The Journal of the Oceanological Society of Korea
Vol. 19, No. 1, p. 44-55, June 1984.

Seasonal Variations in Populations of Small Fishes Concentrated in Shoalgrass and Turtlegrass Meadows

Sung-Hoi Huh
Dept. of Oceanography, National Fisheries University of Pusan, Pusan 608

Shoalgrass와 turtlegrass에 棲息하는 小型魚類 個體群들의 季節的 變動에 관한 研究

許 成 會
釜山水産大 海洋學科

Abstract: Abundances of small fishes that utilized seagrass meadows of Redfish Bay, Texas, were analyzed quantitatively to determine monthly changes of this concentrated subtropical fish community during 1982~1983. An effective quantitative sampler, a 1-m^2 thrown cage, yielded a total of 10,223 fishes that comprised 40 species in 23 families, with average total densities about 15 fishes/m^2 in shoalgrass meadow and 6 fishes/m^2 in turtlegrass meadow. The darter goby, pinfish, code goby, and Gulf pipefish were the four most abundant species, and accounted for approximately 85% of the number of fish collected. However, the two different meadows had different relative abundances of fishes. The darter goby numerically dominated shallower shoalgrass meadow, while the pinfish and code goby were the commonest fishes in deeper turtlegrass meadow.

Seasonal changes in both species composition and abundances of fish populations were major characteristics in these subtropical seagrass medows. Peak abundance of total fishes occurred during spring, with a secondary peak in fall. Lowest abundance of total fishes occurred in winter. Each abundant species showed its own seasonal abundance pattern, and had a peak abundance 1-3 months separated from other species, with some overlap of the increased larval recruitment. Such distinct seasonal abundance patterns with different times of peak recruitment among fish species seem to permit use of the seagrass meadow habitats with reduced, seasonoal competition.

要約: 아열대 seagrass 어류군집의 계절적 변동을 결정하기 위해, 미국 Texas 남쪽해안에 위치한 Redfish Bay의 seagrass meadow 에서 서식하는 소형어류개체군들의 밀도를 1982~1983년동안 매달조사하였다. 23과 40종에 속하는 총 10223개체수가 채집되었으며, 평균밀도는 shoalgrass에서 약 15마리/m^2이었고 turtlegrass에서 약 6마리/m^2 이었다. Darter goby, pinfish, code goby 그리고 Gulf pipefish가 일년을 통해 양 meadows에서 우점종으로 나타났다. 이들 네 어종은 총채집된 개체수의 약 85%를 차지하였다. Darter goby는 얕은곳에 위치한 shoalgrass에서 가장 흔한 어종이었으며 약간, 깊은 곳에 위치한 turtlegrass에서는 pinfish와 code goby가 가장 흔한 어종이었다. 어류의 종구성과 밀도의 계절적 변화는 이들 두 아열대 seagrass meadows에서 뚜렷하게 나타난다. 어류의 최대밀도는 봄에 나타난다. 어류밀도는 여름에 감소하나 가을에 다시 증가한다. 최소밀도는 겨울에 나타난다. 네 우점종은 각기 서로 다른 계절적 밀도변화 양상을 보인다. 이들 사이에는 약간의 중첩이 있지만 일반적으로 다른 종들로부터 1~3개월 분리된 최대밀도시기를 보인다. 이같이 분리된 최대밀도시기를 보이는 주요 어종의 계절적 개체수변화 양상은 높은 어류밀도를 지닌 아열대 seagrass meadows 에서의 이들 주요 어종의 공존을 가능케 하는 것으로 사료된다.

Manuscript received 17 April 1984.

INTRODUCTION

Seagrass communities often cover immense areas in the coastal waters of both temperate and tropical seas (den Hartog, 1977). In addition to the role of seagrasses in primary production of a great quantity of organic material by itself (Odum, 1957, 1963; Buesa, 1974; Greenway, 1974; Zieman, 1975; Thayer et al., 1975), the dense vegetation provides a good habitat for especially dense and often diverse groups of algae and animals(e.g. Humm, 1964; Nagle, 1968). Seagrasses also act as a shelter and nursery ground for economically valuable shrimp and fishes (Hoese, 1960; Skyes and Finucane, 1966), but these fishes are small minorities within the variety of densely concentrated, potentially competing fishes and invertebrates in seagrass meadows.

Considerable literature exists concerning such productive marine seagrass meadows. Many studies have been conducted on fishes, which comprise a both numerically and tropically important component of seagrass meadow food webs (Hellier, 1962; Hoese and Jones, 1963; Livingston, 1975; Adams, 1976a, b, c: Bonin, 1977; Brook, 1977; Weinstein and Heck, 1979; Stoner 1980; Kulczycki et al., 1981;Livingston, 1982; Holt et al., 1983). Although abundances of seagrass fishes have heen studied extensively, temporal partitioning of habitats by seagrass fishes remains largely undetermined. Analysis of such resource partitioning can provide evidence for competition as a mechanism resulting in niche separation and coexistence of concentrated, ecologically similar species.

