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Population dynamics of the nonindigenous brown mussel *Perna perna* in the Gulf of Mexico compared to other world-wide populations

David W. Hicks[1,*], John W. Tunnell Jr[1], Robert F. McMahon[2]

[1]Center for Coastal Studies, Texas A&M University-Corpus Christi, 6300 Ocean Drive, Corpus Christi, Texas 78412, USA
[2]Department of Biology, Box 19498, The University of Texas at Arlington, Arlington, Texas 76019, USA

ABSTRACT: Texas Gulf of Mexico populations of the marine mytilid *Perna perna* (Linnaeus, 1758) were sampled monthly on Fish Pass Jetty (FP) (27° 41′ N) from September 1993 to February 1995 and Mansfield Pass Jetty (MP) (26° 34′ N) from March 1994 to June 1995 within 1 yr of initial colonization. Population density and mussel size distributions allowed identification of annual cohorts. Mean individual tissue and shell ash-free dry weights (AFDW) from subsamples allowed estimation of cohort standing crop shell + tissue biomass. FP was dominated by the 1993 cohort, while 1992 and 1993 cohorts dominated MP. At both sites, poorly recruited 1994 cohorts had negligible biomass or production. FP 1993 cohort density declined from 15 000 to 1000 m^{-2} while those of the 1992 and 1993 MP cohorts declined from 1000 to 100 and 2000 to 1000 m^{-2}, over their respective sampling periods. First-year shell growth was 42 and 53 mm at FP and MP, respectively. AFDW biomass and monthly productivity at both sites remained constant through time. Mean annual FP AFDW biomass = 1.95 kg m^{-2} and production = 2.44 kg m^{-2} yr^{-1}; respective values for MP were 1.35 kg m^{-2} and 1.86 kg m^{-2} yr^{-1}. Spawning periods, marked by reduced mean individual production, extended from March to October at temperatures >18 to 20°C. The MP 1993 cohort did not reproduce. Gamete release accounted for 76 and 74% of total production in the 1993 FP and 1992 MP cohorts, respectively. Laboratory spawned mussels lost 60% of tissue AFDW regardless of sex. Growth rate, biomass, productivity and reproductive effort in Texan populations were similar to those of other *P. perna* populations, suggesting that North American Gulf of Mexico shores can support this species.

KEY WORDS: Biomass · Density · Growth · Invasion · *Perna perna* · Population dynamics · Production · Reproductive effort · Spawning periods

INTRODUCTION

The brown mussel *Perna perna* (Linnaeus, 1758) was first discovered in the Gulf of Mexico as 2 juvenile specimens on jetty rocks at Port Aransas, Texas, in February 1990 (Hicks & Tunnell 1993). *P. perna* populations now occur on other isolated hardshores along 1700 km of coast from Freeport, Texas, to southern Veracruz, Mexico (Hicks & Tunnell 1993, 1995, McGrath et al. 1998). International shipping, particularly from South America, may have transported *P. perna* to the Gulf of Mexico (Hicks & Tunnell 1993), recent molecular genetic evidence suggesting origination from Venezuela populations (Holland 1997). The endemic range of *P. perna* (synonymous with *P. picta* [Born] and *P. indica* Kuriakose and Nair [Siddall 1980, Vakily 1989]) includes southern India, Sri Lanka, Madagascar, the east coast of Africa from central Mozambique to False Bay, and the African west coast from Luderiz Bay north into the Mediterranean from Gibraltar to the Gulf of Tunis, as well as the Atlantic coasts of Brazil, Uruguay, Venezuela, and the West Indies (Berry 1978).

*Present address: Department of Biology, Lamar University, PO Box 10037, Beaumont, Texas 77710, USA.
E-mail: hicksdw@hal.lamar.edu

Population and reproductive dynamics have been described for *Perna perna* in South Africa (Berry 1978, Crawford & Bower 1983, Lasiak 1986, Lasiak & Dye 1989, van Erkom Schurink & Griffiths 1991, Lasiak & Barnard 1995, Tomalin 1995), northern Africa (Abada-Boudjema et al. 1984, Shafee 1989, 1992, Abada-Boudjema & Dauvin 1995), India and Sri Lanka (Appukuttan et al. 1989, Indrasena & Wanninayake 1994), Brazil (Lunetta 1969, Marques et al. 1991) and Venezuela (Vélez & Martinez 1967, Carvajal 1969, Vélez 1971, Acuña 1977). The highly variable growth rates, life spans and spawning periodicities among different populations of *P. perna* (Vélez 1971, Berry 1978, Lasiak & Dye 1989, Indrasena & Wanninayake 1994, Tomalin 1995) makes the potential invasive success of this species in North America difficult to assess. Indeed, the Gulf of Mexico is in many ways (tidal range and frequency, wider temperature range, and lack of continuous rocky shores) uniquely different from the endemic habitats of *P. perna*. In addition, immediate post-invasion population dynamics have not been studied in this economically important, macrofouling species (Rajagopal et al. 1995, Morton 1997). This report describes a study of growth, production, reproductive cycle and reproductive effort of 2 *P. perna* populations within 1 yr of their initial colonization of Fish Pass and Mansfield Pass Jetties on the Texas Gulf of Mexico coast, allowing comparison of results to those published for other endemic populations of this species.

