weight for S. For S–M, individual weights were somewhat higher from January through March.

The dominant or typical species of each community were identified on the basis of abundance, biomass and high frequency (Tables 4 and 5). At system S, there were 21 dominant species and at S–M there were 18 dominant species. Only 39% of the dominant species occurred in both sites. This low similarity is related to species composition. At S 48% were marine species, 36% marine-estuarine, and 16% estuarine, while at the S–M station 6% were freshwater species, 22% estuarine, 66% marine-estuarine and only 6% marine.

Figure 6A and B gives the index of seasonal

Table 3. Ecological parameters of fish community in seagrass/mangroves (S–M) system (Estero Pargo Inlet, Terminos Lagoon).

Months	No. of species	No. of indiv.	Weight (g)	H'n	H'w	D	J'	Biomass g m^{-2}	Density ind. m^{-2}	Popu. size g ind^{-1}
Jan	11	74	1803.5	1.69	1.48	2.51	0.72	0.9	0.04	32
Feb	19	187	8141.3	2.22	1.95	3.53	0.77	4.07	0.09	50
Mar	12	87	1934.3	1.78	1.59	2.55	0.73	0.96	0.04	21
May	15	393	4191.6	1.43	1.84	2.4	0.54	2.09	0.19	11
Jul	14	269	3465.2	1.63	1.9	2.34	0.62	1.73	0.13	12
Sep	14	101	2770.2	1.84	1.8	2.83	0.69	1.39	0.05	26
Nov	10	121	865.9	1.01	1.4	1.78	0.47	0.43	0.06	6

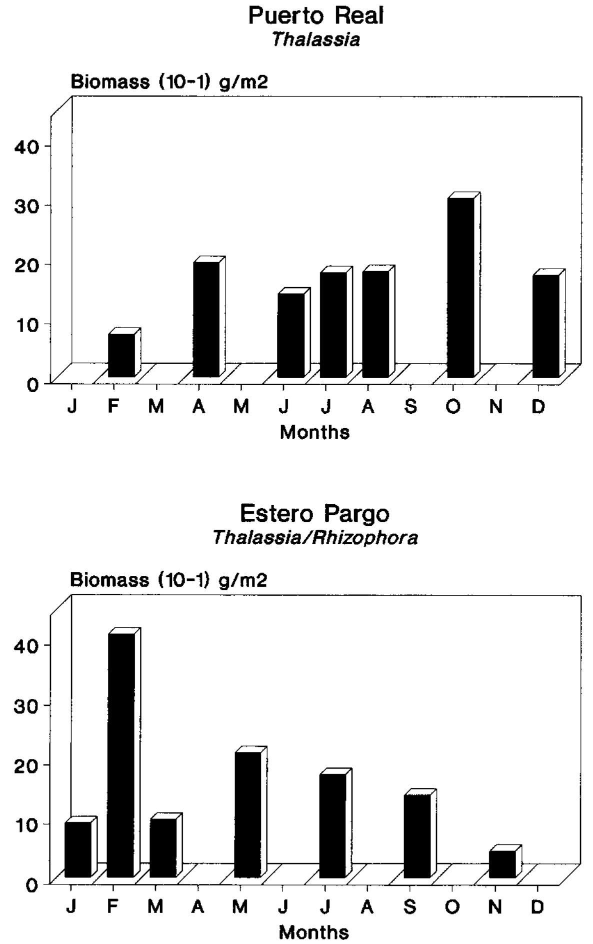

Fig. 3. Fish biomass in seagrass system (*Thalassia*) and seagrass/mangrove system (*Rhizophora*/*Thalassia*) in each month.