In this study, an attempt was made to examine intensively the changes in the fish assemblages of adjacent shoalgrass and turtlegrass meadows in the northwestern Gulf of Mexico. Principal objectives of this study were determinations of the following: (1) fish species composition, (2) comparisions of abundances of fish between shoalgrass and turtlegrass meadows, and (3) seasonal changes in abundances of fish. Particular attention was given to the aspect of temporal partitioning in habitat use among the four most abundant fish species.

DESCRIPTION OF STUDY AREA

The study area was located adjacent to Steadman Island in Redfish Bay, Texas (27°50'N and 97°5'W) (Fig. 1). Redfish Bay, which lies approximately 7km north of Port Aransas, is one of a series of shallow marine lagoons formed by barrier islands characteristic of the Texas coast. Redfish Bay contains extensive meadows of turtlegrass (*Thalassia testudinum*) on a shell-mud bottom and shallower shoalgrass (*Halodule wrightii*).

A well defined band of the shoalgrass is about 10-15m wide, on a soft muddy bottom. Meadows of the turtlegrass extend from the shoalgrass offshore to a depth near 1m. Drifting

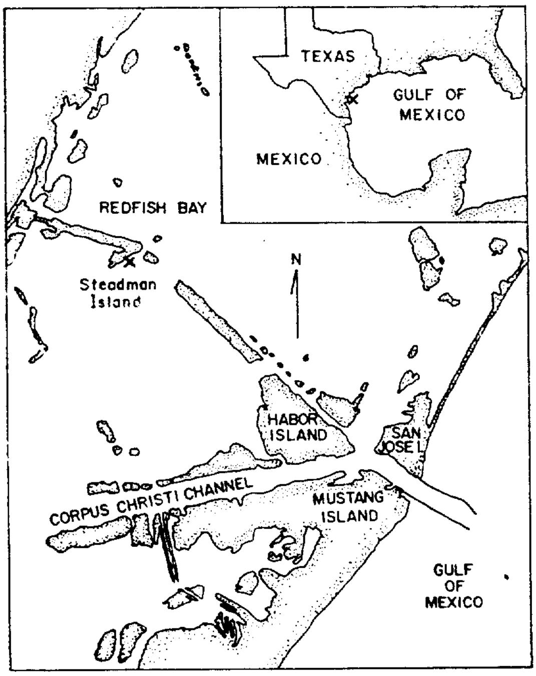

Fig. 1. Location of the study area near Port Aransas, Texas.

red algae were sometimes common, interspersed among the seagrass (Cowper, 1978). Epiphytic algae were always common on the shoalgrass and turtlegrass.

Seasonal differences in average sea level created slightly higher water levels in the spring and autumn months in this areas (Marmer, 1954). The normal tide range in this area is small, generally less than 0.6m (U.S. Department of Commerce Tide Tables, 1982), and is influenced heavily by atmospheric conditions. However, the study area was so shallow that portions of shallower seagrass blades, especially shoalgrass blades, occasionally were exposed to the air during the lowest tides, but always with water trapped near the bases of the blades.

Because of the shallow depths, wide daily and seasonal variations in surface water temperatures were observed in the seagrass. Daily average surface water temperature during the study period ranged from 15°C on December 16, 1982 to 33°C on July 14, 1982. The data yielded on annual average of 23.4°C.

Because Redfish Bay is close to the Gulf of Mexico and lacks any major fresh water sources, it had relatively constant salinity daily and seasonally. Diel changes in salinity, if any, were less than 2ppt. Daily average salinity during the study period varied from 26ppt on May 15, 1982 to 36ppt on August 23, 1982. In general, low salinities were encountered in spring and winter, and high salinities in summer months. Salinity averaged 30.3ppt throughout the year.

METHODS AND MATERIALS

Collections of fish were made every month from March, 1982 through April, 1983 at seagrass meadows of Steadman Island in Redfish Bay, Texas. Water temperature, salinity, and sampling depth were recorded throughout each monthly sampling date.

Fish were sampled quantitatively using a recently improved "throwing cage sampler" (1 m^2). The throwing cage was a square, 20kg frame made of galvanized steel bar, measuring $1\times 1m^2$ on the bottom and 0.75m tall. The sides were covered with 2mm-mesh net. The cage was thrown by two people into an undisturbed area of seagrass. It fell to the bottom within 1 second. It was pressed down into the sediment to ensure that no fish escaped. The area inside the cage was then swept five times with a square net that had 2mm-mesh netting and fitted closely inside the cage to capture virtually all fish present. In the preliminary throws with 6 or more sweeps, five sweeps were determined to be adequate to remove $\geq$95 % of the fish from each cage. Each month during the present study, the cage was thrown five times at each of four times (twice during daylight and twice at night) in each of two adjacent meadows of shoalgrass and turtlegrass. Each meadow was sampled approximately every 6hr over a 24hr period beginning about 1000 hrs. This procedure permitted analysis of the fish community in the seagrass meadows throughout four times of the day and night. All fishes collected were preserved immediately in the field in 10% formalin.