MATERIALS AND METHODS

Study area. Mussels were collected from 2 granite jetties on the Texas Gulf of Mexico coast: the northern jetty at Fish Pass (FP) (also called Corpus Christi Water Exchange Pass) (27° 41′ N); and the northern jetty at Mansfield Pass (MP) (26° 34′ N) (Fig. 1). Average monthly diurnal tidal range (m) on these jetties was 0.37 ± 0.064 SD over the sampling period (n = 22, range = 0.22 to 0.47 m) (data from Conrad Blucher Institute, Division of Near-shore Research, Texas A&M University-Corpus Christi). FP, on Mustang Island, 26 km south of Port Aransas, Texas, is closed by sedimentation (Behrens et al. 1977). The northern FP jetty extends 150 m from shore and is 30 m wide. MP, on North Padre Island, 150 km south of Corpus Christi, Texas, is continuously open. The northern MP jetty extends 700 m from shore and is 30 m wide.

Sampling. *Perna perna* populations were sampled at approximately monthly intervals from September 1993 to February 1995 at FP and from March 1994 to June 1995 at MP. Samples consisted of 4 to 8 clumps of mussels taken without specific selection from boulders in the middle of each jetty (75 m offshore at FP and 350 m offshore at MP). Mussel clumps were cut with a putty knife from continuous, uniformly dense, mussel beds in the upper 25 cm of the *P. perna* population (the lower eulittoral), minimizing errors associated with sampling at different shore heights. The surface areas occupied by removed mussel clumps were determined with a 5 cm^2 grid (range = 200 to 625 cm^2). Monthly removal of mussel clumps did not impact mussel distributions and densities within the sampling area. Daily ambient water temperatures at Mustang Island, 10 km north of FP, were obtained from The University of Texas Marine Science Institute and hourly tidal heights at Bob Hall Pier, 12 km south of FP, from the Conrad Blucher Institute, Division of Near-shore Research, Texas A&M University-Corpus Christi.

Population dynamics and productivity. Mussels were freed from clumps by cutting byssal attachments, and were rinsed free of silt and debris in a 1 mm mesh sieve. Shell lengths (SL: the greatest anterior-posterior dimension) of all individuals were measured to the nearest 0.1 mm with digital calipers. Soft tissues were excised from 48 to 72 randomly selected individuals

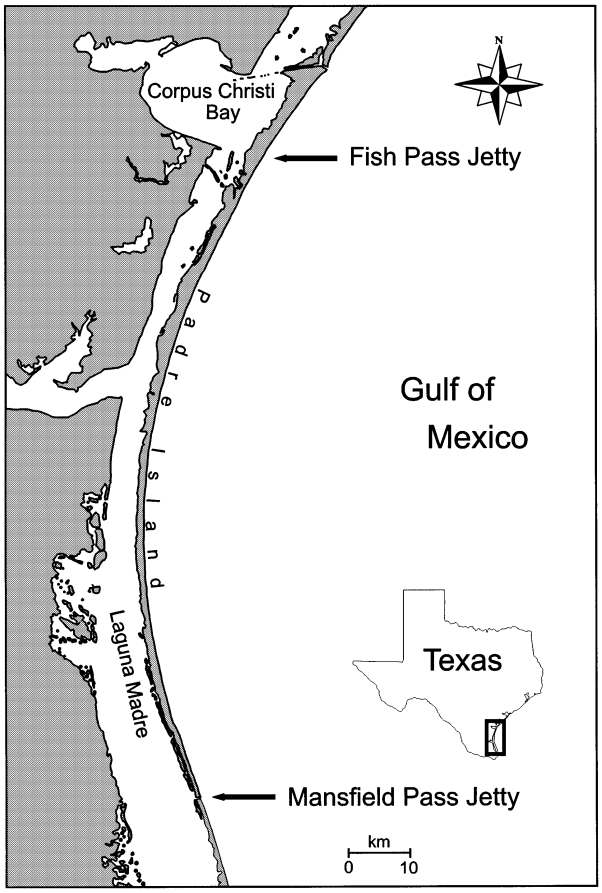

Fig. 1. Locations of sampled populations of *Perna perna* at Fish Pass and Mansfield Pass Jetties (arrowed) on the Texas shore of the western Gulf of Mexico

from each monthly sample at each site. Excised tissues and shells were dried to constant weight at 65°C (>72 h), and thereafter were combusted at 530°C for 3 h to obtain their ash-free dry weights (AFDW) to the nearest 0.1 mg. Least-squares linear regressions of the natural logarithms of shell or tissue AFDW as a dependent variable versus the natural logarithm of SL (Ricker 1973) were utilized in conjunction with sample size distributions, densities, and survivorships to estimate AFDW tissue or shell organic production between successive sampling dates.

