Abstract.-Trawl collections were made for Atlantic threadfin Polydactylus octonemus from 5 to 100 m in the Gulf of Mexico along a cross-shelf transect off Texas during October 1977-August 1981. Threadfin generally mature at 165-210 mm TL as they approach 7-9 months of age. Spawning primarily occurs in one period, mid-December-mid-March, and spans 45-120 days overall; 90% of successful spawning may occur in only 59% of that period. Threadfin in the northwestern Gulf range from <5 to 27 m depths in the demersal stage but are most abundant at <5to 16 m. Young-of-the-year recruit in waters <5-16 m when 2-4 months old. Fish begin to disperse to deeper waters in early summer and form a positive size gradient from the estuaries seaward. Threadfin in the demersal phase are not abundant in the northwestern Gulf after 9-11 months of age and reach only 15 months there. Observed mean and predicted sizes were 135-165 mm TL at 6 months, 165-215 mm at 9 months, and 180-205 mm at 12 months. Fitted von Bertalanffy parameters were 2.17-2.92 (K, annual), 195-230 (L_), and -0.03-0.08 years (t₀). Maximum size in the demersal phase is 230 mm TL in the northwestern Gulf, but more typically only 200-205 mm. Typical maximum life span (t_L) is about 1 year but may exceed that if individuals survive in a pelagic stage after spawning. Apparent mean time and cohort-specific total annual mortality rates are 97-100% in the northwestern Gulf. Population dynamics parameters presented are termed apparent because of the unknown effects of recruitment, movements, random variation, gear selectivity, etc. Spawning grounds seemingly lie along the Outer Continental Shelf, slope, or further offshore, and currents of the cyclonic shelf gyre off Texas and western Louisiana transport the young to estuarine and inshore nurseries.

Reproduction, Movements, and Apparent Population Dynamics of the Atlantic Threadfin *Polydactylus octonemus* in the Gulf of Mexico*

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The Atlantic threadfin Polydactylus octonemus occurs along continental shelves from Massachusetts to Brazil. and in the Gulf of Mexico (Breder 1948, Briggs 1958, Dahlberg 1975, Fischer 1978). Although uncommon on the Atlantic coast (Hildebrand and Schroeder 1928, Anderson and Gehringer 1965, Anderson 1968, Wilk and Silverman 1976), it is abundant in Gulf of Mexico (Gulf) coastal, surf, and estuarine waters (Hildebrand 1954, McFarland 1963, Chittenden and McEachran 1976). However, its annual abundance seems to fluctuate greatly (Reid 1956, Gallaway and Strawn 1974, Ogren and Brusher 1977).

Despite its abundance, the life history of P. octonemus has not been studied in detail, and little supporting data have been published. General notes occur in many faunal studies including Gunter (1938a, 1945), Reid (1955), Miller (1965), and Juneau (1975). These notes indicate P. octonemus is a small, inshore species that occurs from spring through fall in the northern Gulf and spawns from fall through spring. Our paper describes maturation, spawning periodicity, bathymetric distribution, recruitment, movements, age determination and growth using length frequencies, maximum size, life span, mortality, and relationships of length-weight, length-girth, standard-total length and fork-total length of *P. octonemus* in the northwestern Gulf. It also discusses spawning areas and larval dispersal in relation to Gulf hydrography, as well as how recruitment, movements, and randomization affect parameter estimation and interpretation.

Materials and methods

Collections for *Polydactylus octonemus* were made from nearly 3000 trawl tows in 71 monthly or twicemonthly cruises, October 1977–August 1981, along a cross-shelf transect in the Gulf off Freeport, Texas (Fig. 1) aboard a chartered shrimp trawler. Gear used were twin 10.4-m (34-ft) trawls with a 4.4-cm stretched-mesh cod end and a tickler chain. Initial stations usually were located at depths of 9, 13, 16, 18, 22, 27, 36, and 47 m. Sampling was expanded to include stations at 5 and 24 m after November 1978 and at 55, 64, 73, 82,

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86, and 100 m after May 1979. Collections were made during the day through September 1978; thereafter, a day and a night cruise were usually made each month. Usually, two tows of 10 minutes bottom time were made at each depth, except that 8 were made at 16 m, 24 were made at 22 m, and only 1 tow was made at most depths prior to October 1978. We emphasize our spatial sampling design was a single, cross-shelf transect from a sampling frame that encompassed much of the northern Gulf.

All *P. octonemus* were culled from the catch, measured to the nearest millimeter total length, fixed in 10% formalin, and then preserved in 70% ethanol. All individuals collected January-December 1979 were processed to determine the following: total length (TL), fork length (FL), standard length (SL), girth at origin of the dorsal fin (G), total weight (TW), gonad weight (GW), and sex and gonad maturity stage. If available, 200 fish were randomly selected for similar processing in all other months, except standard length and girth were not recorded. Gonad maturity (Table 1) was determined by a modification of the Kesteven classification (Lagler 1978). Fish in the Early Developing and later stages were considered mature to calculate maturity curves (Bowering 1983), which indicate the length when half were mature (M_{50}) . Gonadosomatic indices (GSI) were calculated for individual fish as: GSI = 100 GW/TW.

Age in years was determined by length-frequency analysis, e.g., the modal group progression analysis modification (Jearld 1983) of the Petersen Method (Lagler 1956). Knowing from this that essentially all

Stage and name	Description
1 Immature	Sex undetermined; gonads small or not visible.
2 Maturing Virgin	Sex distinguishable; gonads thin, occupy <10% of body cavity; eggs not visible.
3 Early Developing	Sex distinguishable to naked eye; gonads not flat, occupy 10-25% of body cavity; eggs opaque if present, not visible to naked eye.
4 Late Developing	Gonads occupy 25–50% of body cavity; opaque eggs present, visible to naked eye.
5 Gravid	Gonads occupy >50% of body cavity; up to 50% of eggs translucent.
6 Ripe	Gonads occupy $>50\%$ of body cavity; >50% of eggs translucent.
7 Spawning/Spent	Ovaries flaccid, completely or partially empty.

fish were age 0, we forced through the origin a regression to approximate age in days at observed sizes; this procedure is detailed under the methods used to calculate hatching dates. Cohorts (year classes) were specified on length-frequency figures by the season and year when they were hatched, e.g., winter 1981. Arithmetic means were used to describe central tendencies of length for each cruise, because length frequencies within each cohort were generally normally distributed.