In the laboratory, fishes were sorted to species, counted, and weighed to the nearest gram wet weight and measured to the nearest mm standard length. Temporal overlap in habitat use was calculated using the formula proposed by Pianka (1973):

$$A_{ij}=\frac{(\sum p_{ih}\cdot p_{jh})}{[\sum p_{ih}^2\cdot \sum p_{jh}^2]^{1/2}}$$

where A_{ij} is the temporal overlap of species j on species i; p_{ih} is the proportion of individuals of species i sampled in a particular month h (1-12); p_{jh} is the proportion of individuals of species j sampled in the same month h. Values for the overlap index may vary between 0, if no overlap occurs, and 1 for complete overlap.

RESULTS

I. Species Composition

During the study period, 10,223 fishes from 23 families and 40 species were sampled in these seagrass meadows. These were primarily small fish species or early juveniles of large fish species. Only about 5% exceeded 50mm standard length. Most longer individuals were pipefishes.

The major families represented in the seagrass meadows in both numbers and biomass ranked as the Gobiidae, Sparidae, Syngnathidae, Engraulidae, and Sciaenidae. The four most abundant fish species collected, listed in order of decreasing abundance, were the darter goby (***Gobionellus boleosoma***), pinfish (***Lagodon rhomboides***), code goby (***Gobiosoma robustum***), and Gulf pipefish (***Syngnathus scovelli***). These four most abundant fish species made up 84.7% of the total number of fish and 81.1% of the total biomass of fish collected.

Fish species of secondary importance in abundance and biomass were the bay anchovy (***Anchoa mitchilli***), three species of the sciaenids, i.e. spot (***Leiostomus xanthurus***), silver perch (***Bairdiella chrysura***), and Atlantic croaker (***Micropogon undulatus***), two species of mojarras, i.e. silver jenny (***Eucinostomus gula***), and spotfin mojarra (***E. argenteus***), blackcheek tonguefish (***Symphurus plagiusa***), pigfish (***Orthopristis chrysoptera***), blackedge cusk-eel (***Lepophidium graellsi***), tidewater silverside (***Menidia beryllina***), rainwater killifish (***Lucania parva***), and Gulf toadfish (***Opsanus beta***). This secondary group of fish made up about 12.5% of the total number and 14.5% of the total biomass collected.

The remaining 24 species made up only <3% of the total number and <5% of the total biomass of fish collected. They included juveniles of economically important species such as the spotted seatrout (*Cynoscion nebulosus*), red drum (*Sciaenops ocellata*), southern flounder (*Paralichthys lethostigma*), and Gulf flounder (*P. albigutta*).

II. Comparisons between Shoalgrass and Turtlegrass Meadows

Shoalgrass and turtlegrass meadows were generally similar in fish species present, but the density of fish and proportional species composition of the two meadows were different (Table 1). The annual mean density of total fishes sampled from the shoalgrass meadow during the study period was more than twice that of the turtlegrass meadow (15.1 vs. 6.2 individuals/m^2). All of the four most abundant species, i.e. the darter goby, pinfish, code goby, and Gulf pipefish, were shared commonly between the shoalgrass and the turtlegrass meadows. In the shoalgrass meadow, the darter goby accounted for approximately 45% of the total number of fish collected. In contrast, the pinfish and code goby were almost equally represented among fishes from the turtlegrass meadow, and accounted for 36.2% and 31.1% of the fishes, respectively. Large differences in relative abundances between the two meadows were caused mainly by the concentration of the most abun-

Table 1. Annual mean densities (individuals/m^2) and mean biomass (g wet wt/m^2) of the four most abundant fish species in the two different meadows of Redfish Bay from March, 1982 through April, 1983.

	shoalgrass		turtlegrass	
	density	biomass	density	biomass
darter gody	6.9	1.20	0.6	0.16
pinfish	2.4	2.72	2.3	4.56
code goby	2.7	0.52	1.9	0.49
Gulf pipefish	0.9	0.29	0.4	0.21
other 36 species	2.3	1.33	1.0	1.03
total	15.1	6.02	6.2	6.45

Table 2. Size distributions and annual mean sizes of the four most abundant fish species in the two different meadows of Redfish Bay from March, 1982 through April, 1983. S.=shoalgrass and T.=turtlegrass meadows.