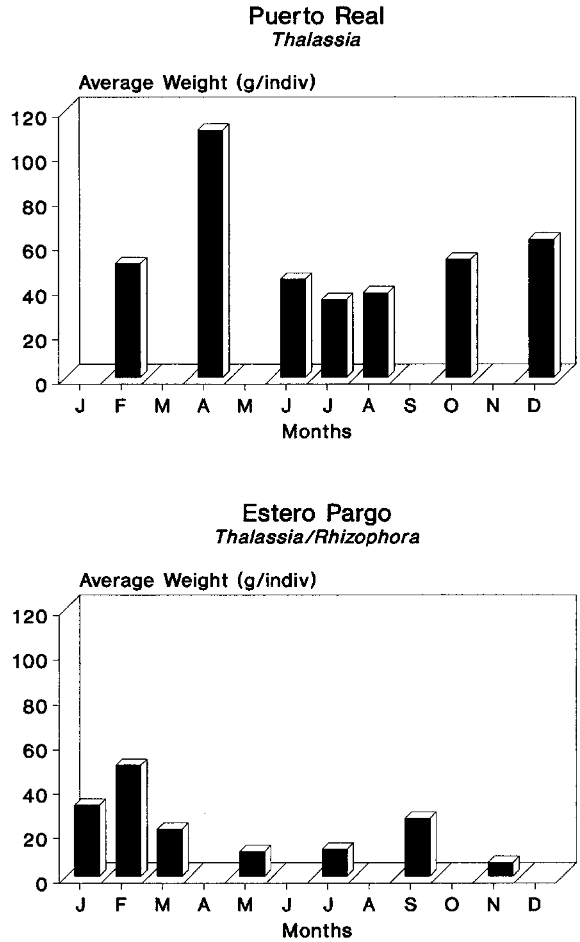

Fig. 4. Average size in weight of fish in seagrass system (*Thalassia*) and seagrass/mangrove system (*Rhizophora*/*Thalassia*) in each month.

abundance for seven dominant species common at both sites. S shows a clear tendency of high abundance during the rainy and 'nortes' seasons (June to December, Fig. 6A), while in S–M the highest species abundance occurred late in the 'nortes' season and during the dry season (December to March, Fig. 6B). Non-dominant species also showed the same usage tendency of the two systems.

Discussion

Seagrass and mangrove habitats in tropical and subtropical areas in the middle western Atlantic are used by many species of nekton and are generally characterized by high fish abundance and diversity. The literature on these two topics is broad and the reader is referred to Yáñez-Arancibia & Lara-Domínguez (1983). Livingstone (1984), and Weinstein (1985).

Overall patterns of biomass, density, number of species and size presented for the fish community in the results section are a function of the patterns of behavior of individual species. When specific species are considered, it is apparent that the use of different habitats has a strong seasonal programming.

It is clear that the utilization of the two habitats by fishes is different. Fishes in seagrass beds

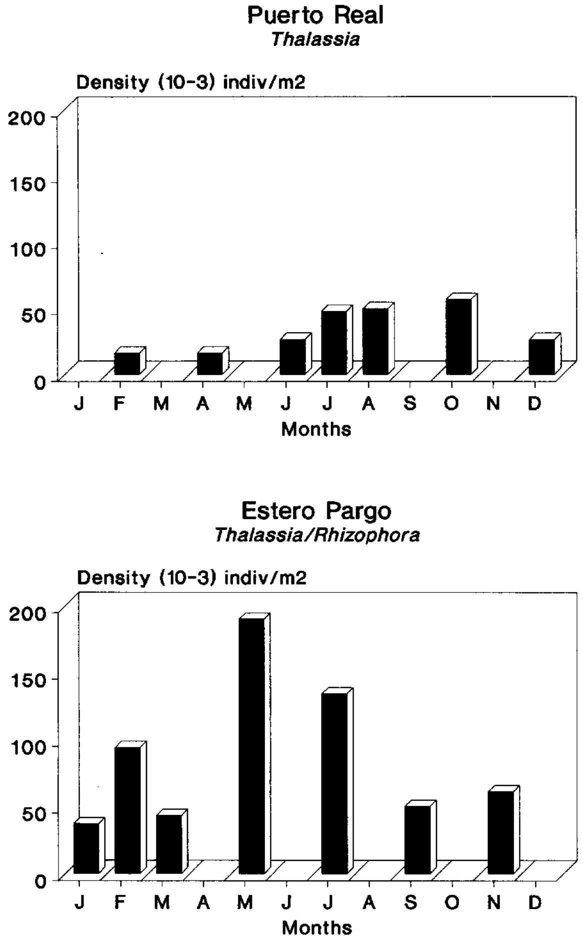

Fig. 5. Density of fish in seagrass system (*Thalassia*) and seagrass/mangrove system (*Rhizophora*/*Thalassia*) in each month.

in Puerto Real inlet were larger and fewer in number while those captured in the seagrass/mangrove system behind Carmen Island were smaller and more abundant. This reflects the predominance of juvenile and preadult fishes in the S–M area compared to mainly adult fishes at the S system. This pattern is also evident when the index of seasonal abundance of individual dominant species is considered (Fig. 6). The dominant species were found more often in the inlet during the end of wet season and all of the 'nortes' season and in the seagrass/mangrove area at the end of the nortes and during the dry season. This means that larger fish use the seagrass beds in the inlet mainly as an area of transit. The movement into and through the inlet during the 'nortes' season is facilitated by the strong net inflow, especially during the frontal passages. The seagrass/mangrove system behind Carmen Island is used mainly as a nursery. The combination of calm water, high organic matter content, mangrove and seagrass habitat, and high densities of invertebrates makes this a rich nursery area (Yáñez-Arancibia *et al.*, 1990).