Descriptions of spawning periodicity (beginnings and ends) using length frequencies assumed the following size and age combinations predicted from regressions of total length on age (Fig. 2): 25-40 mm TL at 1

Figure 2

Mean observed and predicted sizes at age (days) for *Polydactylus* octonemus cohorts with a summary of the iterative process used to calculate final hatching dates (H.D.) and set time-scales for final growth equations (F.E.). Initial growth equations (I.E.) were scaled to a 1 February hatching date. All regressions are significant at a = 0.005. The first two and three collections of the 1980 and 1981 cohorts, respectively, were deleted from calculations; see text on "Maturation and Spawning Periodicity" for explanation.





Apparent duration of the overall spawning period was approximated following Geoghegan and Chittenden (1982), as

Time-specific mean size range early in life Mean growth/day early in life

Calculations were based on fish collected early in life, i.e., May-June; too few were collected before then (1-4 fish/cruise in March and April) to estimate growth. For the numerator, time-specific size range was estimated for each cohort as the mean of the 99% confidence intervals for observations in that period. For the denominator, individual growth increments were estimated as the difference between (1) observed mean total lengths on successive dates and (2) total lengths on successive dates predicted from regressions. Individual estimates of growth/day were then made as the individual growth increment divided by the time between collection dates. Mean growth/day early in life was then estimated as the average of individual growth/day values between successive collections during May-June. Dentzau (1985, table 3) details these calculations. Calculations were also made using 90% confidence intervals to compare how much successful spawning occurred in a period shorter than the overall period.

Hatching dates used to approximate time scales to calculate growth were determined by a one-step iteration process following Standard and Chittenden (1984). An initial hatching date of 1 February was used to start the approximation, because fish 50-90 mm, assumed to be 2-3 months old, first appeared in March-April. Quadratic regressions of total length on age in days after 1 February were then used as models to estimate an initial \bar{x} -intercept for each cohort; linear regression was used if the quadratic term was not significant at $\alpha = 0.05$. Final hatching dates were calculated by using the \bar{x} -intercept for each cohort to readjust the initial x-variable (time) scale, so each final growth curve passed through the origin (Fig. 2).

Recruitment patterns and movements in the Gulf were determined by analyzing length frequencies and catch-per-unit-effort against depth at specified "seasons" (months) of the year; length-frequency data from Galveston Bay, Texas (Gallaway and Strawn 1974), extended our analyses to estuaries. We use the words "recruit" and "recruitment" in two ways: (1) to describe movement to areas by young *P. octonemus* descending to the bottom from their pelagic early stages, and (2) horizontal movements from estuaries



Figure 3

Length frequencies and cumulative percentage of all *Polydactylus* octonemus collected off Freeport, Texas, October 1977–August 1981.

to the Gulf, or within the Gulf, by fishes already in the exploited phase. The former conforms to Beverton and Holt's (1957) meaning of recruitment (t_r) , because these areas are generally exploited, and to Beverton and Holt's (1957) and Ricker's (1975) meaning (t_c) , because fish also then enter the exploited phase of life. Some gear selection for older, larger fish may occur as part of these processes.

Typical maximum life span was approximated by the Beverton-Holt model parameter t_L (Gulland 1969), and typical maximum size was approximated as a corresponding length (l_L) following the definition that only 0.5–1.0% of the catch exceeds age t_L (Alverson and Carney 1975, DeVries and Chittenden 1982). Values of l_L were calculated from the cumulative frequency for all fish captured (Fig. 3). Specific values of t_L were calculated from l_L by solving for time in von Bertalanffy (Gulland 1969) and regression growth equations (Fig. 2).

Time and cohort-specific total annual mortality rates (1 - S) were calculated using $S = N_t/N_0$, where S = rate of survival, and N_t and N_0 are the numbers of fish at age each month or per tow. Observed estimates were compared against theoretical values calculated from the expression $\overline{Z} = 4.6$ /number of years in life span (Royce 1972:238). Total mortality rates, typical maximum life spans, maximum sizes, sizes at age, spawning period durations, and von Bertalanffy parameters



Figure 4

Length frequencies of immature and female *Polydactylus octonemus* by gonad stage.

presented were termed apparent, because they may have been affected by recruitment of larger young from estuaries to the Gulf, by emigration and/or gear avoidance of fish about age I, or by a change from demersal to pelagic behavior; if so, they overestimated mortality, K, and spawning period durations and underestimated life spans, maximum sizes, average sizes at age, and L_{m} .

Von Bertalanffy parameters were calculated using Fabens' (1965) program and the same data used in TL on age regressions (Fig. 2). These points described a curvilinear regression and evidenced an asymptote, so they met the minimum requirements for a von Bertalanffy fit (Knight 1968, Gallucci and Quinn 1979). Unless stated, all length frequencies were moving averages of three and all lengths were total length. The symbol "?L" was used for instances where the type of length was not reported. Conversions between stan-



Percentage of mature female *Polydactylus octonemus* as a function of size.

dard, fork, and total lengths used regressions presented herein.

Results

Maturation and spawning periodicity

Polydactylus octonemus begin to mature at 165–210 mm in late summer-early fall. Sex usually could be determined by eye at 165 mm as many females entered the Early Developing stage (Fig. 4). Fish entered later stages at 180–210 mm. M_{50} was 185–195 mm, about 7–9 months old (Fig. 5), in agreement with gonad-stage length frequencies.

Little somatic growth seemingly occurs after P. octonemus enter later stages of gonad development. Mean sizes were 188 mm in the Early Developing stage (Fig. 4), 197 mm when Late Developing, and 196 mm when Gravid. The only fish collected in the Spawning/Spent stage was 189 mm. Minimum and maximum sizes remained constant after the Early Developing stage.



Figure 6

Monthly length frequencies of *Polydactylus octonemus* off Freeport, Texas, in day (D) and night (N) cruises. Bars in each panel depict cohort size ranges. The letter and first two digits above or within a bar indicate cohorts; the digit to the right of the decimal, age in years.



Polydactylus octonemus primarily spawn in one discrete period from mid-December through mid-March. The well-defined modes in length frequencies from throughout the study (Fig. 6) suggest spawning oc-

curred in one discrete period. Major spawning must have occurred during mid-December-mid-March, because small, young fish recruited mainly during mid-March-mid-May each year, e.g., fish 75-105 mm and



Figure 7 Monthly gonad maturity stages (defined in Table 1) of immature and female *Polydactylus octonemus*.