Population size structure and temporal changes in length-frequency distributions were used to estimate shell growth rate, mortality, and cohort recruitment as previously carried out for other *Perna perna* populations (Acuña 1977, Berry 1978, Crawford & Bower 1983, Marques et al. 1991, Tomalin 1995). Removal of entire mussel clumps and their separation in a 1 mm sieve retained all but the smallest post-larval recruits, avoiding errors in length-frequency analysis associated with gear size selectivity and under-sampling of juveniles. *P. perna* has a short juvenile phase (15 to 20 d) and pediveligers settle directly into adult mussel beds (Lasiak & Barnard 1995). Thus, initial appearance of juveniles <5 mm SL in samples marked recruitment events. New cohorts did not display substantial size overlap throughout the sampling period, allowing accurate determination of growth rates.

Size-frequency data were developed from pooled mussel clumps for each monthly sample at each site. Shell length-frequency distributions, in 2 mm size-class intervals, were fitted to the von Bertalanffy growth curve,

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right]$$

using the MULTIFAN Program of Fournier et al. (1991), where L_t is SL at time t, L_∞ is the asymptotic SL (mm), k is the rate at which SL approaches asymptotic SL, and t_0 is the estimated time when SL = zero.

Cohort survivorship was estimated by fitting natural logarithm-transformed raw density values ($\ln N$) for each monthly sample as the dependent variable to the least-squares linear regression equation,

$$\ln N = \ln C + Zt$$

where the slope, Z, is the instantaneous mortality rate, t is time in years, and $\ln C$ is the intercept (Beverton & Holt 1957). Annual cohort mortality rate was calculated as $1 - e^z$ (Crisp 1971).

AFDW production of shell and soft tissues of each cohort at each site was estimated from cohort growth data (Crisp 1971, Berry 1978). Byssal threads were excluded from analysis of organic production as their contribution in this species is only 1.2 to 3.5% of total organic production (Berry 1978, Shafee 1992).

In production analyses, distinct age/size cohorts represented single annual generations, for which growth, density, and survivorship were calculated separately. Least-squares linear regressions relating lnAFDW to lnSL allowed estimation of shell and tissue AFDW of all individuals in each monthly cohort sample. These values were summed and divided by cohort density to yield mean individual shell and tissue AFDW biomass (reported hereafter as mean ± SE) for each sampled cohort. Mean individual shell and tissue AFDW values were multiplied by corresponding cohort densities in order to estimate cohort shell and tissue standing crop biomasses as kg organic matter m^{-2} at each sampling period. Monthly cohort shell and tissue organic production were then estimated from changes in AFDW biomass and mortality (estimated from the regression of density vs time described above) between sequential samples. These values were divided by average cohort density and time in days between successive samples to obtain the mean daily productivity value of an individual in g AFDW of shell or flesh d^{-1}. Shell and flesh productivity values were summed to yield mean daily, total individual production rates. Monthly AFDW shell and tissue production values were summed over all samples to obtain total AFDW production estimates for each cohort over the entire sampling period.

Reproductive effort. Reproductive effort was directly assessed for large, pre-spawning, gravid individuals (mean SL = 66.0 ± 0.64 mm, range = 60.5 to 79.5 mm) collected from FP during March 1997. After collection, mussels were held at 15°C in a 285 l refrigerated holding tank in continuously aerated artificial seawater. Within 30 d, 20 randomly chosen individuals were stimulated to spawn by isolation in a 40 l plastic aquarium with artificial seawater at 25°C for 24 h. A second control group of 20 mussels, held at 15°C, did not spawn. The sex of spawned individuals was determined by post-mortem examination of the gonads. Individual tissue and shell AFDW biomass were determined for control and post-spawning groups as described above.

RESULTS

Population dynamics

Settlement events in Texan *Perna perna* populations were marked by appearance of individuals <5 mm SL in samples. Recruitment of 1994 cohorts was minor compared to existing FP and MP cohorts (Fig. 2). With densities <300 m^{-2}, they had little impact on population production.