A. Darter goby

Fish size	0~10	11~15	16~20	21~25	26~30	31~35	36~40	mean size
S.	0.6%	13.4%	28.8%	31.7%	18.3%	6.5%	0.7%	21.3mm
T.	0.0%	5.3%	13.8%	25.7%	38.0%	16.7%	0.5%	24.8mm

B. Code goby

Fish size	0~10	11~15	16~20	21~25	26~30	31~35	36~40	mean size
S.	1.1%	32.0%	36.4%	12.4%	11.8%	4.2%	2.1%	18.6mm
T.	0.0%	10.4%	29.6%	27.4%	18.7%	10.3%	3.6%	22.8mm

C. Pinfish

Fish size	0~10	11~15	16~20	21~25	26~30	31~35	36~40	41~45	46~50	51~55	56~60	61~90	mean size
S.	2.2%	13.2%	14.7%	11.9%	14.5%	15.1%	10.4%	9.1%	5.0%	1.5%	1.0%	1.4%	28.5mm
T.	0.0%	3.3%	3.6%	3.8%	5.3%	9.3%	10.2%	22.8%	18.5%	9.8%	6.2%	7.2%	42.4mm

D. Gulf pipefish

Fish size	0~30	31~40	41~50	51~60	61~70	71~80	81~90	91~100	101~110	111~120	mean size
S.	1.6%	5.5%	14.0%	15.7%	15.6%	19.2%	15.7%	8.5%	3.8%	0.4%	67.6mm
T.	0.0%	2.2%	3.4%	6.8%	8.0%	17.0%	34.1%	14.8%	12.5%	1.2%	81.5mm

Fish size: mm SL

dant species, the darter goby, in the shoalgrass vs. turtlegrass meadows. In general, most species had a higher density in the shoalgrass meadows, although some species such as the pinfish were distributed almost evenly between the two meadows throughout the year.

In contrast to the differences in the fish numerical abundance between the two meadows, the biomass based on wet weight of fish per unit area was very similar for both meadows (Table 1). The annual mean biomass was 6.02 g/m^2 for the shoalgrass meadow and 6.45 g/m^2 for the turtlegrass meadows. Biomass of pinfish, which can reach much larger adult size than any other common fish species in the seagrass meadows, predominated in both meadows. In the shoalgrass meadow the pinfish accounted for approximately 45% of the biomass of fish collected. In the turtlegrass meadow the pinfish accounted for 70.7% of the total biomass of fish collected.

Population density of fishes in the shoalgrass meadow was twice that in turtlegrass, while total biomass of fish in the two seagrass meadows was similar; the proportion of large fish in the turtlegrass meadow was higher than that in shoalgrass, and the annual mean size of total fishes sampled from the turtlegrass meadow was larger than that of the shoalgrass meadow. Table 2 summarizes the size distributions and the annual mean sizes of the four common fish species in each meadow. Differences in size distributions were obvious between the two meadows for all of these common fish species. They showed similar size distribution patterns; smaller fish usually inhabited shoalgrass meadows, while larger fish usually inhabited somewhat deeper turtlegrass meadows.

III. Seasonality in Abundances of Fishes

Monthly densities of the four most abundant fish species at both shoalgrass and turtlegrass meadows are shown in Figs. 2 and 3. Data in the figure were based on 20 samples in each meadow each month, and the small standard errors (<5%) indicate statistically significant seasonal changes. Seasonal occurrence patterns of each abundant species was basically similar in the shoalgrass and turtlegrass meadows. A major difference was that the magnitude of peak abundance of each species in the shoalgrass meadow was generally larger than that in the turtlegrass.

1) Darter goby:

Gravid females and early juveniles were present in collections almost every month. This suggests continuous breeding for this species. However, a peak of reproduction occurred during late spring with a smaller peak during fall. This species was most common during late summer and early fall (Figs. 2 and 3). The peak density occurred in both meadows in September. The density of this species decreased in late fall, and reached a minimum during winter. But it increased again during spring.

2) Code goby:

A spawning season appeared to take place in late spring and early summer in the seagrass meadows; adult females had ripe eggs almost exclusively during these periods. The smallest gobies were caught in June along with gravid females. However, most code gobies disappeared from the seagrass meadows during summer months (Figs. 2 and 3) when their major prey items such as amphipods became scarce. Many young fishes started to appear in September and populations reached peak densities during late fall in the shoalgrass meadow and during early winter in the turtlegrass meadow. Density of this species was relatively high during winter months, but decreased during spring.

3) Pinfish:

According to Gunter (1945), spawning of Texas pinfish takes place in the winter, probably in the open Gulf near passes and the young spread into the inshore shallows. The smallest specimens first appeared in the study area in January at a mean length of about 20mm SL. The numbers of young fish continued to increase during early spring and populations reached a peak density in April in the shoalgrass meadow

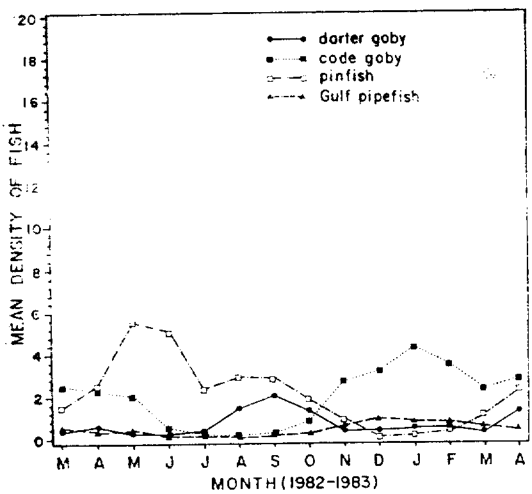

Fig. 2. Seasonal changes in densities (individuals/m^2) of the four most abundant fish species in the shoalgrass mesdow of Redfish Bay.