3-4 months of age recruited in abundance in mid-April-early May 1978, fish 50-70 mm and 2 months old in early April 1979, fish 65-115 mm and 2-4 months old in mid-May 1979, fish 75 mm and 3 months old in mid-March 1980, fish 55-115 mm and 2-4 months old in May 1980, and fish 60-115 mm and 2-4 months old in early April-early May 1981. Few fish 50-115 mm were collected from late August through February, indicating little spawning during late April-late October or November.

Calculated hatching dates were 11 January 1978, 16 February 1979, 26 January 1980, and 7 February 1981 for the 1978–1981 cohorts, respectively (Fig. 2). Other dates could have been calculated depending on data points included; however, the basic spawning period and coefficients of determination would be similar (Dentzau 1985). We deleted the earliest two collections in 1980 and earliest three in 1981 from calculations because mean sizes in these collections were as large or larger than those in subsequent ones and may have reflected incomplete recruitment or gear selection for larger fish, causing an upward size bias.

Gonad maturity data support the major mid-December-mid-March spawning period indicated by length frequencies. Except for one gravid age-I fish collected in April 1979, all fish collected in March-June were immature or maturing virgin (Fig. 7); none were in the Early Developing or later stages. Early and/or Late Developing stage fish were most common in October-December. Except for the one individual caught in April 1979, gravid fish were collected only in December as they approached age I. No ripe fish were collected, and few were gravid or late developing. Mean and/or maximum GSI values, although usually low, were high-





Figure 8

Monthly mean gonadosomatic indices, ranges, and 95% confidence limits about means for female *Polydactylus octonemus*, September 1978-August 1981.

est November-December (Fig. 8), except in August 1980 and 1981, when the few late-developing fish greatly skewed the means, and in mid-April 1979, when one age-I fish was gravid. The latter fish suggests some spawning in April and possibly May.

The apparent overall spawning period spans 45–120 days. Calculated overall spawning periods were 144 and 80 days in 1978, 53 and 80 days in 1979, 46 and 103 days in 1980, and 64 and 121 days in 1981 based on respective observed and predicted growth/day values. The broad 144-day interval for 1978 was based on only 9 fish and may be unreliable. Ignoring that value, spawning encompassed a 45–120 day interval which brackets the 90 day duration length frequencies indicated.

A large fraction of the successful spawning may occur in a period much shorter than the calculated overall spawning period duration. Using mean 90% instead of 99% confidence limits for observations, spawning periods were 78 and 43 days in 1978, 33 and 50 days in 1979, 27 and 60 days in 1980, and 40 and 76 days in 1981, based on respective observed and predicted growth/day values. On average, the duration estimated using 90% confidence limits was 59% of that using 99% limits. This suggests most spawning occurs in a relatively small part of the overall spawning period. Cohorts are apparently produced by fish that first spawn when 10–14 months old, assuming the hatching dates and sizes at early age noted previously. Spawning at 10–14 months of age is supported by (1) the disappearance from collections of all but one fish sometime during late October-late December when 9–11 months old (Fig. 6), (2) the occurrence of large mean and maximum GSI values in October-December (Fig. 8), and (3) the collection of early developing and more sexually mature fish during September-December (Fig. 7).

Polydactylus octonemus exhibit a sex ratio of 1.00 male to 1.78 females. This ratio was observed in 800 fish and differed significantly from 1:1 ($\chi^2 = 64.98$, $\alpha = 0.05$, df = 1).

Bathymetric distribution, recruitment, and movements

Polydactylus octonemus in the northwestern Gulf occur from <5 m depths to at least 27 m off Freeport. Only one specimen was collected deeper than 27 m, a 75-mm fish at 86 m in April, which may represent a pelagic young captured as the net was being retrieved. Greatest abundance generally occurred at 5 m, the shallowest depth occupied (Fig. 9), except in 1978 when this depth was occupied only in December, a time when



Figure 9

Catch/effort (mean number/ 10-min tow) by depth for *Polydactylus octonemus* off Freeport, Texas, each year and pooled, October 1977-August 1981. Tows in January and February were excluded in calculating effort because no fish were captured then.

fish had already begun to move offshore as noted below. Abundance was generally high at 9-16 m, although it often declined with increasing depth in this range. Abundance declined sharply between 18 and 22 m.

Young-of-the-year P. octonemus in the northwestern Gulf recruit to estuaries and coastal waters <5-16 m deep. Many young recruited to Galveston Bay in April and May when 50–110 mm (Fig. 10). In the Gulf, recruitment was greatest at the shallowest depths occupied. Fish 50–120 mm and 2–4 months old mainly recruited to 5–9 m in March-May, although some recruited as deep as 16 m (Fig. 11A, Table 2). Fish were most abundant at 5 m. Their abundance declined with increasing depth and was very low deeper than 13–16 m. Only one recruit was taken deeper than 16 m, the 75-mm fish at 86 m in April that may have been in a pelagic stage.

Polydactylus octonemus gradually disperse to deeper water in early summer and thereafter. Few age-0 fish were captured deeper than 9–13 m in April and May, but they were found at 18–27 m in June and were abundant at 16 m in July (Table 2). This gradual offshore dispersal is supported by the size gradient that existed seaward from Galveston Bay in June–December (Table 3), i.e., the smallest mean sizes were usually in Galveston Bay and the shallowest Gulf depths. Larger *P. octonemus* lead the offshore dispersal. Minimum sizes were similar at each depth in the Gulf and in Galveston Bay during May (Fig. 10, 11A). In contrast, size compositions showed gradients of increasing size with depth in June, July, August, September, and October, suggesting larger, presumably older, fish move offshore first (Fig. 11A,B,C; Table 3).

Peak abundance of *P. octonemus* shifts towards deeper waters as they disperse offshore. Abundance was greatest by far at 5-9 m in May and June, then included 13 and 16 m in July as fish dispersed offshore (Table 2). Abundance peaked at 16 m in August and September, although fish were abundant from 5 or 9 to 18 m, and at 16-24 m in October (Table 2).