In September 1993, the FP population consisted of a single 1993 cohort of small individuals (mean SL = 18.1 ± 0.11 mm) (Fig 2A). Spat <5 mm SL were

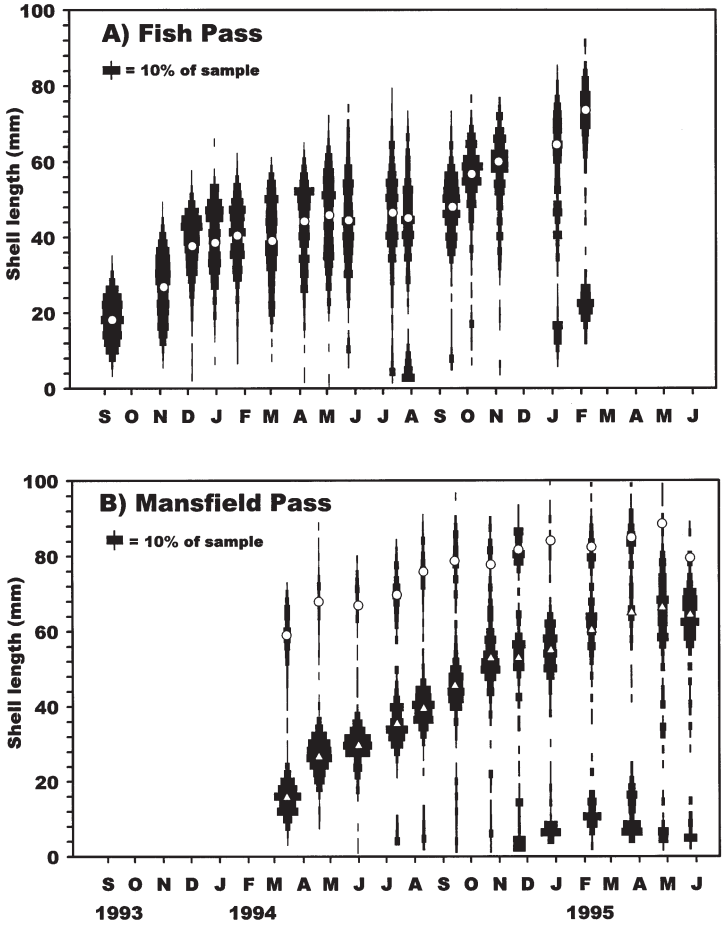

Fig. 2. *Perna perna.* Length-frequency histograms of annual cohorts from monthly population samples at (A) Fish Pass Jetty (September 1993 to February 1995) and (B) Mansfield Pass Jetty (March 1994 to June 1995). (O) Mean shell length for the 1993 cohorts at both sites; (Δ) mean shell length for the 1992 cohort at Mansfield Pass. No mean shell length values are indicated for the poorly recruited 1994 cohorts at either site

observed prior to the onset of sampling on 27 June 1993, suggesting that settlement occurred during the previous May and June. The density of this initial cohort in the September 1993 sample was 15 000 m^{-2}. During the 514 d sampling period, its density declined to <1000 m^{-2} (Fig. 3A), yielding an instantaneous mortality coefficient (Z) of –1.35 ln individuals m^{-2} yr^{-1} (±0.14) or an annual mortality rate of 74%.

When initially sampled in March 1994, the MP population consisted of a 1992 cohort (mean SL = 59.0 ± 0.58 mm) and a 1993 cohort (mean SL = 15.6 ± 0.22 mm) (Fig. 2B). Prior observation of settled spat on 10 December 1993 suggested that the 1993 MP cohort settled during October/November 1993. In the initial, March 1994 sample, this cohort accounted for 71% of individuals (Fig. 2B). Density in the older, 1992 MP cohort declined from approximately 1000 mussels m^{-2} in March 1994 to 100 mussels m^{-2} in June 1995 during the 437 d sampling period (Fig. 3B). Concurrently, 1993 MP cohort density declined from 2000 mussels m^{-2} to less than 1000 mussels m^{-2} (Fig. 3B). Corresponding Z values for the 1992 and 1993 MP cohorts were –1.40 ± 0.37 and –1.60 ± 0.35, yielding respective annual mortality rates of 75 and 80%.

MULTIFAN analysis (Fournier et al. 1991) indicated that FP mussels would attain an SL of 42 mm during their first year of life (k = 0.53 ± 0.15, L_∞ = 101.2 ± 2.82) while MP mussels would reach 53 mm (k = 0.82 ± 0.14, L_∞ = 96.8 ± 1.2). Estimated maximum SL values (L_∞) for FP at 101.2 mm and MP at 96.8 mm were in agreement with actual maximum mussel SL, being 92 and 100 mm, respectively.

Population biomass and production

Cohort biomass at both sites remained relatively stable over sampling periods (excepting biomass reductions at FP associated with gamete release) (Fig. 4). As individuals continued to grow (Fig. 2), total population biomass appeared to have reached the maximum level which could be sustained under the biotic and abiotic conditions specific to each site (mussel mats appeared to reach maximum, sustainable levels of thickness).

