

Abstract.— Collections were made for gulf butterfish *Peprilus burti* along a cross-shelf transect at depths of 5–100 m in the Gulf of Mexico off Texas from October 1977 to July 1980. Butterfish mature at 100–160 mm fork length as they approach age I. Spawning occurs primarily from September through May, but length frequencies indicate it concentrates, or is most successful, in distinct “Winter” (late January–mid-May) and “Fall” (early September–late October) periods that coincide with downcoast, alongshore currents (toward Mexico). Gonad data and persistence of small fish indicate spawning in winter, but at a low level. Spawning probably occurs offshore and upcoast toward the northcentral Gulf. Surface currents of the cyclonic shelf gyre probably transport eggs/larvae inshore and downcoast to recruit to the bottom in water 5–27 m deep, used as nurseries by butterfish when they are 2–5 months old. Butterfish disperse offshore as they mature and congregate in 36–100 m depths when they are 9–12 months old. They average 130–146 mm in fork length at age I in the northwestern Gulf, but 120–124 mm at age I and about 170 mm at age II in the northcentral Gulf. Estimates for the von Bertalanffy growth parameters L_{∞} , K , and t_0 were 164 mm, 1.99/year, and -0.20 years, respectively, for pooled northwestern Gulf Winter cohorts and 141 mm, 2.69/year, and -0.06 years, respectively, for pooled Fall cohorts. Somatic growth ceases as spawning approaches in the northwestern Gulf, but fish from the northcentral Gulf show large annual size increments. Butterfish reach about 200 mm in fork length, the largest ones occurring in the northcentral Gulf. Apparent maximum ages are 1–1.5 years in the northwestern Gulf, and 2–2.5 years in the northcentral Gulf. Differences in population attributes suggest complete mortality at age I in the northwestern Gulf or some unknown combination of an offshore and permanent contranantant spawning or postspawning emigration of adults to the northcentral Gulf. The genus *Peprilus* shows zoogeographic differences in population dynamics near Cape Hatteras, North Carolina.

Manuscript accepted 1 October 1990.
Fishery Bulletin, U.S. 89:101–116 (1991).

Reproduction, Age and Growth, and Movements of the Gulf Butterfish *Peprilus burti**

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The gulf butterfish *Peprilus burti* ranges in the Gulf of Mexico (Gulf from the Yucatan Peninsula to Tampa Bay, Florida (Horn 1970) and may occur along the U.S. southeast Atlantic coast, depending upon its systematic status and range extensions during cold spells (Caldwell 1961, Collette 1963, Horn 1970, Perschbacher et al. 1979). This abundant species is important in the industrial fishery and is commonly discarded by the shrimp fishery in the northern Gulf (Roithmayr 1965, Franks et al. 1972, Guthertz et al. 1975, Chittenden and McEachran 1976). Recent exploratory surveys have found large, commercially valuable concentrations of *P. burti* in the northern Gulf (Vecchione 1987). A preliminary biomass estimate for this area is 177,000 MT per 10,164 square miles (Gledhill unpubl.).

The life history and population dynamics of this species have not been described in detail, only as brief notes in numerous faunal studies including Gunter (1945), Hildebrand (1954), Miller (1965), Franks et al. (1972), Christmas and Waller (1973), Chittenden and McEachran (1976), and Allen et al. (1986). The paucity

of information reflects difficulty in age determination. Allen et al. (1986) found that hard parts such as otoliths, scales, opercula, and vertebrae were not useful in age determination.

In this paper we use an extensive set of length frequencies to infer age of *P. burti* and to describe size and age at maturity, spawning seasonality and areas, recruitment, seasonal distribution and movements, growth, maximum size and age, and weight-length, girth-length, and total, fork, and standard length relationships. We also discuss hydrographic conditions associated with spawning areas and recruitment, and zoogeographic differences in population dynamics in *Peprilus* near Cape Hatteras, North Carolina.

Methods

Collections for *Peprilus burti* were made along a cross-shelf transect in the Gulf off Freeport, Texas (Fig. 1) from October 1977 through July 1980 aboard a chartered shrimp trawler using twin 10.4-m (34-ft) shrimp trawls with a tickler chain and 4.4-cm stretched mesh in the cod end. Initial stations 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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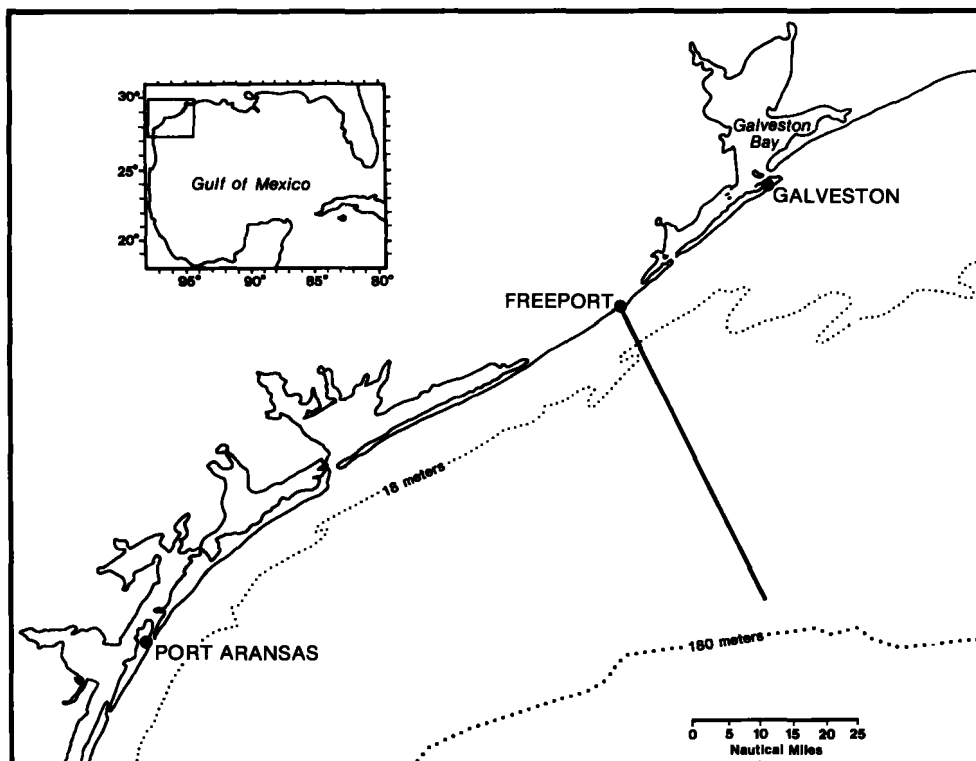


Figure 1
Location of sampling area off Freeport, Texas.

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

All *P. burti* were culled from the catch, measured for total length (TL), fixed in 10% formalin for 2–4 days, and then stored in 70% ethanol. For the period December 1978–November 1979 a total of 300 fish, if available, was selected each month after stratifying the catch into cohorts determined by length-frequency analysis (see below). Specimens were then randomly selected within strata to determine total length, fork length (FL), standard length (SL), total weight (TW), gonad weight (GW), and girth (G) measured vertically from the dorsal fin to the preanal pterygiophore. Sagittal otoliths were removed from individuals larger than 75mm, teased free of saccular and labyrinthian tissue, and then stored dry for later immersion in water and viewing with reflected light under a dissecting microscope. Female and immature fish were assigned gonad maturity stages (Table 1) modified from Kesteven's system (Bagenal and Braum 1971). Gonad weight and

Table 1

Description of gonad maturity stages assigned to immature and female *P. burti*.