Polydactylus octonemus abandon estuaries and inshore portions of the Gulf (<5-9 m) in late fall and occupy only the offshore portions (13-24 m) before disappearing in November and December. Two fish at 9 m in November were the only individuals captured shallower than 13 m in the Gulf in November and December (Table 2), although peak abundance was at 5-9 m in May and June. Gallaway and Strawn's (1974) data show a similar abandonment of estuaries by late fall (Fig. 10).

Polydactylus octonemus were most abundant in July-September and least abundant November-April



Flgure 10

Monthly length frequencies of *Polydactylus octonemus* in Galveston Bay, Texas, 1968 and 1969. Adapted from seine and trawl data of Gallaway and Strawn (1974); length frequencies are not moving averages of three.

(Fig. 12). Usually no *P. octonemus* were captured December-February.

Age determination and growth

Only one cohort of P. octonemus usually occurs at any one time in the northwestern Gulf. The only exceptions to this we found were in April 1979 when two cohorts appeared, albeit on separate cruises, and possibly in November of 1977 and 1980 (Fig. 6), when the second cohort was represented by only one individual.

Polydactylus octonemus is not abundant in the demersal phase in the northwestern Gulf after 8–11 months of age and apparently reaches only 15 months. Cohorts were present only until their first November or December after which they were not captured again (Fig. 6), except for the 194-mm fish in April 1979 that was the only fish older than 12 months.

Apparent growth of *P. octonemus* varied between cohorts, but observed mean sizes, and von Bertalanffy and quadratic regression predictions, averaged 135-165 mm at 6 months, 165-215 mm at 9 months, and 180-205 mm extrapolated to 12 months (Table 4). Regardless of the growth model, for a given cohort, predicted sizes agreed within 6 mm or less at 6 and 9 months and within 11 mm at 12 months.

Fitted von Bertalanffy equations were:

 $(1978): l_t = 195.2[1 - e^{-0.007999(t-30.40)}];$ annual K = 2.92; annual $t_0 = 0.0833$ $(1979): l_t = 230.4[1 - e^{-0.005955(t-11.69)}];$

annual K = 2.17; annual $t_0 = -0.0320$

where $l_t = TL$ in millimeters at time t in days.

Maximum size, life span, and mortality

Polydactylus octonemus in the demersal phase apparently reach a maximum size of about 230 mm in the northwestern Gulf but more typically only 200-205 mm. The largest of 4324 specimens collected was 229 mm; 99% were <202 mm and 99.5% were <206 mm (Fig. 3). The latter two sizes estimate an apparent l_L .

The apparent typical maximum life span in the demersal phase of *P. octonemus* in the northwestern Gulf is only 1 year. A value of $t_L = 1$ seems reasonable because (1) l_L values of 202 and 206 mm can be substituted into hatching-date regressions and von Bertalanffy equations to predict values of 0.69–1.00 year; (2) observed and predicted mean sizes at 9 months are 165–215 mm and predicted sizes at 12 months are 180–205 mm; (3) the largest specimen was about 11 months old when collected in December 1978; and



Figure 11 Length frequencies by

Length frequencies by depth for *Polydactylus* octonemus off Freeport, Texas, in March-June (A), July-August (B), September-October (C), and November-December (D). Data in each panel were pooled over the period October 1977-August 1981.



(4) *P. octonemus* almost completely disappeared from trawl catches off Freeport at 9–11 months of age. The collection of one specimen seemingly 15 months old in April 1979 (Fig. 6) suggests a few age-I fish survive

and remain in the white shrimp community, an inshore fauna described by Hildebrand (1954) and Chittenden and McEachran (1976). However, this would not greatly affect our estimate of t_L .

<i>tytus octonemus</i> by depth off Freeport, Texas. Depth (m)							
Period	5	9	13	16	18	22-24	27
MarApr.	0.4	0.2	0.1	0.1	0	0	0
May	18.7	5.8	1.4	0.5	0	0	0
June	14.8	8.6	2.5	1.4	0.8	0.4	0.1
July	17.2	10.7	18.0	9.1	0.5	0.1	0
Aug.	1.8	9.9	11.1	27.8	12.6	1.6	1.2
Sep.	3.8	3.9	4.0	12.2	4.1	2.7	0
Oct.	1.1	0.9	1.3	5.0	5.0	2.3	0
Nov.	0	0.2	0	0.4	0	0.1	0
Dec.	0	0	0.1	0.5	0.1	0.5	0

Polydactylus octonemus in the demersal phase have an apparent total annual mortality rate off Texas that approaches 100%, mean time- and cohort-specific values being 97–100%. Only one winter cohort was present in 31 of 32 months off Freeport (Fig. 6), so timespecific estimates were 100% in each of these instances. Cohort-specific values were 100% in 6 of 7 months for 1978, 8 of 8 months for 1979, and 5 of 5 months for 1980 fish because N_t was zero. A time-specific estimate for April 1979 and a cohort-specific estimate for April 1979 and a cohort-specific estimate for April 1979 and 3.00), respectively, but the former value may be an underestimate because the younger cohort was incompletely recruited in April.

Table 3

Mean total length (mm) for *Polydactylus octonemus* in Galveston Bay, 1968 and 1969 (adapted from Gallaway and Strawn 1974), and by depth in the Gulf off Freeport, Texas. Data at each depth in the Gulf are for age-0 fish pooled over the period October 1977-August 1981.

Month	Galveston Bay		Gulf of Mexico (depth in m)							
	1968	1969	5	9	13	16	18	22-24	27	86
Mar.			74.0				<u> </u>			·
Apr.	77.2	65.7	70.7	80.5						75.0
May	78.3	81.6	84.9	86.7	76.9	80.7				
June	86.6	92.7	109.4	127.1	132.1	123.2	139.2	147.7	164.0	
July	93.1	117.5	133.6	148.6	142.8	156.4	163.5	157.0		
Aug.	102.3	129.5	140.6	157.1	159.9	164.5	173.4	165.5	164.9	
Sep.	109.7	132.0	168.2	169.4	168.5	164.7	168.8	175.7		
Oct.	114.1	140.3	163.0	160.1	167.2	165.0	173.6	185.5		
Nov.	104.8					194.7		189.7		
Dec.	123.9				164.0	185.9	186.0	181.8		
Jan.	158.0									



Figure 12

Catch/effort (mean number/10-min tow) by month of *Polydactylus octonemus* off Freeport, Texas, each year.