Annual population AFDW tissue production values for a 12 mo period of concurrent sampling at FP and MP (March 1994 to February 1995) were 1.41 and 0.86 kg m^{-2} yr^{-1}, respectively. Annual population AFDW shell organic production was nearly equivalent to tissue production at 1.03 and 1.00 kg m^{-2} yr^{-1}, respectively. Average annual biomass (tissue and organic shell AFDW) at FP was 1.95 kg AFDW m^{-2}, and at MP 1.35 kg m^{-2}. Annual turnover ratios (annual tissue + shell AFDW production ÷ average annual tissue + shell AFDW biomass, P:B ratio) were 1.25 and 1.38 for FP and MP, respectively, indicative of similar individual growth rates in both populations (Fig. 2).

At FP, the 1993 cohort accounted for 99% (5.16 kg AFDW m^{-2}) of total AFDW production (5.22 kg AFDW m^{-2}) over the 514 d sampling period. The 1992 and 1993 MP cohorts accounted for 23% (0.52 kg AFDW m^{-2}) and 60% (1.57 kg AFDW m^{-2}) of total production (2.24 kg AFDW m^{-2}), respectively, over the 437 d sampling period. At FP and MP, newly settled 1994 cohorts accounted for only 1% (0.06 kg AFDW m^{-2}) and 7% (0.15 kg AFDW m^{-2}) of total production.

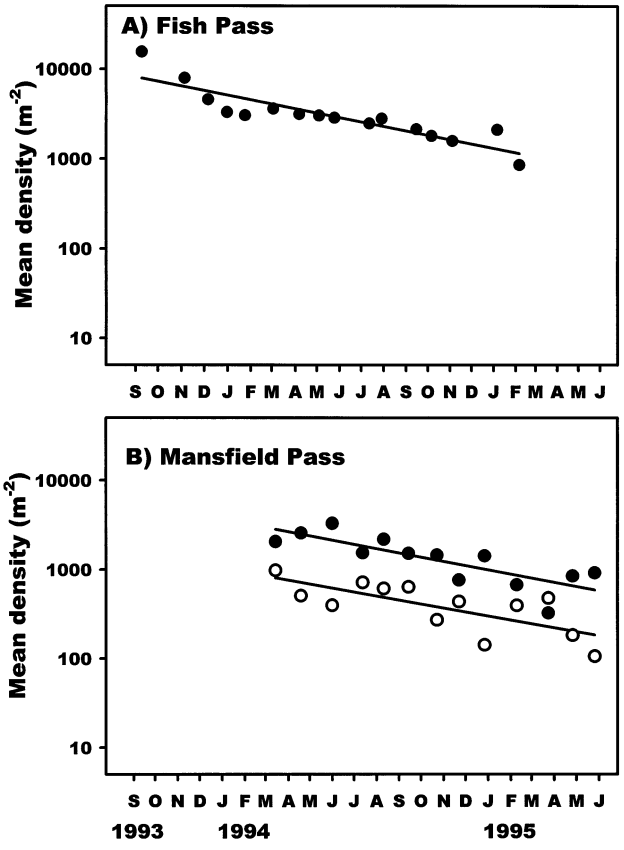

Fig. 3. *Perna perna.* Natural logarithmic transformations of mean densities (vertical axis) over duration of collection for annual cohorts in populations on (A) Fish Pass Jetty (September 1993 to February 1995) and (B) Mansfield Pass Jetty (March 1994 to June 1995). (●) Densities of 1993 cohorts at both sites; (○) density of 1992 cohort at Mansfield Pass. Lines associated with cohort density values represent fitted annual survivorship curves as follows: Fish Pass 1993 cohort, ln density m^{-2} = 8.98 – 1.35 (yr) (r = 0.88, F = 45.7, p < 0.0001); Mansfield Pass 1992 cohort, ln density m^{-2} = 7.15 – 1.40 (yr) (r = 0.53, F = 14.1, p = 0.001) and Mansfield Pass 1993 cohort, ln density m^{-2} = 8.46 – 1.60 (yr) (r = 0.59, F = 20.7, p = 0.0001)