Stage	Description
1 Immature	Gonads barely or not visible; sex indistinguishable to naked eye.
2 Maturing Virgin	Gonads small, opaque; usually thin, streamer-like, running along posteroventral wall of body cavity; sex indistinguishable to naked eye.
3 Early Developing/ Resting	Sex distinguishable; individual eggs not visible to naked eye but ovarian lamellae visible; ovaries occupy <20% of body cavity.
4 Late Developing I	Ovaries occupy 20–50% of body cavity; individual eggs visible in close examination; eggs opaque.
5 Late Developing II	Ovaries occupy 50–80% of body cavity; individual eggs distinguishable; eggs opaque.
6 Gravid	Ovaries occupy >50% of body cavity; translucent eggs present, but make up <50%.
7 Ripe	Ovaries occupy >50% of body cavity; >50% of eggs translucent.
8 Spawning/Spent	Ovaries flaccid, pink, with few eggs present; fish large enough to have spawned.

Table 2

Final quadratic growth regressions, calculated hatching dates, and von Bertalanffy equations for individual *Peprilus burti* cohorts and pooled Fall and Winter cohorts. Fits regress mean observed fork lengths (mm FL) on age in days (Days) for the quadratic and on age in years (Years) for the von Bertalanffy growth equations. All regressions are significant at $\alpha = 0.05$.

Cohort	Final quadratic growth equation	r^2	Final calculated hatching date	von Bertalanffy growth equation
Fall ₇₇	FL = 0.09 + 0.6004(Days) - 0.0007(Days) ²	0.93	25 Sep 77	FL = 139(1 - exp(-2.22(Years + 0.050)))
Fall ₇₈	FL = -0.14 + 0.6971(Days) - 0.0009(Days) ²	0.87	8 Sep 78	FL = 138(1 - exp(-3.81(Years + 0.122)))
Fall ₇₉	FL = -0.16 + 0.7234(Days) - 0.0010(Days) ²	0.97	15 Sep 79	Data not adequate to fit alone
Fall pooled	FL = 4.04 + 0.6386(Days) - 0.0008(Days) ²	0.91	— — —	FL = 141(1 - exp(-2.69(Years + 0.063)))
Winter ₇₈	FL = -0.10 + 0.1741(Days) - 0.0011(Days) ²	0.95	30 Jan 78	FL = 133(1 - exp(-3.06(Years + 0.055)))
Winter ₇₉	FL = 0.14 + 0.6931(Days) - 0.0008(Days) ²	0.94	16 Mar 79	FL = 170(1 - exp(-1.98(Years + 0.043)))
Winter ₈₀	FL = -0.09 + 0.6975(Days)	0.93	22 Mar 80	Data not adequate to fit alone
Winter pooled	FL = 8.18 + 0.6327(Days) - 0.0007(Days) ²	0.93	— — —	FL = 164(1 - exp(-1.99(Years + 0.200)))
Fall and Winter pooled	FL = 6.28 + 0.6362(Days) - 0.0008(Days) ²	0.91	— — —	

stage were also determined for randomly selected fish in October 1978 and during December 1979–February 1980 to verify spawning seasons. All lengths presented are fork lengths, and all length frequencies are moving averages of three, unless specified otherwise.

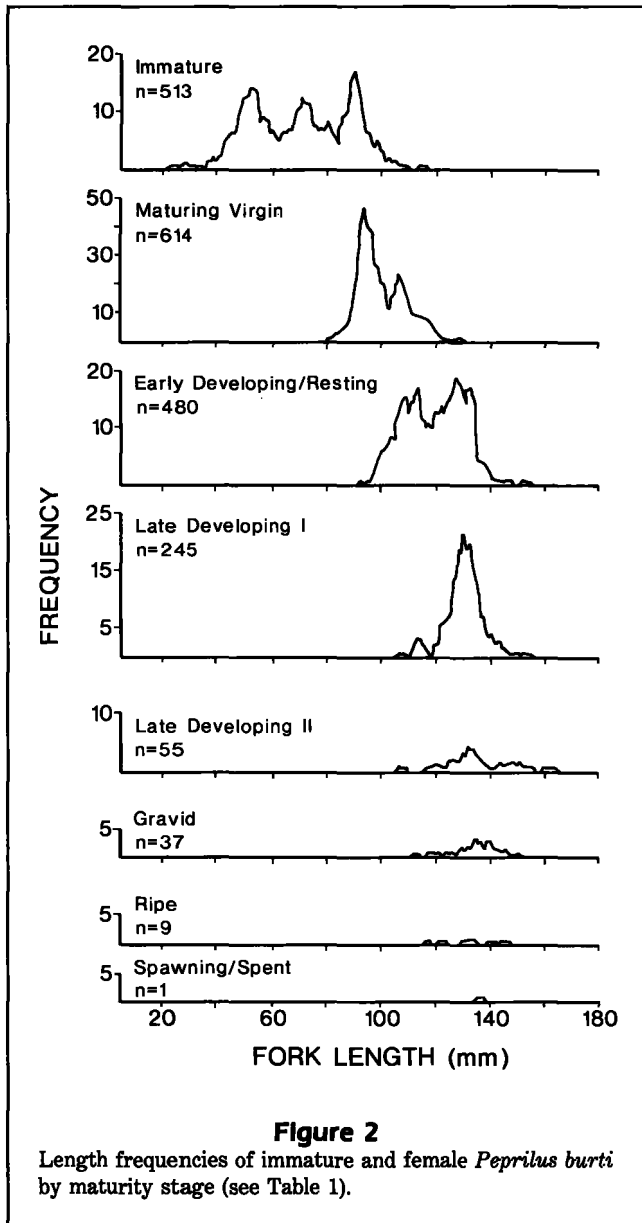
We also made collections in the northcentral Gulf, at depths of 9–91 m, aboard the FRS *Oregon II* east (89°00'W–89°30'W) and west (89°30'W–91°30'W) of the Mississippi River during 10–19 April 1980 and 21 April–1 May 1980, respectively (Rohr et al. 1980). Fish were sampled from these catches without randomization and measured (FL) to compare with size and age compositions in the northwestern Gulf.

Age was determined by length-frequency analysis, that is, the modal group progression analysis modification (Jearld 1983) of the Petersen method (Lagler 1956, Tesch 1971). Cohorts were specified by the season and year when they hatched, for example, Fall₇₉. Cohorts hatched during the periods January–May and September–October are hereafter referred to as Winter and Fall cohorts, respectively; this abbreviated terminology corresponds with the major spawning each period (see “Maturation and Spawning Periodicity”). Arithmetic means were used to describe central tendencies in cohort length frequencies.

Mean hatching dates used to approximate time scales to calculate growth were determined by a one-step iterative process following Standard and Chittenden (1984). A hatching date of 1 March was assigned to start iterations for the Winter₇₉ and Winter₈₀ cohorts because, in those groups, fish 30–75 mm, assumed to be 2–4 months old, first appeared mid-May to mid-June.

A hatching date of 1 February was assigned to start iterations for the Winter₇₈ cohort because, in that group, fish 20–50 mm, assumed to be 1–3 months old, became abundant in mid-April. A hatching date of 1 September was assigned to start the approximation for Fall cohorts because fish 30–75 mm, assumed to be 2–4 months old, first appeared November through early December. Quadratic regression of length-on-age in days was then used to estimate initial x-intercepts for each cohort. Final hatching dates were calculated by using x-intercepts to readjust the initial x-variable (time) scale, so that each final quadratic growth curve passed through the origin (Table 2). Descriptions of spawning periodicity using length frequencies assume early size and age combinations (see Results) predicted from quadratic regression of length-on-age pooling all Winter and Fall cohorts (Table 2). Von Bertalanffy growth equations were fit to length and age (in years) data using the nonlinear least-square parameter estimation procedure in FSAS (Saila et al. 1988). Data points described a curvilinear regression and evidenced an asymptote, so equations presented met the minimum requirements for a von Bertalanffy fit (Knight 1968, Gallucci and Quinn 1979).