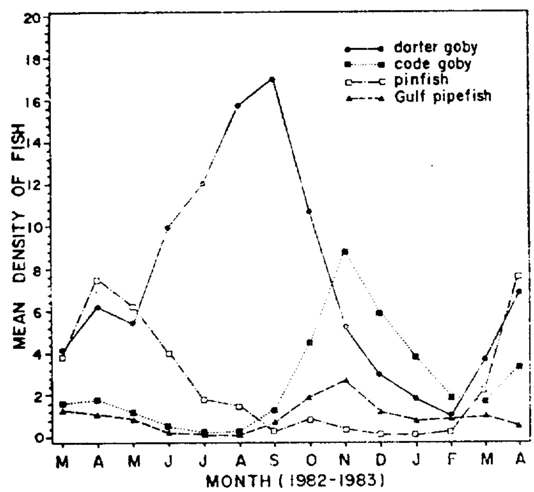

Fig. 3. Seasonal changes in densities (individuals/m^2) of the four most abundant fish species in the turtlegrass meadow of Redfish Bay.

and in May in the turtlegrass meadow (Figs. 2 and 3). The density of the pinfish decreased gradually during summer and early fall. Most pinfish emigrated from the seagrass meadows in October as 46 to 60mm (SL) size classes of juveniles. They probably moved toward the Gulf or deep bay waters. During winter only few larger specimens (>61mm SL) were caught.

4) Gulf pipefish:

The presence of male pipefish with developing embryos in their brood pouches and of gravid females in almost every month indicates continuous breeding. However, there appears to be a spring peak of reproduction in the study area since a higher percentage of males were breeding and were carrying larger broods than in any other season. Peak abundance of the Gulf pipefish occurred during late fall in both meadows (Figs. 2 and 3). But abundance of this species began declining in spring. And like the code goby, most Gulf pipefish disappeared from the seagrass meadow during summer month. Fall data showed a proliferation of young pipefishes on the seagrass meadows and their numbers increased to the late fall peak.

5) Temporal partitioning among the four abundant species:

Table 3 summarizes temporal overlap among these common species. The smallest temporal overlap occurred between pinfish with a spring peak abundance and code goby or Gulf pipefish with a fall peak abundance. Moderate overlap occurred between darter goby with a summer peak and the other species. The code goby appeared to have had a large overlap in temporal utilization with Gulf pipefish. However, the code goby was nearly always observed on the bottom, while the Gulf pipefish was usually observed in the water column near seagrass blades.

6) Other species:

Generally, the secondarily important fish species utilized the seagrass meadows as nursery grounds only for 2-4 months. According to the season of their appearance in the seagrass meadows, the secondary group of fish species can be divided into four seasonal groups. The first seasonal group included the bay anchovy, spot, southern flounder, and Gulf flounder, which were the fish species characteristic of early spring. The second group included the silver perch, pigfish, and skilletfish, which appeared during late spring and early summer, and two species of majorras, which appeared in late summer. The third seasonal group included the spotted trout and red drum, which appeared mainly in fall. The fourth seasonal group included the Atlantic croaker and blackedge cusk-eel, which appeared in winter.

7) Overall fish density:

Monthly densities of total fishes in each meadow are shown in Fig. 4. Although the den-

Table 3. Summary of time of peak abundance and temporal overlap in habitat use among the four most abundant species from seagrass meadows of Redfish Bay from March, 1982 through March, 1983. Temporal overlap index was calculated using the formula proposed by Pianka (1973).

	A. shoalgrass meadow					B. turtlegrass meadow				
fish species	time of peak abundance	temporal overlap index				time of peak abundance	temporal overlap index			
		1	2	3	4		1	2	3	4
1. darter goby	Aug. & Sep.	1.00	0.48	0.51	0.55	Sep.	1.00	0.41	0.46	0.52
2. code goby	Nov. & Dec.	—	1.00	0.92	0.28	Dec. & Jan.	—	1.00	0.93	0.34
3. Gulf pipefish	Nov. & Dec.	—	—	1.00	0.33	Dec. & Jan.	—	—	1.00	0.36
4. pinfish	Apr. & May	—	—	—	1.00	May & Jun.	—	—	—	1.00