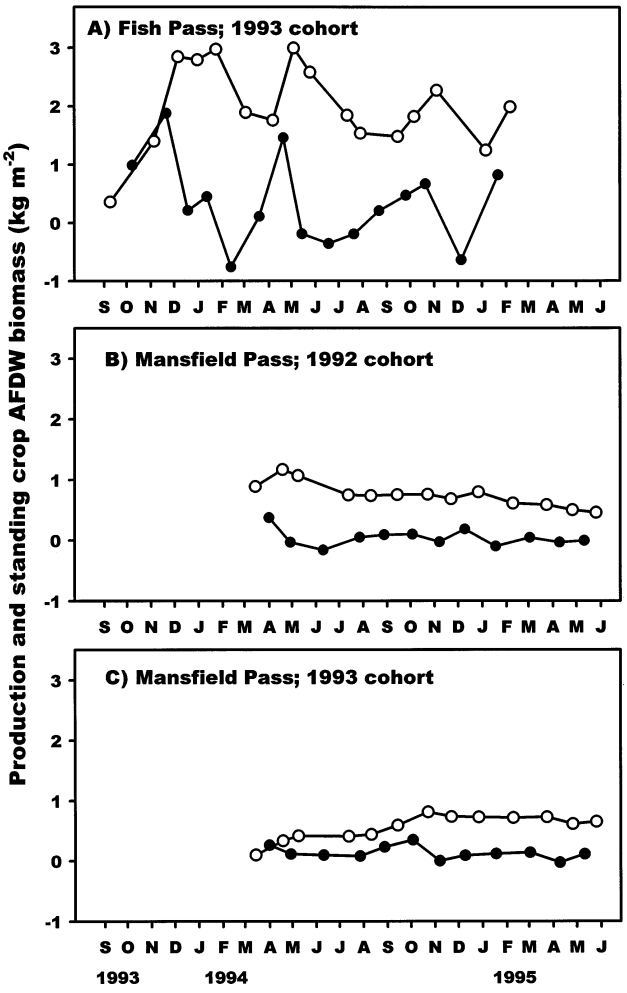

Fig. 4. *Perna perna.* Monthly values of shell plus tissue ash-free dry weight (AFDW) production (●) and standing crop AFDW biomass (○) over duration of sampling for (A) the Fish Pass 1993 cohort (September 1993 to February 1995) and the (B) 1992 and (C) 1993 cohorts at Mansfield Pass (March 1994 to June 1995)

Mean individual biomass, production and reproduction

At both sites, mean individual shell AFDW biomass of all cohorts progressively increased with time, indicating relatively constant shell growth (Fig. 5B,C,D). In the 1993 MP cohort, tissue AFDW increased in direct proportion to increases in shell AFDW (Fig. 5D). In contrast, mean individual AFDW tissue biomass in the 1993 FP and 1992 MP cohorts distinctly declined relative to shell AFDW biomass from early spring through late fall relative to winter periods (Fig. 5B,C). Decline in mean individual tissue AFDW among these cohorts was not associated with shell degrowth, because shell AFDW increased throughout these periods (Fig. 5B,C). Rather, biomass declines resulted from gamete release during spawning as marked by emaciation of adult gonads and settlement of 1994 cohorts (Fig. 5B,C). In contrast, lack of both concurrent reduction in mean individual tissue AFDW biomass and formation of gravid gonads in the 1993 MP cohort indicated that it did not mature in its first year of life. This result suggests that reduction in tissue biomass in the mature 1993 FP and 1992 MP cohorts was due to gamete release.

Mean individual tissue AFDW was nearly twice that of shell AFDW in the 1993 FP cohort during non-spawning periods. In contrast, it was essentially equivalent to shell AFDW throughout sampling in the 1993 MP cohort (Fig. 5D). This result suggests that organic

energy stores accounted for a greater proportion of mean individual tissue AFDW biomass in the 1993 FP cohort which spawned within its first year than in the 1993 MP cohort which did not spawn within its first year of life.

Reduction in individual tissue AFDW as a marker for spawning periods has been documented for a number of mytilid species, including *Perna perna*, by microscopic examination of gonad sections (Baird 1966, Griffiths 1977, Dix & Ferguson 1984, Shafee 1989, van Erkom Schurink & Griffiths 1991) and weight loss in pre- versus post-spawned individuals (Griffiths 1977, Thompson 1979). Spawning, marked by decline in individual tissue AFDW, was initiated in the 1993 FP and 1992 MP cohorts in early spring 1994 as average ambient water temperatures rose to 18–20°C from mid-winter lows of 12–15°C (Fig. 5A,B,C). Continued depression of tissue AFDW in these cohorts indicated that spawning activity occurred from early spring into November/December, ceasing only after water temperatures fell below 18 to 20°C. Based on tissue AFDW depression, the 1992 MP cohort exhibited a single extended spawning period (May to December 1994) (Fig. 5C), while the 1993 FP cohort had 2 apparent spawning episodes, the first extending from March to April 1994, followed by an increase in tissue AFDW from May to June, leading to a second reproductive effort from July through November 1994 (Fig. 5B).