Maximum age was approximated by the Beverton-Holt model parameter t_L (Gulland 1969) following the definition that only 0.5–1.0% of the catch exceeds age t_L or its corresponding length (Alverson and Carney 1975, DeVries and Chittenden 1982). Maximum sizes and ages, and sizes-at-age, presented are termed apparent, because they may be affected by emigration of fish approaching age I; if so, they underestimate maximum size and age, and sizes-at-age.



Results

Maturation and spawning periodicity

Peprilus burti mature at 100–160mm in length. Few fish larger than 100mm were immature (Fig. 2). Males were identifiable at 100–110mm when the testes became creamy white, but they were difficult to stage macroscopically. Females were 95–155mm and 105–165mm in Early Developing and Late Developing stages, respectively. Most Gravid and Ripe females were 120–150mm, the smallest being 113mm. These sizes-at-maturity are supported by regressions of gonad weight on fork length (Fig. 3) in which x-intercepts for

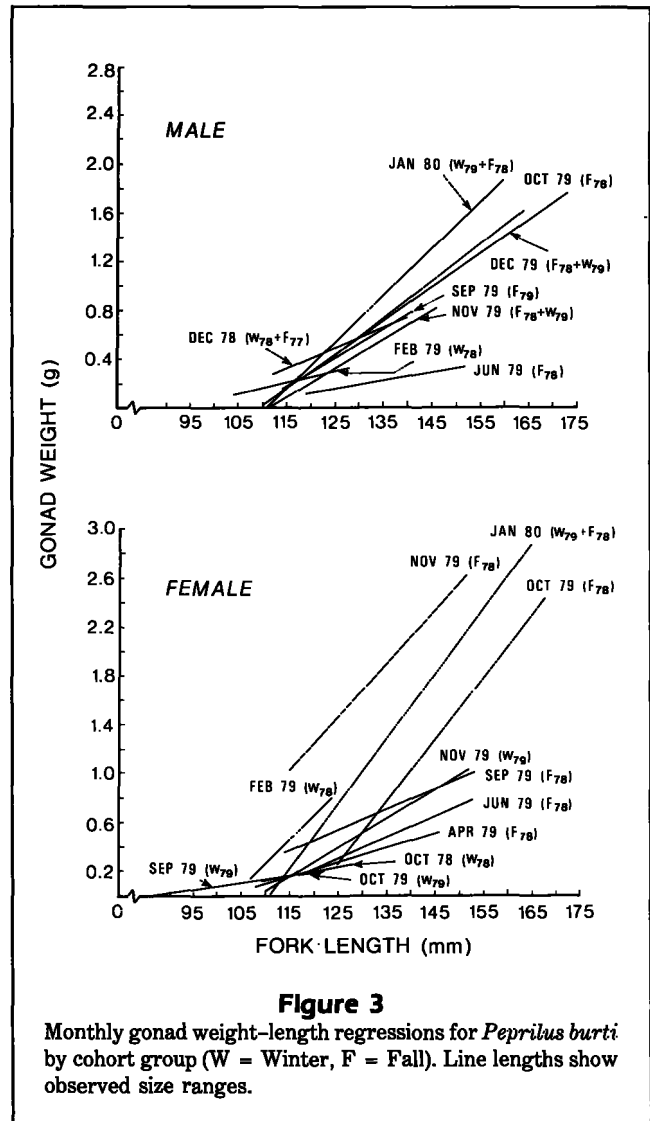


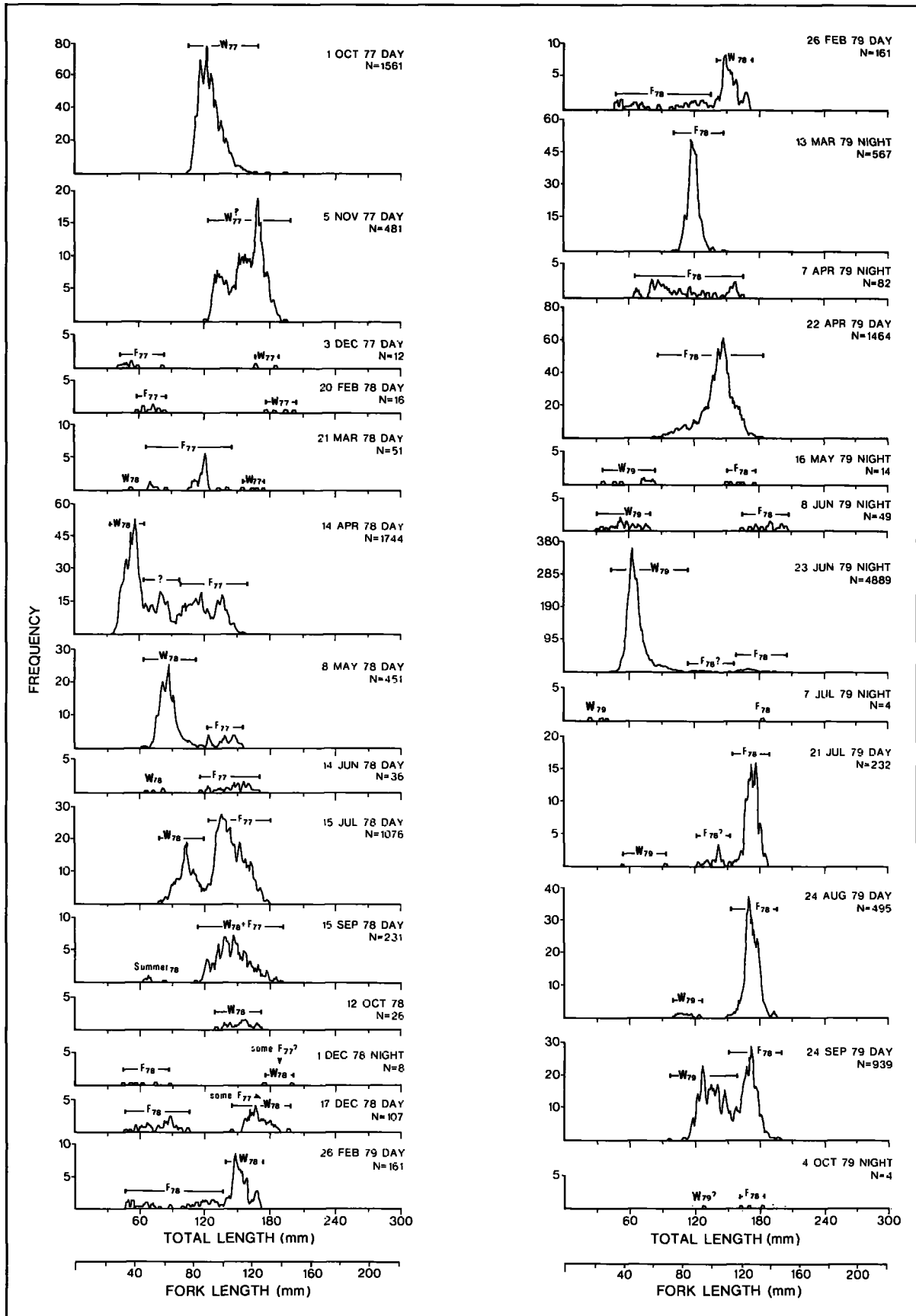
Figure 4
(facing page and overleaf)

Monthly length frequencies of *Peprilus burti* off Freeport, Texas.

both sexes usually were 95–110mm during September through February, a period that brackets much of the broad spawning period when fish should be maturing. Age compositions and sizes-at-age presented later indicate *P. burti* mature to first spawn at 9–16 months.

Peprilus burti spawn primarily during the broad period of September through May. Fish 30–40mm, which occurred mid-November to early July (Fig. 4), were 1.5 months of age April–July and mid-November–December based on quadratic regressions of size-on-age for pooled Winter and Fall cohorts (Table 2).