Such patterns of the use of estuarine habitats by migratory nekton species has been shown for a wide variety of coastal systems (Boehlert & Mundy, 1988; Shaw *et al.*, 1988). For Terminos Lagoon Chavance *et al.*, (1986), and Yáñez-Arancibia & Lara-Domínguez (1988) have documented life history patterns. As indicated before, there are a number of advantages of using estuarine habitats including protection, calm waters, abundant food resources, and a diversity of habitats. Our results indicate that adult fish enter the lagoon through Puerto Real inlet in the fall during the wet and 'nortes' seasons. These fish often spawn nearshore in the vicinity of the inlets or in the inlet itself. This ensures that eggs and larvae are swept into the lagoon and distributed widely by prevailing currents. Therefore, there are at least three main patterns of use of the seagrasses in Puerto Real inlet and the seagrass-mangroves areas behind Carmen Island: (1) There are marine species which spawn in or near the inlet and the eggs and larvae are transported into and distributed throughout the lagoon by the predominant currents. Two important species which follow this pattern are *Archosargus rhomboidalis* and *Orthopristis chrysoptera*. (2) There are estuarine-marine species which spawn in different habitats of the lagoon and use the seagrass/mangrove system as a nursery area, e.g. *Bairdiella chrysoura*, *Arius melanopus*, *Arius felis*. (3) Finally, there are species which complete their life history in the inlet seagrass and seagrass/mangrove systems, e.g. *Urolophus jamaicensis*, *Opsanus beta*.

It seems clear that life history patterns have evolved to ensure the distribution, migration, biomass, and habitat use. But which factors have

Table 4. Dominant fish species of seagrass (S) system (Puerto Teal Inlet, Terminos Lagoon): monthly catch in number and weight (g), total frequency, total number and total weight.

Species	Feb Wt (No.)	Apr Wt (No.)	Jun Wt (No.)	Jul Wt (No.)	Aug Wt (No.)	Oct Wt (No.)	Dec Wt (No.)	Total Wt (No.)	Freq. %
Urolophus jamaicensis	3985.8 (7)	3692.7 (10)	2882.8 (7)	4197.9 (24)	1255.8 (8)	5749.5 (21)	9773.4 (27)	31537.9 (104)	62
Arius melanopus					366.6 (8)	17301.8 (232)	884 (13)	18552.4 (253)	9
Arius felis	654.6 (10)	3294.9 (37)	824.0 (5)	144.3 (2)	438.7 (10)	1850.9 (46)	8057.9 (59)	15265.3 (169)	50
Opsanus beta	656.5 (9)	854.6 (16)	310.0 (7)	2213.2 (24)	1571.6 (24)	1513.9 (17)	1006.2 (19)	8126.0 (116)	50
Lutjanus griseus	523.8 (8)	764.7 (7)	731.8 (4)	114.0 (1)	3165.1 (33)	2693.6 (37)	2421.2 (34)	10414.2 (124)	54
Eucinostomus gula		76.3 (7)	100.7 (19)	521.7 (116)	188.3 (45)	202.6 (39)	40.5 (7)	1130.1 (233)	58
Orthopristis chrysotera	227.4 (24)	550.1 (44)	3824.1 (244)	10279.5 (520)	11331 (465)	7537.4 (242)	1520.3 (111)	35269.8 (1650)	92
Haemulon aurolineatum			5.3 (2)	205.4 (39)	266.6 (51)	298.5 (20)	7.1 (1)	782.9 (113)	36
Haemulon bonariense	408.5 (5)	628.3 (10)	909.6 (10)	220.6 (7)	144.5 (21)	1168.1 (47)	660.2 (41)	4139.8 (141)	55
Haemulon plumieri	299.3 (27)	641.2 (18)	1080.4 (20)	857.6 (38)	1247.8 (31)	1830.2 (113)	1073 (75)	7029.5 (322)	86
Anisotremus virginicus	847.4 (12)	5470.0 (21)	2243.0 (14)	282.5 (5)	682.1 (7)	1289.4 (37)	1714.6 (23)	12529.0 (119)	56
Archosargus rhomboidalis	3027.1 (20)	10031.0 (74)	4281.0 (45)	12047.3 (274)	16544.9 (486)	38754.7 (435)	11924.7 (69)	96610.7 (1403)	94
Archosargus probatocephalus	461 (3)	23923.9 (27)	14248.3 (17)	2698.6 (12)	795.7 (3)	2507.2 (11)	4558 (8)	49192.7 (81)	49
Bairdiella chrysoura		219.5 (8)	42.8 (6)	143.7 (12)	1066.1 (88)	471.7 (35)	197.3 (8)	2141.1 (157)	45
Odontoscion dentex	22.9 (1)	26.7 (1)				1230.5 (74)	394.7 (23)	1674.8 (99)	24
Corvula sanctae-luciae	2052.5 (193)	1599.4 (117)	2676.9 (268)	2008.8 (136)	1430.1 (90)	3063.5 (237)	5043.9 (314)	17875.1 (1355)	86
Nicholsina usta	1049.3 (48)	799.8 (19)	326.9 (3)	303.4 (2)		3442.6 (138)	872.5 (42)	6794.5 (252)	55
Stephanolepsis hispidus	10.8 (5)	67.4 (9)	378.6 (29)	1666.6 (62)	1110.9 (31)	309.1 (8)		3543.4 (144)	53
Sphoeroides testudineus	1928.3 (15)	2369.6 (14)	1627.3 (12)	1210.7 (9)	2303.3 (27)	4526.2 (45)	4812.8 (44)	18778.2 (166)	69
Chilomycterus schoepfi	1278.7 (12)	1876.2 (9)	1097.9 (21)	2173.8 (38)	2098.3 (50)	2591.8 (35)	1435 (23)	12551.7 (188)	68
Diodon hystrix	1514.1 (25)	1332.6 (16)	3401.7 (27)	2448.6 (18)	989.9 (5)	2816.4 (54)	1037.6 (25)	13540.9 (179)	68