Table 4

Observed mean sizes (mm TL), size ranges, and predicted sizes by hatching-date regressions (Fig. 2) and von Bertalanffy models for 1977-80 *Polydactylus octonemus* cohorts at 6, 9, and 12 months of age. Observed values are pooled data from July-August at 6 months and October-November at 9 months. Dentzau (1985, table 4) gives more detail.

		Observe	ed sizes			
		6 mo		9 mo		
Year	Mean	Size range	Mean	Size range		
1977			178	144-200		
1978	153	125-176	178	160-214		
1979	154	107-194	183	157-212		
1980	148	86-197	207	194-214		
1981	160	103-223	-	-		
			Pred	icted sizes	<u>·</u> ·	
		6 mo		9 mo		12 mo
	Regression	von Bertalanffy	Regression	von Bertalanffy	Regression	von Bertalanffy
1978	133	136	172	166	192	181
1979	163	157	186	187	_	205
1980	141	_	212	_	_	_

Table 5

Total weight-total length, girth-total length, and length-length regressions for *Polydactylus octonemus* with supporting statistics. All regressions were significant at $\alpha = 0.05$. The symbol v is from Ricker's (1973) GM regression. Measures are grams and millimeters. See Methods for symbols.

Equation	n	Range	$100 r^2$	v
Log_{10} TW = $-5.72 + 3.27$ Log_{10} TL (males + females + immatures)	2398	51-226	99.0	3.29
$Log_{10} TW = -6.29 + 3.53 Log_{10} TL$ (males + females)	800	107-226	94.2	3.64
$Log_{10} TW = -6.50 + 3.63 Log_{10} TL$ (males)	286	126-207	92.8	3.76
$Log_{10} TW = -6.25 + 3.51 Log_{10} TL$ (females)	514	107-226	94.8	3.60
TL = 15.10 + 1.70 G	847	51-226	94.8	1.74
G = -4.22 + 0.56 TL	847	51-226	94.8	0.57
TL = -1.04 + 1.42 SL	847	51-226	99.1	1.43
SL = 1.74 + 0.70 TL	847	51-226	99.1	0.70
TL = -2.77 + 1.26 FL	2398	51-226	99.5	1.27
FL = 2.80 + 0.79 TL	2398	51-226	99.5	0.79

Weight, girth, and length relationships

Total weight-total length regressions for males and females (Table 5) were not significantly different in slope (F = 2.91, df = 1, 798), but they differed in elevation (F = 7.73, df = 1, 799). Therefore, equations are presented for each sex and for males and females pooled. Total weight-total length regressions for all fish and for males and females pooled were significantly different in slope (F = 99.10, df = 1, 2056); however, the one equation that pools all fish may be useful at this stage of management.

Discussion

Spawning periodicity

The primary winter-spring spawning period we found for *Polydactylus octonemus* in the northwestern Gulf,

Table 6

Available information on larval, young (see text footnotes 1 and 4), and juvenile specimens of *Polydactylus octonemus* collected in western Gulf of Mexico surface waters by plankton net, dip net, meter net, and neuston net. Reference numbers correspond to locations in Figure 13.

forma	Location collected		Collection	Donth	Longeth		
iumber	(lat.°N)	(long.°W)	date	(m)	(mm)	Reference	
			Texas and Lo	uisiana			
1	Gulf off B Lor	arataria Bay, jisiana	Apr. 33	<22	$50~\mathrm{TL}$	Gunter 1938b	
2	26°40′	92°00′	8 May 54	1602	_	Springer and Bullis 1956	
3	26°05′	95°25′	27 May 54	1890		Springer and Bullis 1956	
4	26°15′	95°00′	7 Mar. 65	≅2300	44–54 TL	Pequegnat (text footnote 3	
5	27°52′	93°48′	Mar. 72	137	57-71 TL	Bright and Cashman 1974	
6	27°33′	96°06′	Jan.–Feb. 76	134	35-36 TL	Pequegnat et al. 1977	
7	26°57′	96°32′	Jan.–Feb. 76	106	38–47 TL	Pequegnat et al. 1977	
8	26°10′	96°24′	27 Feb. 76	91	21-52 TL	Pequegnat et al. 1977	
9	27°17′	96°23′	25 Mar. 76	131	40 TL	Pequegnat et al. 1977	
10	27°30′	96°44′	8 Apr. 76	49	56 TL	Pequegnat et al. 1977	
11	27°17′	96°23′	10 Apr. 76	131	43-80 TL	Pequegnat et al. 1977	
12	26°58'	97°11′	29 May-8 June 76	25	_	Pequegnat et al. 1977	
13	27°17′	96°23′	20 Apr. 77	131	65–72 TL	Wormuth et al. 1979	
14	27°34′	96°07′	15-21 May 77	134		Wormuth et al. 1979	
15	26°10′	96°24′	15–21 May 77	91	_	Wormuth et al. 1979	
16	Gulf of	f Freeport	6 May 79	54	56-66 TL	Rockett ¹	
17	28°14′	94°57′	23 Apr. 59	47		Bullis and Thompson 1965	
18	26°00'	96°00′	22 Apr. 82	200	44 SI.	Liehv ²	
19	26°30'	94°30'	24 Apr. 82	200	39-51 SL	Lieby	
20	27°00'	92°00'	25 Apr. 82	200	40-48 SL	Lieby	
21	27°30′	92°30′	10 May 82	200	41-44 SL	Lieby	
22	27°30'	93°30'	10 May 82	200	45 SL	Lieby	
23	28°00′	94°00′	9 May 82	58	38-45 SL	Lieby	
			Mexico				
24	20°01′	92°27′	14 May 54	1467	_	Springer and Bullis 1956	
25	19°13′	95°34′	17 May 54	1260	_	Springer and Bullis 1956	
26	20°34′	95°37′	20 May 54	2160	_	Springer and Bullis 1956	
27	21°42′	93°35′	22 May 54	2736		Springer and Bullis 1956	
28	24°00′	96°50′	25 May 54	1035	_	Springer and Bullis 1956	
29	24°54′	96°05′	27 May 54	1530	_	Springer and Bullis 1956	
30	25°08′	94°58′	9 Mar. 65		48 TL	Pequegnat (text footnote	
31	23°14′	96°08′	23 Apr. 75	_	49-60 TL	Kennicutt (text footnote 3	
32	23°00′	96°52'	24 Apr. 75	_	53-66 TL	Kennicutt (text footnote 3	
33	20°40′	92°55′	25 Nov. 56	2088	_	Bullis and Thompson 196	
34	20°40′	96°05′	2 Apr. 56	1782	_	Bullis and Thompson 196	
35	19°35′	95°28′	11 Apr. 56	2300	_	Bullis and Thompson 196	

mid-December-mid-March and continuing at a lower level through April or May, generally agrees with the limited literature. Gunter (1938b, 1945) suggested fallwinter or late winter-early spring spawning, because 28-100 mm young appeared from April through June. Winter-spring spawning is also supported by: (1) collection of neustonic "larvae"¹ 21-80 mm² in water 25-134 m deep over the south Texas continental shelf primarily from mid-January through early April, but also into early June (Pequegnat et al. 1977); (2) collection at the surface of fish (a) 44–54 mm in water 2300 m deep in early March off south Texas ($26^{\circ}15'N$, $95^{\circ}00'W$)³, (b) 57–71 mm (41–51 mm SL) in water 137