Little spawning of *P. burti* occurs June through August. Fish 30–40mm, 1.5 months-old, were not captured late July to early November (Fig. 4). No distinct,

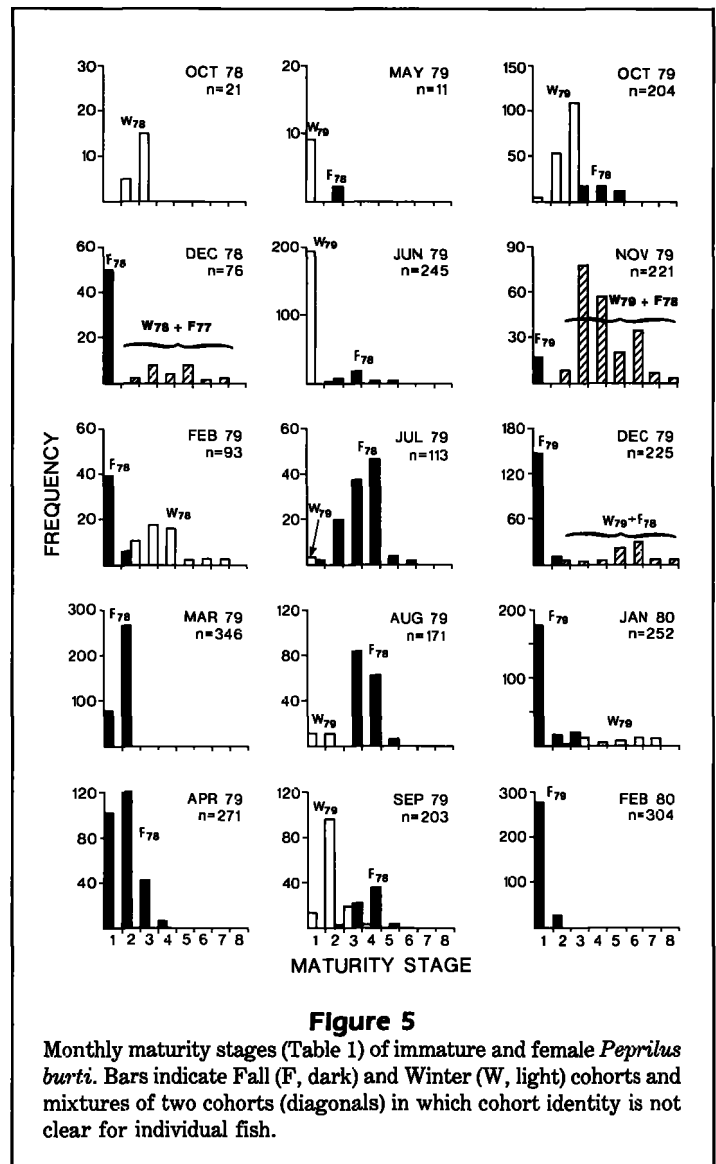


abundant groups of fish 30–60 mm originated then, and the smallest fish caught then usually reflected the more slowly growing Winter-spawned individuals. The few fish 50–60 mm, about 2.5–3 months of age on average, caught September to mid-November, and the one Gravid fish captured in July, probably indicate some summer spawning (Fig. 5).

Peprilus burti spawn primarily during discrete Winter (late January–mid-May) and Fall (early September–late October) periods. Length compositions were consistently bimodal off Texas, and modal groups originated from Winter and Fall spawning periods (Fig. 4). Winter-spawned fish first appeared mid-April to early July at lengths of 30–75 mm at an average age of 1.5–4.5 months, which indicates spawning from about late January to mid-May. Fall-spawned fish first appeared mid-November to early December at lengths of 30–75 mm and an average age of 1.5–4.5 months, which indicates spawning from about early September to late October. Modes for Winter cohorts are readily followed in the periods: (1) mid-April 1978–late February 1979, (2) mid-May 1979–mid-June 1980, and (3) late May–late July 1980. Modes for Fall cohorts can be followed in the periods: (1) early December 1977–mid-July 1978, (2) December 1978–mid-October 1979, and (3) mid-November 1979–late July 1980. Calculated mean hatching dates occurred during late January to March for Winter groups and during September for Fall groups (Table 2).

In contrast to length frequencies, gonad weight and maturity data indicate *P. burti* spawns during much of the fall and winter. Gonad weight regressions had maximum slopes and elevations and usually were significant September through February (Fig. 3). Regressions had lower slopes and elevations and usually were not significant March through August (Murphy 1981, Table 2). Most Gravid and/or Ripe fish were captured November through February (Fig. 5).

The end of the Fall spawning period is not clear, but length frequencies suggest low-level spawning, or spawning success, during late fall and early winter. The consistently bimodal length frequencies must reflect some temporal separation in spawning that originates then. Fall₇₉ fish recruited in abundance by mid-January to mid-February 1980 when they were 60–105 mm long and 3–7 months of age (Fig. 4). Fall₇₈ fish recruited in abundance by mid-March 1979 when they were 90–110 mm and 5.5–7.5 months of age. These data suggest peak fall spawning ends by about late October. No abundant, distinct groups of fish 30–60 mm and 1.5–3 months of age originated during any late-fall or



early-winter period studied (Fig. 4), although 30–75 mm fish—which we labeled Fall-spawned fish—persisted January through May in 1979 and 1980 and probably reflect some winter spawning.

Cohort spawning and recruitment periodicity vary within and between years. Winter₇₈ fish appeared as an abundant, distinct group in mid-April, but few recruited thereafter (Fig. 4). In contrast, Winter₇₉ and ₈₀ fish did not form abundant, distinct groups until June, although a few fish appeared in May. Fall groups first appeared mid-November to early December. However, the bimodal size frequencies of the Fall₇₉ cohort in the period mid-February to early June 1980 suggest intragroup variation in spawning or recruitment success and periodicity similar to that for winter cohorts. We have interpreted the lower mode

of the Fall₇₉ cohort as actually being part of that cohort; the lower mode first became distinct in February 1980 when those fish were primarily 55–75 mm long and about 4 months of age, which would suggest early October to early November hatching.

Recruitment, movements, and nurseries

Fall cohorts of *P. burti* seemingly recruit in abundance at an older age (4–5 months) than Winter fish (2–4 months) off Texas. Winter fish formed abundant, distinct groups soon after first appearing mid-April to early June at 30–75 mm in length when 1.5–4.5 months old (Fig. 4). Fall fish did not form abundant, distinct groups until winter to early spring, although they first appeared mid-November to early December when 30–75 mm and 1.5–4.5 months old.

Young *P. burti* recruit to the bottom off Texas primarily in 5–27 m depths when 2–5 months old. Winter₇₉ fish 2–4 months old and 35–70 mm were captured only at 22 m in May 1979 (Figs. 4, 6). They occurred from 16–55 m during the period June through August 1979 (primarily June) but were most abundant at 22–27 m; few were shallower than 22 m or deeper than 36 m. Recently hatched Fall₇₉ fish 25–70 mm long were captured only at 5–9 m in mid-November 1979 (Figs. 4, 6). Fall₇₉ fish occurred only at 5–27 m (primarily 22–27 m) December 1979 through February 1980 when 3–5 months old. Similarly, Fall₇₈ fish were abundant at 5–27 m March through May when 7–9 months old, but few occurred in deeper water.

Juvenile *P. burti* disperse offshore as they mature and approach age I. Winter₇₉ fish were most abundant at 13–27 m depths September through November 1979 when 6–8 months old (Fig. 6). However, none occurred shallower than 22 m December 1979 through February 1980, when they were 9–11 months old; most were at 36–100 m. The largest Fall₇₉ individuals occurred in the deepest water December 1979 through February 1980, the size gradient suggesting gradual movement offshore. Fall₇₈ fish were almost exclusively at 5–27 m from March through May 1979 when 7–9 months old, but they were at 36–100 m from June through August when 10–12 months old.