ANCOVA, with lnSL as a covariant, indicated that tissue biomass reductions among male (n = 9) and female (n = 11) laboratory-spawned specimens of *Perna perna* were not different (df = 1, 18, $F = 2.40$, p = 0.1392), allowing pooling of male and female data for subsequent analyses. Least-squares linear regressions of lntissue AFDW versus lnSL as the independent variable for pre- and post-laboratory-spawned individuals were significant (lnpre-spawning mg tissue AFDW = –15.78 + 3.84 ln mm SL , n = 20, $F = 7.61$, p = 0. 0.013; lnpost-spawning mg tissue AFDW = –10.95 + 2.47 ln mm SL, n = 20, $F = 9.26$, p = 0.007) (Fig. 6). ANCOVA with lnSL as a covariant indicated that tis-

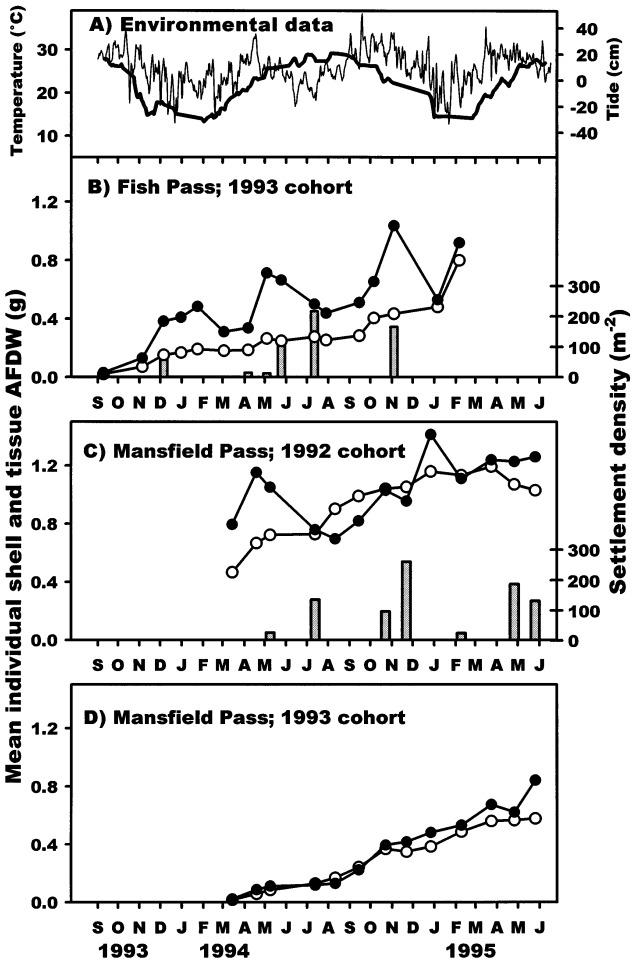

Fig. 5. *Perna perna.* Mean individual shell (○) and tissue (●) ash-free dry weight (AFDW) biomass of annual cohorts in Texan populations (left vertical axis) over the duration of collection (B,C,D). (A) Mean daily seawater temperatures (thick solid line) and daily tidal deviations from mean sea level (thin solid line). (B) Mean individual shell and tissue AFDW biomass for the Fish Pass 1993 cohort (September 1993 to February 1995), and the (C) 1992 and (D) 1993 cohorts at Mansfield Pass (March 1994 to June 1995). Histograms in (B) and (C) represent densities of the newly recruited 1994 cohorts (shell length <5 mm) (right vertical axis) recorded in monthly samples at each site

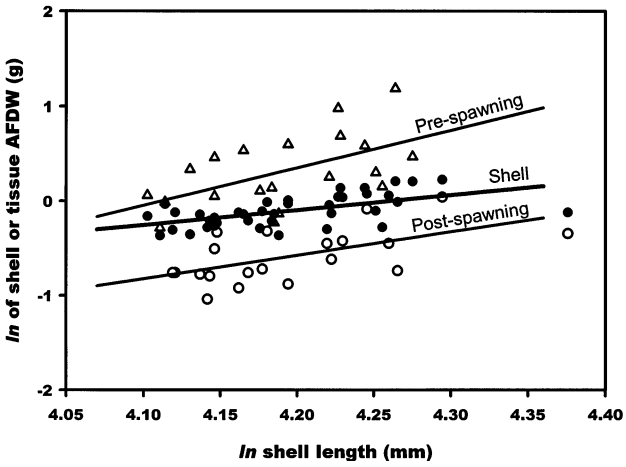

Fig. 6. *Perna perna.* Natural logarithmic transformations of shell or tissue ash-free dry weight (AFDW) biomass (g) (vertical axis) versus natural logarithmic transformation of shell length (mm) (horizontal axis) of pre- and post-laboratory-spawned individuals from Fish Pass Jetty, Texas. (△) AFDW tissue biomass of pre-spawned individuals; (○) AFDW tissue biomass of post-spawned individuals; (●) AFDW shell biomass of pre- and post-spawned individuals combined. Lines are fitted least-squares linear regressions for pre- and post-spawning tissue AFDW and shell AFDW as labeled (see 'Results' for regression equation parameters)