Table 5. Dominant fish species of seagrass/mangrove (S–M) system (Estero Pargo Inlet, Terminos Lagoon): monthly catch in number and weight (g), total frequency, total number and total weight.

Species	Jan Wt (No.)	Feb Wt (No.)	Mar Wt (No.)	May Wt (No.)	Jul Wt (No.)	Sep Wt (No.)	Nov Wt (No.)	Total Wt (No.)	Freq. %
Anchoa mitchilli	293.2 (380)	7.0 (8)	1.8 (2)			5.7 (4)	93.5 (314)	401.2 (708)	27
Arius melanopus	3577.4 (51)	3501.1 (71)			86.3 (1)	800.0 (19)	302.7 (4)	8267.5 (146)	17
Arius felis	1315.2 (21)	2088.5 (38)	125.2 (1)	784.2 (8)	1566.4 (54)	3400.0 (104)	158.5 (7)	9438.0 (233)	54
Opsanus beta	972.9 (8)	21810.7 (123)	6257.2 (37)	7793.9 (53)	2848.6 (11)	1155.9 (10)	725.4 (3)	41564.6 (245)	57
Scorpaena plumieri	847.3 (6)	1396.4 (15)	344.9 (3)	247.7 (6)	639.3 (2)	269 (2)	219.3 (2)	3963.9 (36)	26
Lutjanus griseus	748.7 (26)	5195.6 (135)	1121.0 (30)	2600.6 (52)	924.5 (12)	550.1 (22)	87.1 (3)	11227.6 (280)	66
Eucinostomus gula	408.2 (83)	1898.3 (394)	512.8 (146)	486.0 (285)	1983.4 (960)	316.5 (189)	1926.0 (558)	7531.2 (2615)	96
Diapterus rhombeus	40.4 (11)	26.7 (8)	2.6 (1)	23.1 (4)	0.7 (1)	10.0 (2)	211.1 (184)	314.6 (211)	34
Orthopristis chrysoptera	314.5 (13)	1228.1 (174)	1383.2 (361)	15047.6 (2467)	10636.9 (1176)	3841.8 (199)	120.7 (6)	32572.8 (4396)	74
Archosargus rhomboidalis	2695.5 (66)	16470.5 (488)	3018.8 (93)	5837.1 (1158)	5724.3 (514)	8992.1 (230)	1608.5 (14)	44346.8 (2563)	83
Archosargus probatocephalus		3099.7 (52)	215.1 (4)	942.5 (15)	891.7 (10)	276.9 (5)	292.4 (2)	5718.3 (88)	43
Cynoscion nebulosus	74.5 (2)	1504.1 (28)	150.3 (8)	225.3 (13)	641.8 (23)	458.4 (13)	245 (10)	3299.4 (97)	60
Bairdiella chrysoura	508 (46)	5934.2 (307)	822.7 (125)	3163 (413)	1353.8 (230)	3061.0 (163)	726.6 (54)	15569.3 (1338)	88
Bairdiella ronchus		1503.7 (22)	20.5 (1)	609.7 (16)	38 (16)	44.8 (2)	3.4 (2)	2220.1 (59)	23
Cichlasoma urophthalmus		404.7 (11)	364.7 (14)	270.8 (5)				1040.2 (30)	10
Acanthostracion quadricornis	282.8 (5)	501.3 (23)	644.2 (9)	224.2 (6)	958.6 (18)	158.4 (5)	1.5 (1)	2771.0 (67)	46
Sphoeroides testudineus	5432.0 (44)	18874.2 (142)	1666.7 (11)	9360.5 (83)	10558.3 (78)	4376.8 (40)	1079.0 (7)	51347.5 (405)	76
Chilomycterus schoepfi	606.0 (3)	5233.0 (51)	3913.5 (34)	1571.4 (22)	1382.2 (22)	1692.8 (15)	2.2 (1)	14401.1 (148)	61