Age determination using otoliths

Whole otoliths of *P. burti* apparently cannot be readily aged. Only 984 of 2461 whole otoliths examined had apparent internal features. Many were entirely opaque or lacked a distinct boundary between opaque and hyaline zones, possibly due to initial preservation or storage fluids, though fresh otoliths showed similar features. Only 11 of the 984 legible otoliths had an apparent annulus. These 11 fish were 120–160 mm in

length and could have been about age I by length-frequency analysis. Annuli frequently were not apparent for fish that were age I by length frequencies.

Growth and age determination by length frequency

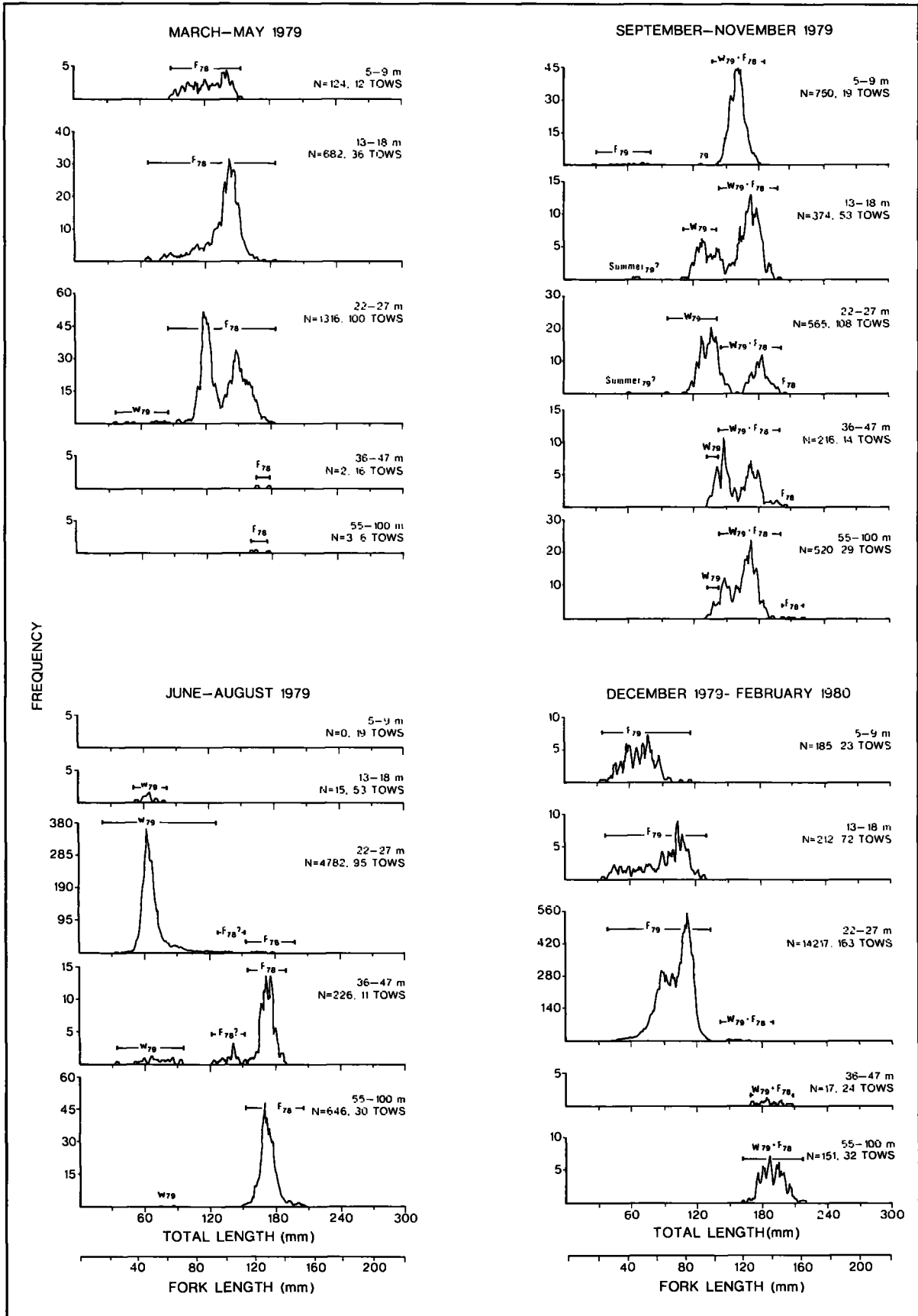
Length frequencies could be used to determine age of *P. burti* through at least 13–16 months of age in the northwestern Gulf and apparently 20–27 months of age in the northcentral Gulf. No more than two cohorts occurred off Texas in any one month, except in March and December 1978, November 1979 through January 1980, and May through June 1980 when a few members of a third group were present (Fig. 4). Each cohort was followed easily until it disappeared when 13–16 months old. In contrast, in the northcentral Gulf in April 1980 there were three cohorts west of the Mississippi River and four to the east (Fig. 7). Fish were abundant at 20 months of age west of the Mississippi and were as old as 27 months to the east (Table 3).

Early sizes for *P. burti* average 25 mm in length at 1 month of age, 42 mm at 2 months, 57 mm at 3 months, 72 mm at 4 months, and 84 mm at 5 months. These values are predicted from quadratic regressions of length-on-age in days pooling all Winter and Fall cohorts (Table 2). Similar size-age combinations may be predicted from quadratic regressions for individual cohorts, and for pooled Winter groups and pooled Fall groups.

Peprilus burti average about 65–100 mm in length at 6 months, 120–145 at age I, and about 170 mm at age II, but fish in the northcentral Gulf were smaller at age than off Texas. Quadratic and von Bertalanffy growth equations both fit observed data from off Texas well, and they predict similar sizes-at-age over most of the observed size range (Fig. 8). For Winter fish quadratic and von Bertalanffy equations predicted lengths of 99 and 100 mm at 6 months, respectively, and 146 and 141 mm at age I (Fig. 8). Observed lengths show many Winter fish were as large as 120 mm at 6 months and 155 mm at age I (Fig. 4; Murphy 1981, Table 1). For Fall fish, quadratic and von Bertalanffy equations predict lengths of 93 and 97 mm at 6 months, respectively, and 131 and 130 mm at age I. Observed lengths show many Fall fish were as large as 105 mm at 6 months and 145 mm at age I. Winter-spawned fish from the northcentral Gulf averaged 120–124 mm at

Figure 6 (facing page)

Length frequencies of *Peprilus burti* by depth: March–May 1979, June–August 1979, September–November 1979, December 1979–February 1980.



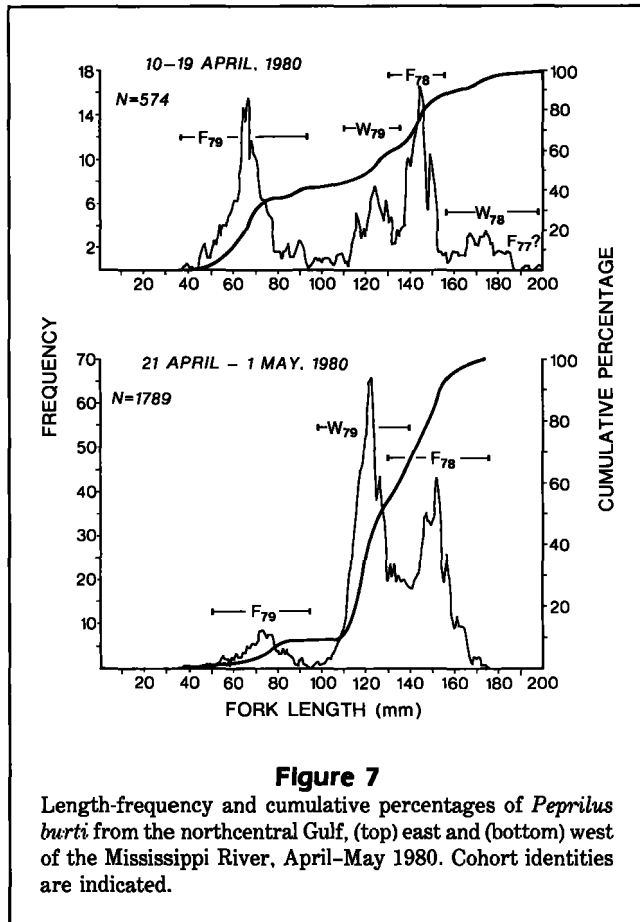


Figure 7

Length-frequency and cumulative percentages of *Peprilus burti* from the northcentral Gulf, (top) east and (bottom) west of the Mississippi River, April-May 1980. Cohort identities are indicated.