¹Larvae as used by Pequegnat et al. (1977) and Wormuth et al. (1979) may encompass the juvenile stage defined by Moyle and Cech (1982). ²We obtained sizes from specimens deposited at the Texas Cooperative Wildlife Collection (TCWC), Texas A&M University, College Station, TX.

³Fish were collected by W. Pequegnat and M. Kennicutt (Dep. Oceanogr., Texas A&M Univ.), and deposited in TCWC.

m deep in March over the West Flower Garden Bank off Texas (27°52'N, 93°48'W; Bright and Cashman 1974), (c) 50 mm in water <22 m in April off Barataria Bay, LA (Gunter 1938b), and (d) 56–66 mm in water 54 m deep in early May off Freeport (M. Rockett, Appalachian State Univ., Boone, NC 28608, pers. commun., March 1981); (3) collection at the surface in early May of "young"⁴ off south Texas (26°05'N, 95°25'W) and off the Louisiana continental shelf (26°40'N, 92°00'W) in water 1890 and 1602 m deep, respectively (Table 6; Springer and Bullis 1956); and (4) collection of neustonic "larvae" (footnote 1) 65–72 mm in water 91–134 m deep in mid-April-mid-May off south Texas (Wormuth et al. 1979).

Our calculated spawning-period duration of 45-120 days assumes large fish hatch before small ones and all grow at the same rate (Geoghegan and Chittenden 1982). The latter assumption appears reasonable, because 99% confidence intervals for observations (in Dentzau 1985, table 3) were fairly constant between cruises within each May–June period. Our calculated duration may be an overestimate because continued recruitment of small fish to the Gulf would tend to depress estimates of mean growth/day, the denominator in our spawning-duration equation. The numerator, mean size range, is less affected; larger recruits gradually disperse offshore to deeper waters, but we collected throughout and beyond the bathymetric range of the species. Comparisons of spawning-period durations from 90 and 99% confidence intervals are valid, however; such calculations use the same values except t.

Our calculated hatching dates indicate mid-Januarymid-February spawning, these being mean spawning dates because regression predicts averages. They are in error to the extent that regression curves do not pass through the origin and that they are asymptotic to the x- or y-axis in very early life. The latter is an unknown; the former problem does not seem serious, because Shirota (1970, in Hunter 1981) found length at first feeding in many species is four times the egg diameter. Egg diameter is not known in *P. octonemus* (Martin and Drewry 1978, deSylva 1984), but it averages 0.76 mm in the closely related *Eleutheronema tetradactylum* (deSylva 1984). This suggests *P. octonemus* is 3-3.5 mm at hatching, so only a few days error occurs in x, at most.

Spawning areas

Any spawning of *P. octonemus* in the northern or northwestern Gulf presumably occurs in the water column. Our data and the literature (Chittenden and McEachran 1976; Wohlschlag et al. 1977, 1979) indicate they basically disappear as demersal fish from the white and brown shrimp communities of the northern Gulf in November-December. They may assume a pelagic behavior then, which would explain their apparent absence in January-February, because Hastings et al. (1976) observed this species in December in habitat typical of pelagic fish—open water areas around an offshore platform in water 18 m deep in the northeastern Gulf off Panama City, Florida.

Catch records for young in the literature and the disappearance of P. octonemus from the white and brown shrimp communities in their primary winter spawning period, if the latter does not simply reflect gear selectivity following assumption of a pelagic habit. suggest this species spawns along the outer continental shelf, the continental slope, or further offshore. Although pelagic "larvae" (footnote 1) and juveniles have been collected at the surface in or near waters of the white shrimp community off Texas and Louisiana in April-early June (collections 1 and 12, Fig. 13) or the brown shrimp community in late February-May (collections 8, 10, 15, 16, and 23, Fig. 13), more frequent collections in U.S. waters have been made along the outer continental shelf at 106–137 m in January-May (collections 5, 6, 7, 9, 11, 13, and 14, Fig. 13), and even further offshore at $\geq 200-2300$ m in March-May (collections 2, 3, 4, 18, 19, 20, 21, and 22, Fig. 13). Several collections of "young" (footnote 4) and juveniles have been made in Mexican waters 1035-2736 m deep between Laguna Madre Tamaulipas and Campeche Bank in March-May (collections 24-32, Fig. 13). Similarly, young of other *Polydactylus* spp. also occur off continental shelves although adults are common in inshore waters; e.g., Klawe and Alverson (1964) found young P. opercularis and P. approximans <48 mm 250 nm offshore in the eastern tropical Pacific Ocean.

In contrast to the abundance of *P. octonemus* larvae and juveniles in the western and northwestern Gulf, they have not been identified in extensive collections off the west coast of Florida from Pensacola on the north, south to the Florida Keys (Vick 1964; Houde et al. 1979; M. Lieby, Bur. Mar. Res., St. Petersburg, FL 33701, pers. commun., Feb. 1986). This suggests little or no spawning in that area and in the eastern side of the Loop Current, which contributes water to the western Florida shelf (Austin and Jones 1974).