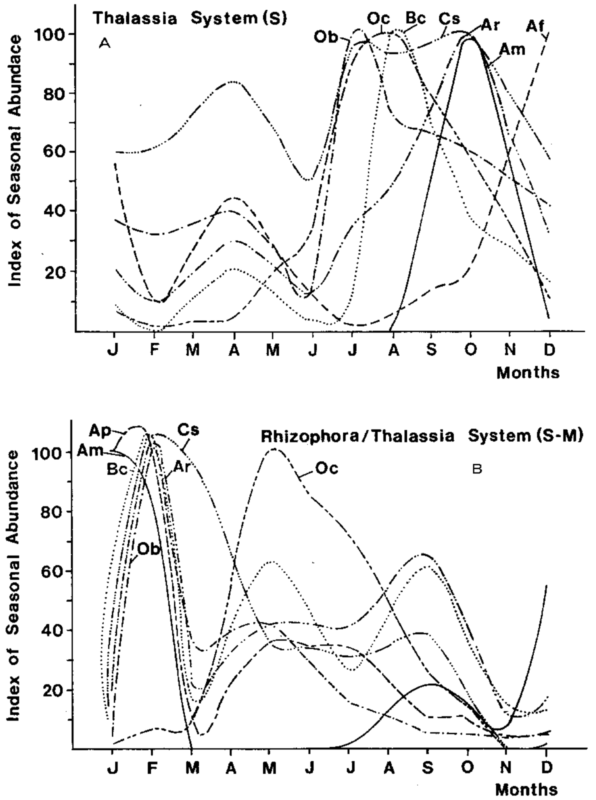

Fig. 6. Temporal variation in abundance of dominant fish population assemblages, as measured by trawl catch. In A) the seagrass system (S) and B) the seagrass/mangrove system (S–M) show Ob = *Opsanus beta*, Oc = *Orthopristis chrysoptera*, Bc = *Bairdiella chrysoura*, Cs = *Corvula sanctae-luciae*, Ar = *Archosargus rhomboidalis*, Ap = *Archosargus probatocephalus*, Am = *Arius melanopus*, Af = *Arius felis*.