13 months and 171 mm at 27 months (Table 3). Fall-spawned fish averaged 66–73 mm at 7 months and 142–149 mm at 20 months.

Male and female *P. burti* reach a similar size off Texas. The largest male sexed was 173 mm and the largest female was 163 mm. Both sexes were equally abundant among fish greater than 150 mm.

Peprilus burti showed little apparent somatic growth off Texas as spawning approached, but fish from the

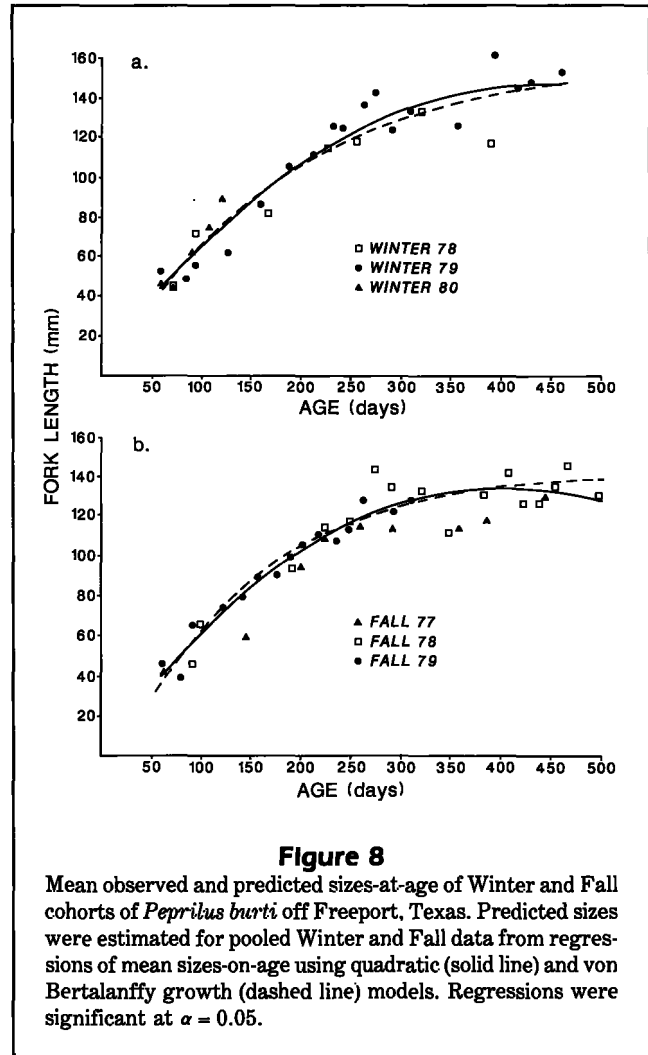


Figure 8

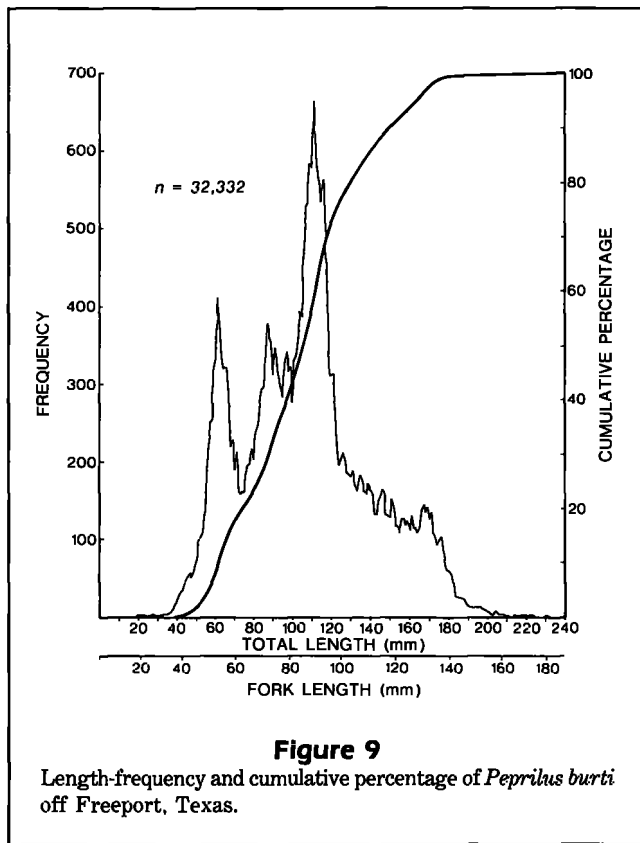
Mean observed and predicted sizes-at-age of Winter and Fall cohorts of *Peprilus burti* off Freeport, Texas. Predicted sizes were estimated for pooled Winter and Fall data from regressions of mean sizes-on-age using quadratic (solid line) and von Bertalanffy growth (dashed line) models. Regressions were significant at $\alpha = 0.05$.

northcentral Gulf had large annual growth increments. Off Texas, fish grew little after reaching modal sizes of 110–160 mm at 7–15 months in Winter groups and 120–150 mm at 9–16 months of age in Fall groups (Figs. 4, 8). Growth ceased or greatly slowed between

Table 3

Size-at-age (mm FL) data for *Peprilus burti* from the northcentral Gulf, east and west of the Mississippi River. Ages assume hatching dates assigned to cohorts off Freeport, Texas.

Spawned group	Approx. age (mo.)	West of Mississippi River			East of Mississippi River		
		n	Size range	Mean FL	n	Size range	Mean FL
Fall ₇₉	7	150	50–95	73	235	37–93	66
Fall ₇₈	20	743	132–176	149	196	130–155	142
Fall ₇₇	33	0	—	—	0	—	—
Winter ₇₉	13	1029	98–139	120	105	110–135	124
Winter ₇₈	27	0	—	—	61	155–200	171
Winter ₇₇	38	0	—	—	0	—	—



the Late Developing and Ripe stages when sizes formed a plateau (Fig. 2). In contrast, growth of Winter and Fall cohorts in the northcentral Gulf continued for fish 7–13 months of age and 20–27 months of age (Table 3).

Maximum size and age

The maximum size of *P. burti* is about 200 mm in length. The largest of 32,332 fish we captured off Texas was only 180 mm, though a 198 mm specimen was measured among only 574 fish from the northcentral Gulf east of the Mississippi River (Fig. 7). Off Texas, 90% of the fish were less than 122 mm, 99% were less than 142 mm, and 99.5% were less than 145 mm (Fig. 9).

The maximum age of *P. burti* typically was only 1–1.5 years in the northwestern Gulf but appeared to be 2–2.5 years in the northcentral Gulf where the largest individuals occur. A t_L of 1–1.5 years seems reasonable off Texas, because fish larger than 142–145 mm, which made up less than 0.5–1.0% of the catch, approximate the average size there at age I. A larger t_L is appropriate for the northcentral Gulf (Fig. 7), because 99–99.5% of the fish west of the Mississippi River were less than 163–167 mm long and 99–99.5% of those to the east were less than 182–184 mm. These sizes approximate the average at age II in the northcentral Gulf and the oldest fish collected there was about age II, so a reasonable estimate of t_L is 2–2.5 years.