Polydactylus octonemus eggs, larvae, and juveniles, pelagic like other polynemids (Breder and Rosen 1966, Kagawade 1970), presumably use current transport to reach their estuarine and shallow Gulf nurseries. Standard and Chittenden (1984), based on Murphy and Chittenden (unpubl.), suggested spawning in Larimus fasciatus and other Gulf fishes is timed to coincide with

⁴Springer and Bullis (1956) defined young as postlarval, juvenile, and young specimens.



the occurrence of downcoast alongshore coastal currents (towards Mexico) and onshore surface Ekman transport caused by downcoast wind stress along much of the Texas and western Louisiana coast from August-September through April-May (Kelly et al. 1981). When alongshore currents are downcoast, an eastward or northeastward counterflow along the shelf break forms a cyclonic gyre on the continental shelf off Texas and western Louisiana (Kelly et al. 1984). The alongshore components of this gyre probably transport, in merry-go-round fashion, eggs, larvae, and juvenile P. octonemus from the outer shelf and slope to their shallow nurseries. Portions of this current not diverted westward at the Mississippi Delta (Kelly et al. 1983) may carry eggs and larvae east towards the west coast of Florida where older stages of P. octonemus have been collected in the surf and estuaries (Powell et al. 1972, Ogren and Brusher 1977) even though, as noted, larvae have not been found. Shaw et al. (1985) suggested a similar model for Gulf menhaden Brevoortia patronus.

Onshore surface Ekman transport components of the gyre seemingly could transport young P. octonemus directly inshore in the northwestern Gulf; however, this does not seem to be the case. Unlike P. octonemus, fishes of the brown shrimp community which spawn offshore and have pelagic eggs and larvae do not appear to be transported into the white shrimp community; they are basically absent there (Chittenden and McEachran 1976).



Depending on how long the young remain pelagic, current regimes are such that the spawning areas that produce young P. octonemus of the northwestern Gulf can lie almost anywhere in the western or central Gulf. Recent studies (Parker et al. 1979) cited in Rezak et al. (1983) found almost all surface drifters released west of a line from the Mississippi delta to the middle of the Yucatan Straits washed ashore along Texas; those released to the east were almost all found outside the Gulf along the Atlantic coast of Florida. This probably reflects a well-documented picture of Gulf circulation (Nowlin and McLellan 1967, Nowlin 1972, Behringer et al. 1977, Merrell and Morrison 1981, Merrell and Vasquez 1983): The major driving force for nearsurface circulation in the deep eastern Gulf is the Loop Current which enters the Gulf via the Yucatan Straits. loops toward Alabama, and turns back to exit the Gulf via the Florida Straits. The major driving force in the western Gulf is a large, permanent anticyclonic gyre, centered at 23.5°N, and maintained by consistent pinching off and westward drift of Loop Current rings (Merrell and Morrison 1981) or wind stress curl across the western Gulf (Sturges and Blaha 1976, Merrell and Vasquez 1983). South of this gyre is a cyclonic gyre in the Bay of Campeche from which water joins a predominantly northerly flow along the Mexican shelf (Nowlin 1972, Merrell and Morrison 1981, Rezak et al. 1983). Pelagic early stages of P. octonemus have been collected along much of the western Gulf margin (Fig. 13). The northerly flow there could transport pelagic young towards Texas. The coastal area off south Texas and northern Mexico has converging currents much of the year, water which at least in part heads easterly or northerly along the shelf edge after leaving the coast near 26°N. Whatever their source, pelagic young transported to and entrained in the gyre of the Texas-western Louisiana shelf could be transported to inshore and estuarine nurseries there.

Bathymetric distribution, recruitment, and movements

Our finding that *P. octonemus* is most abundant at depths ≤ 22 m in the northwestern Gulf agrees with Hildebrand (1954) and Chittenden and McEachran (1976), who only captured it in the demersal phase and considered it a member of the white shrimp community. Maximum depths recorded for the demersal form of this species in the Gulf are 66 m off Louisiana (Springer and Bullis 1956) and 65 m off Texas (Wohlschlag et al. 1979).

Our finding that P. octonemus appears late March-April and basically disappears late October-late December agrees with the literature for Texas and Louisiana including Gunter (1938b, 1945), Perret et al. (1971), and Gallaway and Strawn (1974). Some reports indicate a few fish occur in winter in the white and brown shrimp communities throughout the northern Gulf: (1) in January in Galveston Bay, Texas (Gallaway and Strawn 1974, Sheridan 1983), (2) at 18-22 m in January off Texas (Chittenden and McEachran 1976), (3) in shallow waters in January and February at Sabine Lake and Holly Beach, Louisiana (Perry and Carter 1979), and (4) at 40 m in early February off Alabama (Bullis and Thompson 1965). The similar periodicity of reported occurrence suggests similar movements and spawning periodicity throughout the northwestern and north-central Gulf.

The spring recruitment we found in *P. octonemus* agrees with data in several studies from the northern Gulf including Gunter (1945) and Miller (1965) in Texas, Gunter (1938b) and Perret et al. (1971) in Louisiana, and Ogren and Brusher (1977) in northwestern Florida. Recruitment appears concurrent in estuaries and the shallow Gulf, because we collected fish 50–105 mm in the Gulf off Texas at ≤ 9 m in April, the same period when Gallaway and Strawn (1974) and Landry (1977) collected fish in Galveston Bay 56–97 mm (40–69 mm SL) and 74–101 mm (53–72 mm SL), respectively. Moreover, demersal phase fish first appeared the same month in both Barataria Bay and the shallow Gulf off Louisiana (Gunter 1938b).

Our finding that P. octonemus disperse offshore beginning in early summer agrees with the literature. Gunter (1945), Gallaway and Strawn (1974), and Perret et al. (1971) found abundance declined in estuaries in June-August or September, at about the same time (July-September) we found greatest abundance in the Gulf and size gradients from estuaries to offshore. We found the largest, oldest fish in the deeper areas of the white shrimp community or in the transition community (Chittenden et al. 1982) as they dispersed offshore. This pattern has also been suggested for other species of the Gulf white shrimp community such as *Micropogonias undulatus*, *Peprilus burti*, *Cynoscion arenarius*, and *Larimus fasciatus* (White and Chittenden 1977, Murphy 1981, Shlossman and Chittenden 1981, Standard and Chittenden 1984).

Age determination and growth

Age determination, size at age, and von Bertalanffy parameters have not been previously described for P. *octonemus*. Our calculations for growth are based on sizes at known time scaled to calculated hatching dates to give age. Regression coefficients and K values are the same regardless of hatching date, however, because curves are fitted to the same time dimension between the first and last collections of a cohort.