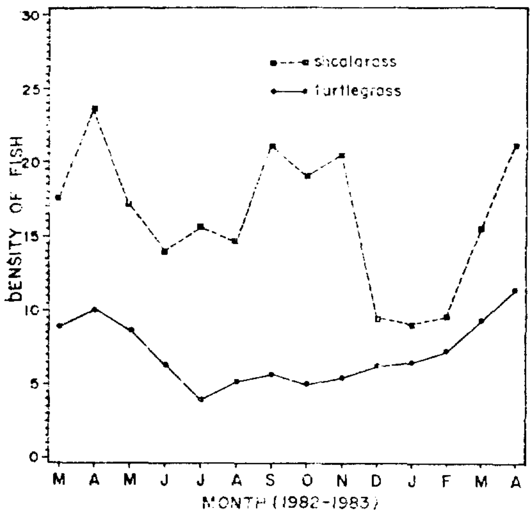

Fig. 4. Seasonal changes in density (individuals/m^2) of total fishes in the shoalgrass and turtlegrass meadows of Redfish Bay.

sities of total fishes collected from each meadow showed seasonal changes, the variations of these totals were not as distinct as changes in each species abundance. Because peak abundances of different fish species occurred in different times of the year, the certain level of overall numerical abundance was retained throughout the year.

In the shoalgrass meadow the lowest densities of total fishes occurred during the cold months between December and February. The density of fishes increased sharply during early spring. A peak in density of fishes occurred in April. Following the spring peak, the density of fishes decreased during summer, but rose again in late summer. The second and the third peaks in fish densities occurred in September and November, respectively.

In the turtlegrass meadow the lowest densities of fishes occurred during summer months, when the pinfish predominated. The density of fishes increased slowly during fall and winter, and reached its maximum during spring. In late spring the density of fishes decreased toward the summer minimum.

DISCUSSION

Forty fish species including several groups of closely related species utilized these two seagrass meadows of Redfish Bay. Among them, the darter goby, pinfish, code goby, and Gulf pipefish were very highly concentrated most of the year in the study area, but very rarely found outside the meadows in numerous samples on open mud (pers. obs.). Most fish species of the secondary group in abundance appeared in seagrass meadows as young juveniles. During their short residence in the seagrass meadows individuals of these species grow rapidly. Assemblages of small fishes and their rapid growth during their short residence in seagrass meadows indicate that seagrass meadows apparently function as nursery areas, probably providing these fish with abundant food and protection. These basic results were found to be generally similar to those of other studies conducted near the study area (Gunter, 1945; Hildebrand, 1954; Hoese and Jones, 1963; Cameron, 1969; Bonin, 1977). These studies agreed that gobies, pinfish, and Gulf pipefish were among the most abundant fish species in subtropical seagrass meadows of Texas.

Studies on species composition and abundances of fish in subtropical seagrass meadows outside Texas bays have been conducted by Livingston (1975) within Gulf of Mexico, and by Roessler (1965) and Brook (1975) within the Florida Atlantic coast. And species composition and abundances of fish in temperate and tropical seagrass meadows have been reported by Adams (1976a) in North Carolina's eelgrass meadows and by Weinstein and Heck (1979) in turtlegrass meadows of Panama, respectively. Comparisons of mean densities of fish between different study areas are difficult because most studies above provided only the total number of fish collected during the study period and it is difficult to estimate fish densities from those data. Only Adams (1976a) reported an average fish density of 2.09/m^2 in eelgrass meadows in North Carolina. The annual fish density of 15.1 /m^2 in shoalgrass meadows and 6.2/m^2 in the turtlegrass meadows found in this study are much higher than that reported by Adams for the eelgrass community, and are probably the highest recorded in seagrass meadows.

In general, smaller individual fish inhabited the shallower shoalgrass meadows, while larger individual fish inhabited the deeper turtlegrass meadows (Table 2). Based on supplementary, qualitative observations of what may keep small animals in such hiding areas, a possible explanation of this trend is as follows: Larval and early young fish of some species that were recruited into seagrass meadows were first concentrated in the shallower meadows of densest shoalgrass along the shore. As fish grew, they moved to the deeper, less crowded turtlegrass meadows, which may have more large fish (eating smaller fish) but less bird predation. Smaller individuals of several invertebrates such as the blue crab and brown shrimp also appeared concentrated in the shoalgrass meadow. Food availability of these fishes (amphipods, etc.) was similar in the shoalgrass and turtlegrass, although epiphytic algae eaten by invertebrate herbivores appeared more common among shoalgrass (Kitting, pers. comm.).

Seasonal changes in both species composition and abundance were major characteristics of the ichthyofauna utilizing these subtropical seagrass meadows of Redfish Bay. Although the four numerically dominant species were present in the study area thorughout the year, each of these species exhibited its own distinct seasonal occurrence pattern and had a different time of peak abundance. Peak abundance was closely related with rapid increase of larval recruitment. Peak larval recruitment and abundance of one species was separated 1-3 months from other species, with some overlap with another species before and after its peak. Generally, one fish population increased rapidly, sustained peak abundance for only two or three months, and decreased rapidly. Subsequently, another fish population increased and reached peak abundance. In this way, the seagrass meadow habitats were partitioned temporally by these abundant fish species.