Total weight-length, girth-length, and length-length relationships

Regressions of total weight on fork length (Table 4) were significantly different (at $\alpha = 0.05$) in elevation between sexes ($F = 9.19$, 1, 1615 df) but not in slope ($F = 3.25$, 1, 1614 df). Calculated slopes did not significantly differ from $\beta = 3.0$ (males: $t = 0.97$, 789 df; females: $t = 1.60$, 825 df) except when all fish were pooled ($t = 20.08$, 2734 df). Girth-fork length and length-length regressions are in Table 4.

Discussion

Spawning periodicity and its regulation

The broad primary spawning period of September through May we suggest for *Peprilus burti* is realistic. Our data agrees with reports of fish 20–40 mm in length from December through June (Gunter 1945, Hoese 1965, Miller 1965) and, in part, with a suggested fall and winter spawning (Miller 1965). Moreover, Finucane et al. (1979) collected larvae off Texas from September through May.

Table 4

Weight-length, girth-length, and total, fork, and standard length regressions for *Peprilus burti*. All regressions were significant at $\alpha = 0.05$. Measures are grams and millimeters.

Equation	n	FL range	r ²
$\log_{10} TW = -4.5517 + 2.9640 \log_{10} FL$ (males)	791	100–163	0.89
$\log_{10} TW = -4.7095 + 3.0477 \log_{10} FL$ (females)	827	94–164	0.93
$\log_{10} TW = -4.8621 + 3.1201 \log_{10} FL$ (males, females, immatures)	2736	25–164	0.99
$G = 10.38 + 0.99 FL$	2736	25–164	0.95
$FL = -4.31 + 0.96 G$	2736	25–164	0.95
$FL = 8.35 + 0.73 TL$	2662	25–164	0.99
$TL = -9.35 + 1.35 FL$	2662	26–164	0.99
$SL = 3.22 + 0.69 TL$	2668	25–164	0.99
$TL = -2.88 + 1.42 SL$	2668	25–164	0.99
$FL = 5.05 + 1.05 SL$	2734	25–164	0.99
$SL = -4.46 + 0.95 FL$	2734	25–164	0.99

We interpret our data to mean *P. burti* spawns primarily—or most successfully—in temporally separate, discrete, Winter (late January–mid-May), and Fall (early September–late October) periods. The consistently well-separated, bimodal length frequencies—on which we place great emphasis—must reflect a temporal separation in spawning activity or success, or growth and mortality, that originates during late fall and early winter. However, the well-developed gonads and Gravid/Ripe fish we observed suggest spawning could occur throughout that period, possibly at a low level. Allen et al. (1986) and Vecchione (1987) also found consistently bimodal size distributions of *P. burti* in the northcentral Gulf. Allen et al. (1986) considered them separate spawning peaks in a continuous, not temporally separated, spawning. The actual degree of temporal separation in spawning of *P. burti* may be important to resolve, because it may influence (1) appropriate management practices, (2) how many populations and stocks exist in *P. burti*, concepts which are not necessarily the same, and (3) how speciation occurs in *Peprilus*. Given properly randomized geographical sampling, age determination by daily otolith increments (Jones 1986) might resolve the question of how intense is late-fall to early-winter spawning and whether or not, and to what degree, spawning is temporally separate.

Although *P. burti* appear to spawn primarily in two main periods, Winter and Fall, it also appears that in each period there is much variation in cohort spawning periodicity or success, or in recruitment periodicity. We observed Winter cohorts to appear as distinct abundant groups in April in one year but not until June in two other years. Similarly, one Fall cohort was distinctly bimodal over a several-month time period. A more exact method of age determination than length frequencies, however, is needed to more clearly interpret these phenomena.

Our interpretation of spawning periodicity in *P. burti* is similar to findings that other Gulf species spawn in discrete Winter–Spring and Late Summer–Fall periods related to current transport, including *Cynoscion arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *Larimus fasciatus* (Standard and Chittenden 1984), *Menticirrhus americanus* (Harding and Chittenden 1987), and *Polydactylus octonemus* (Dentzau and Chittenden 1990). Spawning of *P. burti* in the northwestern Gulf, and for many of these other fishes, probably is timed to coincide with currents (Shlossman and Chittenden 1981) that transport eggs and larvae from spawning areas to nurseries, assuming *P. burti* has pelagic eggs and larvae like *P. alepidotus* and *P. triacanthus* (Martin and Drewry 1978). Spawning, or its absence, coincides with wind-induced, up- or downcoast, alongshore coastal

currents which drive circulation in the northwestern Gulf with seasonal reinforcement from the Mississippi–Atchafalaya discharge (Kelly et al. 1981). Average winds are downcoast (toward Mexico) during August/September–April/May but upcoast (toward Florida) during May/June–July/August. Nearshore currents parallel the coast. Upcoast wind stress causes upcoast alongshore currents which (1) are reflected in high inshore salinity off Galveston/Freeport and falling sea levels during early to midsummer (Marmer 1954, Kelly et al. 1981), and (2) coincide with the summer period of little spawning we observed in *P. burti* and which is reported in other species just cited. Downcoast wind stress causes downcoast (toward Mexico) alongshore currents, onshore surface Ekman transport, and downwelling which (1) are reflected in rising sea levels February–May and August–October, (2) transport low-salinity water downcoast causing a salinity minimum off Galveston/Freeport during September and October, and May and June, and (3) coincide with the two major spawning periods we suggest for *P. burti* and which are reported as major or minor periods in other species just cited. Alongshore currents continue downcoast from late fall to early winter. Seemingly, however, no distinct, abundant groups of *P. burti* originated then, which may reflect low-level spawning or spawning success. Similarly, little or no spawning occurs then in the other species just cited. Temporal variation in the average meteorological and hydrographic patterns may be the primary reason for the variation we noted in cohort spawning and recruitment periodicity between and within years.

Age determination and growth, maximum size and age, and mortality

Our findings on age and growth in *P. burti* are new, because this species has not been aged previously. It would be desirable to corroborate them by analysis of daily otolith increments (Jones 1986). However, that may not prove feasible, because recent studies using scales, opercula, vertebrae, and thin-sectioned otoliths, fail to consistently show clear daily increments or annuli (Allen et al. 1986). Therefore, it appears length frequencies are the only way to age *P. burti* at present. As in our study, supporting length collections must be frequent in time and over a long duration, because cohort boundaries and age are not clear every month. However, they are quite clear in certain months (for examples, the Winter₇₉ and ₈₀ groups in May or June 1979 and 1980, the Fall₇₈ and ₇₉ groups in December 1978 and 1979). From the clear groups, one can work chronologically backward and forward in time and gradually assign age and cohort boundaries with reasonable certainty. This process, however, is not as

simple in species with a complex life history like *P. burti* as it is in species that spawn during one major period a year.

The apparent cessation of somatic growth as *P. burti* approach spawning in the northwestern Gulf contrasts with large annual increments in the northcentral Gulf. This difference, combined with their disappearance from the northwestern Gulf at 13–16 months of age and their smaller maximum sizes and younger maximum ages there (see below), indicate fish from the northwestern Gulf (1) spawn and die at age I, or more probably (2) in some presently unclear combination emigrate offshore and to the northcentral Gulf prior to, or immediately after, spawning.

Few *P. burti* apparently exist larger than 190–200 mm in length. The largest we captured (180 mm, Texas; 198 mm, northcentral Gulf) are similar to maxima in other studies' sampling to at least 80–100 m depths (173 mm, Hildebrand 1954; 184 mm, Franks et al. 1972; 169 mm, Chittenden and McEachran 1976; 193 mm, Allen et al. 1986). Maxima are even smaller from estuaries or the shallow Gulf (154 mm, Gunter 1945; 131 mm, Miller 1965; 122 mm, Perret et al. 1971; 133 mm, Christmas and Waller 1973), which agrees with our findings that *P. burti* disperse to deep water as they mature. The largest records were from the northcentral Gulf (Allen et al. 1986; our study).