We determined age in months and years by lengthfrequency analysis because we had almost 4 years of data from cruises so close in time that modes were easily followed, and only one cohort usually occurred at a given time. As in Stenotomus caprinus (Geoghegan and Chittenden 1982) and Larimus fasciatus (Standard and Chittenden 1984), modal-group progression analysis can be a superior method of age determination in P. octonemus because (1) spawning primarily occurs in one discrete period, (2) growth of large and small fish in a cohort appears uniform because variances were generally constant between cruises, (3) length frequencies are reasonably normally distributed within cohorts. and (4) age need only be determined for 1 or 2 years, ideal conditions for using length frequencies (Lagler 1956, Bagenal and Tesch 1978).

Although it would be desirable to support our aging findings by the more time-consuming analysis of daily otolith increments (Jones 1986), the growth and other parameters we present provide useful upper or lower boundaries for true values (see comments in Methods). We reiterate that our sizes at age and von Bertalanffy parameters are apparent ones; they are affected to an unknown degree by a combination of recruitment, and, especially as the fish approach age I, emigration, gear avoidance, and change from demersal to pelagic behavior. Because of similar problems, Knudsen and Herke (1978) suggested length frequencies should not be used to estimate growth in *Micropogonius undulatus*. We do not agree, however, because the fundamental problem is not the length-frequency method. Rather, it is how best to draw a random sample in time and space to characterize the population. The time dimension has three major aspects of variation (diel, annual, and monthly or seasonal), as does the spatial (alongshelf, across-shelf and estuary, and vertical). No published Gulf study to our knowledge addressed all six aspects, and few addressed any to the extent we did. Our design directly addressed all three time aspects and the across-shelf spatial dimension. We addressed along-shelf and estuarine variation indirectly by referencing the considerable literature. We were not able to address vertical variation, but apparently no published work has done that. The problem of getting representative data for P. octonemus-indeed. for many other Gulf species-may not be fully solved till all six aspects of sampling are concurrently addressed in one study.

Maximum size, life span, and mortality

The largest P. octonemus we collected in the northwestern Gulf (229 mm) is very close to that reported from off Virginia (233 and 235 mm ?L. Hildebrand and Schroeder 1928), the only Atlantic coast location with published sizes. Breder (1948) noted this species reaches one foot in length but gave no details to support the figure; it is only 2-3 inches larger than our maximum sizes and might reflect a rough rounding-off by him. The largest P. octonemus we found is slightly larger than maximum sizes in other Gulf studies [off Texas: 213 mm (Gunter 1945), 210 mm (Compton and Bradley 1963), 213 mm (171 mm FL) (Chittenden and McEachran 1976); Off Mississippi: 197 mm (Christmas and Waller 1973); Off Florida: 209 mm ?L (Powell et al. 1972)]. However, these reported maximum lengths are similar to the apparent typical maximum size of 202–206 mm we found. Smaller maximum sizes in other Gulf reports such as Gunter (1938b). Perret et al. (1971), Gallaway and Strawn (1974), and Perry and Carter (1979) may reflect gear selectivity or the fact they collected largely in estuaries, surf, and shallow Gulf areas. The studies cited, however, took place over much of the northern Gulf so the demersal stage of P. octonemus appears to show little, if any, east-west spatial variation in maximum sizes.

Our finding the largest, oldest *P. octonemus* in the deeper areas of the white shrimp community may reflect a broad life-history pattern for species there, many of which show a positive size gradient towards offshore. This has been reported for strongly estuarine dependent species such as *Micropogonius undulatus* and *Cynoscion arenarius* (White and Chittenden 1977, Shlossman and Chittenden 1981), and more marine forms such as *Peprilus burti* and *Larimus fasciatus* (Murphy 1981, Standard and Chittenden 1984).

The apparent typical maximum life span of 1 year we found for P. octonemus in the northwestern Gulf agrees with Chittenden and McEachran (1976) and appears reasonable, at least for the demersal stage, because the maximum and typical maximum sizes we observed are similar to, or larger than, all other values reported for the Gulf. The value of $t_L = 1$ year might be a little low because P. octonemus disappears at 9-11 months of age to spawn in winter, and because we collected one fish 15 months of age in April. That one fish is the only instance in 71 cruises in which a second year class co-occurred with young-of-the-year, so our data clearly indicate that at least the demersal phase of life basically ends at 1 year. Though the literature indicates no east-west spatial variation in maximum size, and age by inference, P. octonemus might survive their first spawning and assume a pelagic behavior. Bullis (1961) observed a dense ball of small Polydactylus sp., which could have been young or adult P. octonemus, P. virginicus, or P. oligodon (Fischer 1978), at the surface along the 500-fm curve in August in the western Caribbean.

Midwater and surface collections are needed to resolve the duration of a pelagic phase in adult P. octonemus; that would clarify the validity of the several life-history parameter values we have termed "apparent." In addition, collections with trawls larger than we and other workers have used would clarify if and how gear-avoidance affects parameter values. Despite these possible problems, however, it seems clear that few adult P. octonemus resume a demersal existence in the white or brown shrimp communities after age I. We collected only one fish older than 12 months, and Chittenden and McEachran (1976) caught no fish older than 12 months even though they caught 33 specimens on the white shrimp grounds in January.

The apparent mean time- and cohort-specific total annual mortality rates we observed for P. octonemus (97-100%) agree with theoretical estimates of 90-100% (Royce 1972:238) if maximum life span is typically only 1-2 years. Though these are also apparent values, they are not that far from the range of values for another well-studied, exploited pelagic species, Brevoortia *patronus*. In that species, total annual mortality rate is 83-95% depending on age (Nelson and Ahrenholz 1986). Moreover, the population dynamics of P. octonemus in the northwestern Gulf appear generally similar to those reported for many other species there including Micropogonius undulatus (White and Chittenden 1977), Cynoscion arenarius (Shlossman and Chittenden 1981), Cynoscion nothus (DeVries and Chittenden 1982), Peprilus burti (Murphy 1981), Stenotomus caprinus (Geoghegan and Chittenden 1982), Larimus fasciatus (Standard and Chittenden 1984), and Leiostomus xanthurus (Hata 1985). This similarity over a variety of species supports the suggestions (Chittenden and McEachran 1976, Chittenden 1977) that fishes of the white and brown shrimp communities, at least in the northwestern Gulf, have evolved a common pattern of population dynamics which stresses small size, early maturity, short life spans, high mortality rates, and rapid turnover of biomass.

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