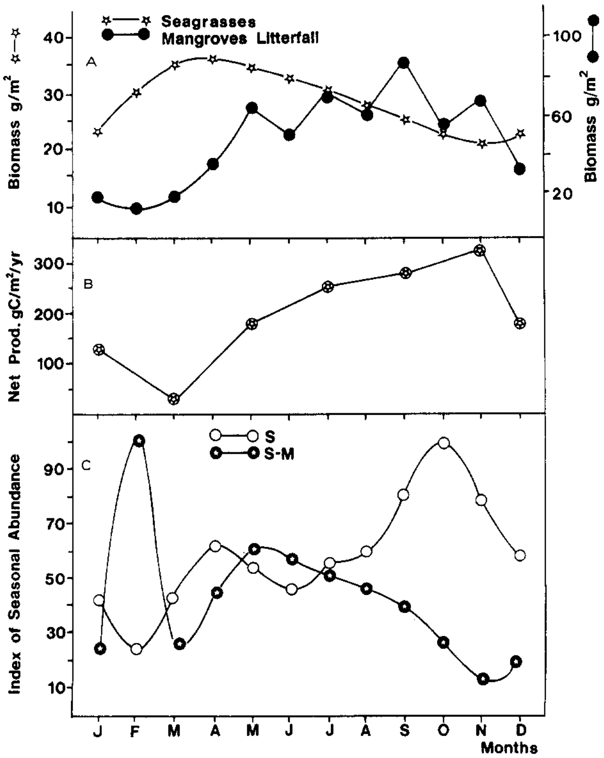

Fig. 7. A) Temporal variation of plant biomass in the seagrass and the seagrass/mangrove systems. B) Temporal variation of net aquatic primary productivity in Terminos Lagoon. C) Monthly index of fish abundance in the seagrass (S) and seagrass/mangrove (S–M) systems.

influenced the evolution of these patterns? We have found that there is a strong correlation between the life history patterns of migratory fish and the patterns of primary production (see Table 1, Fig. 7). In general fish tend to use habitats during periods of high primary production. We will illustrate this pattern with the fish species which use inlet seagrass meadows and the seagrass/mangrove systems behind Carmen Island. The index of seasonal abundance shows that the period of greatest use of the inlet area is during the rainy season, June to October (Fig. 7c). The fish which occur there are mainly adults, many of which spawn in or near the inlet and the eggs and larvae are swept into the lagoon. These eggs and larvae arrive at a time when there is a high availability of organic matter in the central lagoon (Day *et al.*, 1988a). This is due to high levels of phytoplankton productivity at that time as well as to high riverine input (Day *et al.*, 1982, 1988a; Soberón-Chávez & Yáñez-Arancibia, 1985; Deegan *et al.*, 1986). Thus it is likely that the young fish feed directly and indirectly on these sources of organic matter in the open waters of the lagoon.

With the end of the rainy season, river flow diminishes thus reducing riverine input of organic matter and nutrients. Aquatic primary productivity in the central lagoon is lowest during the dry season probably because of low nutrient input from the river (Day *et al.*, 1988a). In contrast to the open lagoon waters, tidal creeks and shallow waters associated with seagrass beds and mangroves have the highest levels of aquatic primary productivity during the dry season (7b, S–M system). Studies have shown that this high level of production is at least partially the result of stimulation of primary production by water draining from mangroves (Day *et al.*, 1987, 1988b). In addition, the productivity of seagrasses is highest during the dry season as a result of higher water clarity (Fig. 7a, Day, *et al.*, 1982; Moore & Wetzel, 1988).

During the dry season, the density and biomass of fishes is highest in the seagrass/mangrove area (Fig. 7c). The great majority of these fishes are small juveniles and preadults. Thus these organisms use the seagrass/mangrove areas during the period of highest primary production and during the most rapid growth period of the life cycle.

In summary, we have shown that for nekton species using seagrass and mangrove habitats in Terminos Lagoon, the pattern of migration seems to be strongly coupled to patterns of primary production in the lagoon. The idea of migratory nekton species using coastal habitats because of the high productivity is a generally accepted tenant of estuarine ecology, see paper in Yáñez-Arancibia (1985), Yáñez-Arancibia *et al.* (1988, 1990), Day *et al.* (1989), and Pinto (1988). However, this is one of the first times that we are aware of where this behavior has been specifically shown both for an entire community (in terms of such parameters on total biomass and density, and diversity) as well as for individual species in the community (as revealed by the index of seasonal abundance). One of the reasons that these patterns are evident have is that they are easier to observe in a tropical system. In temperate systems, seasonal patterns of migration and productivity are strongly controlled by the strong seasonality of temperature and light. In this tropical system where light and temperature are more constant, the adjustment of ecological interaction and processes to more uniquely estuarine forcing functions (e.g., riverflow, prevailing currents, nutrient concentrations) is more evident.

From a standpoint of natural selection, it is not surprising that such patterns would evolve. Larval, juvenile and preadults find using habitats during periods of high primary productivity have higher growth rates. These young give rise to adults which are more successful. The annual patterns of high productivity would continue to reinforce the utilization of habitats during periods of high primary productivity.

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