Our estimate that $t_L = 1-1.5$ years in the northwestern Gulf agrees with Chittenden and McEachran (1976) who suggested a 1–2 year maximum age. A higher t_L (2–2.5 years) in the northcentral Gulf appears realistic, because the largest records there are not much larger than the mean size at age II. Based on these maximum ages, theoretical estimates (Royce 1972, Hoenig 1983) of total annual mortality rate ($1 - S$) are nearly 100% in the northwestern Gulf and 82–90% in the northcentral Gulf. Murphy (1981) calculated similar values of $1 - S$ for the northwestern Gulf (99%) from observed time-specific abundance data for consecutive Winter or Fall cohorts. If mature fish from the northwestern Gulf emigrate offshore and to the northcentral Gulf, as we suggest, our values for maximum age and total mortality are under- and over-estimates, respectively, for *P. burti* in the northwestern Gulf.

The presence of the largest *P. burti* in the northcentral Gulf follows a pattern in other marine and estuarine, demersal and pelagic species (*Cynoscion nothus*, DeVries and Chittenden 1982; *Stenotomus caprinus*, Geoghegan and Chittenden 1982; *Microgobias undulatus*, Rivas and Rothmayr 1970, Guthertz et al. 1975, White and Chittenden 1977; *Brevoortia patronus*, Nicholson 1978; *Larimus fasciatus*, Standard and Chittenden 1984; and probably *C. arenarius*, Shlossman and Chittenden 1981). Small differ-

ences between areas also exist in other population attributes of *P. burti*, as in *C. nothus* and *L. fasciatus*: younger age compositions and maximum ages, smaller maximum sizes, and higher total annual mortality rates occur in the northwestern Gulf. At least three explanations could account for this: (1) There may be no basic differences between areas, just much greater biomass (Moore et al. 1970) at age in the northcentral Gulf; (2) differences may be real, not related to biomass, implying slight, but fundamental, population dynamics differences between areas; and (3) differences reflect some presently unclear combination of an offshore and spawning or postspawning movement of older, larger fish from the northwestern to the northcentral Gulf. The first implies Chittenden and McEachran (1976) and Chittenden (1977) are correct that shrimp communities on the Gulf continental shelf have a common population dynamics pattern. The other explanations imply that their arguments need modification for slightly longer life spans and lower mortality rates in the northcentral Gulf, and that shrimp communities are a little more sensitive to fishing than Chittenden's (1977) simulations indicate.

Movements, recruitment, and spawning areas

Peprilus burti probably spawn offshore. We found fish congregate in 36–100 m depths as they mature and size gradients that indicate an offshore dispersal. In agreement, Allen et al. (1986) found a positive correlation between mean size and depth at 200–290 m. Finucane et al. (1979) collected larvae in water 22–182 m deep on the continental shelf off Texas. The young make their way inshore to 5–27 m depths off Freeport, Texas—the white shrimp community (Hildebrand 1954, Chittenden and McEachran 1976)—where they recruit to the bottom. At least two mechanisms could explain their arrival inshore. For one, Ekman surface transport, associated with prevailing downcoast alongshore currents in the spawning season, could, in theory, bring the young inshore. However, Dentzau and Chittenden (1990) rejected this idea. It implies fishes of the brown shrimp community would also recruit inshore, but, in actuality, there is a clear separation between the two communities (Chittenden and McEachran 1976). A more likely alternative, suggested for *Polydactylus octonemus* (Dentzau and Chittenden 1990), is based on the hydrography and cyclonic gyre of the northwestern Gulf (Kelly et al. 1981, 1983, 1984): The eastward counterflow of the gyre is diverted inshore at the Mississippi River delta and ultimately extends downcoast as an alongshore current. Members of the white shrimp community could spawn anywhere in this flow, in the offshore northeastward flowing arc or in the

alongshore southwestward flow: the young just need to be entrained in waters already in the white shrimp community, or enter them using the eastward counterflow, and be transported in a "downstream manner" (see next paragraph). This interpretation is similar to the current transport model Shaw et al. (1985) suggest for *B. patronus*.

Besides being offshore, spawning grounds for *P. burti* found off Texas may lie towards or in the north-central Gulf. We suggest some unknown combination of offshore and spawning or postspawning movement to the northcentral Gulf explains between-area population dynamics differences. Such upcoast movement may be required within the white shrimp community, given the coincidence of spawning with downcoast currents. Mean alongshore surface current speed is 23 cm/second in water 22m deep off Freeport, Texas from September through June (Kelly et al. 1981), so spawning areas could lie 320 nmi upcoast assuming passive transport for 30 days before the young recruit to the bottom. This estimate depends on many poorly known factors, including (1) routes followed, (2) alongshore current speeds, (3) duration of the transport period, and (4) behavior of the young. However, alongshore currents could transport young great distances—conceptually "downstream"—and Texas recruits could be spawned off Louisiana where low-salinity waters propagate along Texas when alongshore wind components turn downcoast during August and September (Kelly and Randall 1980, Kelly et al. 1981). Mature fish must move toward spawning areas, conceptually in an upstream, contranatal direction from the northwestern Gulf, to maintain a fixed, proven spawning ground following Harden Jones (1968).

Zoogeographic considerations

Peprilus burti fill a niche in the Gulf similar to the one *P. triacanthus* occupies on the Atlantic coast. However, their population dynamics differ, and this may reflect zoogeographic variation suggested for other taxa whose ranges traverse the Cape Hatteras area, including *Micropogonias* and *Alosa* (White and Chittenden 1977), *Cynoscion* (Shlossman and Chittenden 1981), and *Stenotomus* (Geoghegan and Chittenden 1982). It appears for *P. burti* that (1) maturity occurs at 100–160 mm in length as they approach age I and spawn, (2) maximum size is only about 200 mm, but most are much smaller, (3) maximum age is no more than 2.5 years, and (4) total annual mortality rate is not lower than about 82%.

The life history of *P. triacanthus* north of Cape Hatteras is complicated by north-south and onshore-offshore movements (Horn 1970), but they appear to (1) mature at lengths of 110–130 mm in their second

year (Hildebrand and Schroeder 1927, Bigelow and Schroeder 1953, Horn 1970, DuPaul and McEachran 1973), (2) reach maximum sizes of 300 mm (Murawski and Waring 1979), (3) have maximum ages of 3–6 years (Draganik and Zukowski 1966, DuPaul and McEachran 1973, Waring 1975, Kawahara 1977), and (4) have total annual mortalities of 67–84% (Murawski and Waring 1979).

Little has been published for *P. triacanthus* south of Cape Hatteras, but the largest fish collected in extensive trawling in this area was 150 mm (Wenner et al. 1979). This size range is more similar to *P. burti* than *P. triacanthus* north of Cape Hatteras and may reflect an intrageneric, Carolinian Province similarity in sizes, maximum ages, and mortality.

Acknowledgments

We are much indebted to M. Burton, T. Crawford, P. Geoghegan, J. Pavela, M. Rockett, J. Ross, P. Shlossman, B. Slingerland, G. Standard, H. Yette, and Captains Hollis, Mike, and Robby Forrester, P. Smirch, and A. Smircic for assistance in field collections. T. Fehrman and R. Grobe recorded the data. R. Case was of invaluable help for writing and assisting with computer programs. B. Rohr and E. Gutherz allowed the senior author to participate in NMFS groundfish survey 106. R. Darnell, G. Grant, E. Klima, D. Stilwell, K. Strawn, and K. Sulak reviewed drafts of the manuscript. Financial support was provided, in part, by the Texas Agricultural Experiment Station; by the Strategic Petroleum Reserve Program, Department of Energy; and by the Texas A&M Sea Grant College Program, supported by the NOAA Office of Sea Grant, U.S. Department of Commerce. Final preparation and revisions of this manuscript were made while the authors were at Florida Marine Research Institute, Florida Department of Natural Resources (MDM) and College of William and Mary, Virginia Institute of Marine Science (MEC). This manuscript was based on a thesis submitted by the senior author as partial fulfillment of the M.S. degree, Texas A&M University.

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