Fish species of the secondary group in abundance generally appeared in the seagrass meadows for only 2-4 months as post-larvae or young juveniles in a certain season of the year. Among this secondary group, one clear result was temporal partitioning of seagrass meadows among the sciaenids, which are closely related to each other and potentially a guild of competitors. In general, each sciaenid species utilized the seagrass meadows in different times of the year; the spot utilized the study area in spring, the silver perch in summer, the spotted seatrout and red drum in fall, and Atlantic croaker in winter. A temporal overlap index between the sciaenid species calculated by Pianka's formula was less than 0.2.

In the past, several researchers suggested physical factors such as temperature and/or salinity (Gunter 1945; Adams, 1976; Bonin, 1977) and tidal level (Hoese and Jones, 1963) as the major factors affecting the abundance of fish in seagrass meadows. Some of the physical factors should be important in affecting the abundance for many species inhabiting the study area; wide seasonal variations in water temperature were observed in the study areas, and each fish species appeared in the seagrass meadows within a certain range of water temperatures. For example, the mojarras and skillet fish were collected almost exclusively at water temperature above 24°C, while the blackedge cusk-eel was collected exclusively at water mperature below 22°C. However, the year-und presence of the four most abundant ecies in the study area indicates tolerance to mewhat wide fluctuation in temperature.

Salinity did not appear to be related to such sh abundance patterns. Annual fluctuations of linity were not large in the study area, and ost of the species of the study area are condered to be euryhaline (Gunter, 1945). Tidal vel did not appear to be an important factor fecting abundances of most seagrass fish pecies except for extremely low tides, which ay have forced some fishes from the shallower eagrass meadows into deeper water. Such low des affected the distribution of fish only emporarily.

In addition to physical factors, some biologial factors such as the biomass of seagrass, ood availability, and interactions among fish pecies also appeared to be related to abundance f some fish species. For example, the abundance of the darter goby showed a tendency to coincide with the biomass of seagrass. In cold months, when the biomass of shoalgrass was the lowest, the densities of the darter goby were the lowest. But as the biomass of the shoalgrass increased during spring, the abundance of the darter goby also increased. Dense vegetation might provide protection from predation pressure (Holt et al., 1983) or aggressively competing species. Seasonal prey availability appeared to be an important factor related to the abundance of the carnivorous code goby and Gulf pipefish; most code gobies and Gulf pipefish disappeared from the seagrass meadows when their preferred animal prey items became scarce. A major decrease in abundance of pinfish, a subsequent sharp increase in abundance of code gobies, and then the decrease in abundance of darter gobies suggests that interactions among these common fish species might be important factors influencing their abundances in the seagrass meadows.

Shallow seagrass meadows are dynamic systems subject to (1) periodic recruitment of larval fish from seagrass meadows themselves or from the ocean, (2) growth and mortality during their stay in the seagrass meadow, and (3) emigration of some species from seagrass meadows after 2- or 4-month stay. Whatever the major factors affecting the abundance of fish in the seagrass meadows, a temporal partitioning in habitat use occurs dramatically among seagrass fish species. The occurrence of larval and young juvenile fishes of the different species in seagrass meadows at different times of the year leads to an almost continuous concentration of one small fish or another in this productive and potentially protective habitat of seagrass meadows.

ACKNOWLEDGEMENTS

I am very grateful to Drs. C.L. Kitting and D.E. Wohlschlag for their patience, encouragement and excellent advice throughout the course of this study. Drs. C. Hubbs, L.E. Gilbert, M.C. Singer, and D.M. Checkley provided welcome advice on this paper. Mr. J. Eldred of the University of Texas (Department of Zoology) accompanied me on collecting trips in all seasons of the year and in all kinds of weather. Mr. S. Holt of the UT Marine Science Institute cooperated in the use of much of the sampling equipment. Thanks are due to all these people, and the others who provided additional suggestions and advice. Financial support was provided by the Sid Richardson Foundation and Caesar Kleberg Foundation Programs in Living Resources, University Research Institute, a Union Pacific Fellowship, and a Summer Fellowship of the University of Texas at Austin.

REFERENCES

Adams, S.M. 1976a. The ecology of eelgrass, *Zostera* *marina*(L.), fish communities. I. Structural analysis. J. exp. mar. Biol. Ecol. 22:269-291.

Adams, S.M. 1976b. The ecology of eelgrass, *Zostera marina*(L.), fish communities. II. Functional analysis. J. exp. mar. Biol. Ecol. 22:293-311.

Adams, S.M. 1976c. Feeding ecology of eelgrass fish communities. Trans. Am. Fish. Soc. 105:514-519.

Bonin, R.E. 1977. Juvenile marine fishes of Harbor Island, Texas. M.S. Thesis, Texas A&M Univ., College Station, Texas. 108p.

Brook, I.M. 1975. Some aspects of the trophic relationships among the higher consumers in a seagrass community in Card Sound, Florida. Ph.D. Dissertation, Univ. Miami, Coral Gables, Florida. 133p.

Brook, I.M. 1977. Trophic relationships in a seagrass community (*Thalassia testudinum*), in Card Sound, Florida. Fish diets in relation to macrobenthic and cryptic faunal abundance. Trans. Am. Fish. Soc. 106:219-229.

Buesa, R.J. 1974. Population and biological data on turtle grass (*Thalassia testudinum* Konig,1805) on the northwestern Cuban Shelf. Aquaculture 4:207-226.

Cameron, J.N. 1969. Growth, respiratory metabolism and seasonal distribution of juvenile pinfish (*Lagodon rhomboides* Linnaeus) in Redfish Bay, Texas. Contr. Mar. Sci. Univ. Texas 14:19-36.

Cowper, S.W. 1978. The drift algae community of seagrass beds in Redfish Bay, Texas. Contr. Mar. Sci. Univ. Texas 21:125-132.

den Hartog, C. 1977. Structure, function and classification of seagrass communities. In: C.P. McRoy and C. Helfferich (eds.) Seagrass ecosystems. Marcel Dekker Inc., New York. p.89-121.

Greenway, M. 1974. The effects of cropping on the growth of *Thalassia testudinum* (Konig) in Jamaica. Aquaculture 4:199-206.

Gunter, G. 1945. Studies on marine fishes of Texas. Publs. Inst. Mar. Sci. Univ. Texas 1:1-190.

Hellier, T.R., Jr. 1962. Fish production and biomass studies in relation to photosynthesis in the Laguna Madre of Texas. Publs. Inst. Mar. Sci. Univ. Texas 8:1-22.

Hildebrand, H.H. 1954. A study of the fauna of the brown shrimp (*Penaeus azetecus* Ives) grounds in the western Gulf of Mexico. Publs. Inst. Mar. Sci. Univ. Texas 3:1-366.

Hoese, H.D. 1960. Juvenile panaeid shrimp in the shallow Gulf of Mexico. Ecology 41:592-593.

Hoese, H.D. and R.S. Jones. 1963. Seasonality of larger animals in a Texas turtle grass community. Publs. Inst. Mar. Sci. Univ. Texas 9:37-47.

Holt, S.A., C.L. Kitting and C.R. Arnold. 1983. Distribution of young red drums among different seagrass meadows. Trans. Am. Fish. Soc. 112:267-271.

Humm, H.J. 1964. Epiphytes of the sea grass, *Thalassia testudinum* in Florida. Bull. Mar. Sci. Gulf & Carib. 14:306-341.

Kulczycki, G.R., R.W. Virnstein and W.G. Nelson. 1981. The relationship between fish abundance and algal biomass in a seagrass-drift algae community. Estuarine, Coastal and Shelf Science 12:341-347.

Livingston, R.J. 1975. Impact of kraft pulp mill effluents on estuarine and coastal fishes in Apalachee Bay, Florida. Mar. Biol. 32:19-48.

Livingston, R.J. 1982. Trophic organization of fishes in a coastal seagrass system. Mar. Ecol. Prog. Ser. 7:1-12.

Marmer, H.A. 1954. Tides and sea level in the Gulf of Mexico. In: Gulf of Mexoco, its origin, waters, and marine life. Fsih. Bull. U.S. 89. p.108-118.

Nagle, J.S. 1968. Distribution of the epibiota of macrobenthic plants. Contr. Mar. Sci. Univ. Texas 13:105-144.

Odum, H.T. 1957. Primary production of eleven Florida spring and a marine turtlegrass community. Limnol. Oceanogr. 2:85-87.

Odum, H.T. 1963. Productivity measurements in Texas turtle grass and the effects of dredging an intracoastal channel. Publ. Inst. Mar Sci. Univ. Texas. 9:48-58.

Pianka, E.R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4:53-74.

Roessler, M. 1965. An analysis of the variability of fish populations taken by otter trawl in Biscayne Bay, Elorida. Trans. Am. Fish. Soc. 94:311-318.

Skyes, J.E. and J.H. Finucane. 1966. Occurrence in Tampa Bay, Florida, of immaure species dominant in Gulf of Mexico commercial fisheries. Fish. Bull.

65:369-379.

Stoner, A.W. 1980. Feeding ecology of *Lagodon rhomboides* (Pisces: Sparidae): Variation and functional responses. Fish Bull. 78:337-352.

Thayer, G.W., D.A. Wolfe and R.B. Willimas. 1975. The impact of man on seagrass systems. American Scientist 63:288-296.

Weinstein, M.P. and K.L. Heck, Jr. 1979. Ichythyofauna of seagrass meadows along the Caribbean Coast of Panama and in the Gulf of Mexco: Composition, structure. and community ecology. Mar. Biol. 50:97-107.

Zieman, J.C. 1975. Quantitative and dynamic aspects of the ecology of turtle grass, *Thalassia testudinum*. In: L.E. Cronin (ed.) Estuarne Resarch. Vol. 1, p. 541-562.