sue AFDW was significantly greater in pre-spawning mussels (df = 1, 38, F =101.71, p < 0.00001). In contrast, shell AFDW did not differ between pre- and post-spawning individuals (df = 1, 38, F = 0.01, p = 0.904) and was highly correlated to SL (ln mg shell AFDW = –6.77 + 1.56 ln mm SL , n = 40, F = 18.66, p = 0.0001) (Fig. 6). There was no SL × spawning condition interaction over the examined SL range (60.5 to 79.5 mm, mean SL = 66.0 ± 0.64). Adjusted mean tissue AFDW of pre- and post-spawning mussels were 1.38 and 0.55 g, respectively; thus gamete release accounted for a 60% reduction in tissue biomass, a value similar to the 40 to 50% spawning reductions in individual tissue AFDW recorded among the 1993 FP and 1992 MP cohorts (Fig. 5B,C). In the laboratory study, tissue AFDW of pre-spawning individuals was well above that of shell AFDW and fell well below it in post-spawning individuals (Fig. 6). Similarly, among the reproductive 1993 FP and 1992 MP cohorts, tissue AFDW exceeded shell AFDW during nonreproductive periods and was equivalent to or less than it during reproductive periods, suggesting that tissue biomass reduction marked spawning periods in field populations (Fig. 5B,C).

During spawning, reduction of mean individual tissue AFDW (Fig. 5B,C) in 1993 FP and 1992 MP cohorts led to reductions in mean individual daily production rates (Fig. 7A,B). In contrast, there was no reduction in mean individual tissue AFDW or daily production in the immature 1993 MP cohort (Figs. 5D & 7C). As indicated by laboratory spawning studies, reduced productivity in these mature cohorts during spawning seasons resulted from gamete release. If the difference in the energy content between gravid individuals prior to spawning and post-spawned individuals represents energy lost in gamete release (Crisp 1971, Thompson 1979), individual reproductive effort can be estimated by integrating the total loss of production during spawning periods between adjacent nonreproductive periods marked by maximal individual productivity. Thus estimated, mean individual 1994 reproductive effort (indicated by hatched areas in Fig. 7A,B) was 3.83 g AFDW for the 1993 FP cohort and 6.11 g for the 1992 MP cohort. While spawning in the 1992 MP cohort was continuous, that of the FP 1993 cohort occurred in separate early and late periods, with respective mean individual reproductive efforts of 1.65 and 2.18 g accounting for 43 and 57% of its total 1994 reproductive effort.

From initial settlement through the end of spawning in November 1994, the FP 1993 cohort mean individual tissue plus shell AFDW production was 1.21 g, while that for the 1992 MP cohort, estimated from initial collection in March 1994 through cessation of spawning in December 1994, was 1.47 g. Addition of the mean

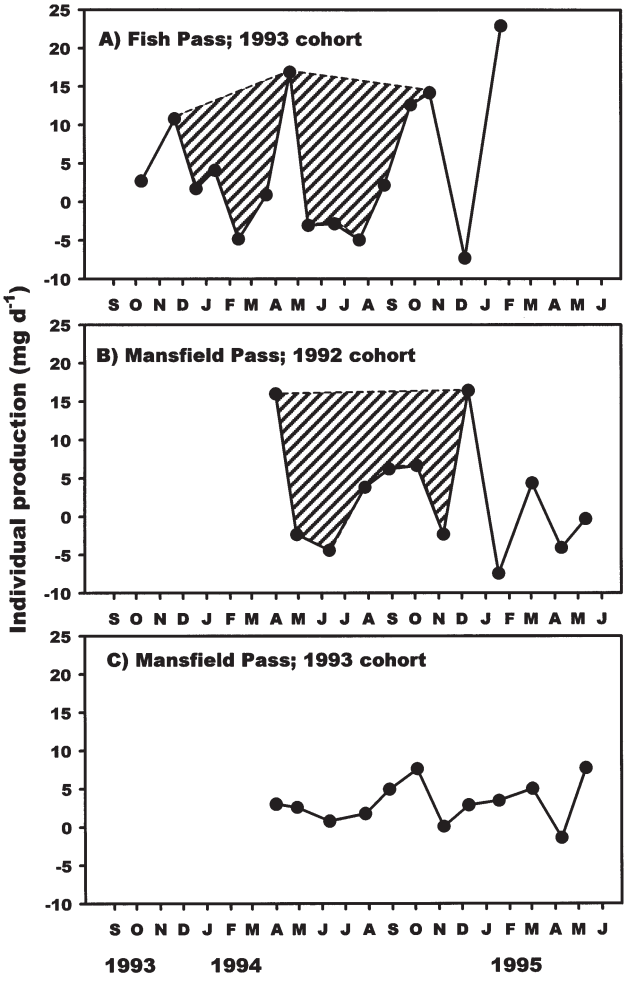

Fig. 7. *Perna perna*. Mean individual daily flesh plus shell ash-free dry weight (AFDW) production values (mg AFDW d^{-1}) over the duration of collection for specimens in the (A) 1993 cohort at Fish Pass, and the (B) 1992 and (C) 1993 cohorts at Mansfield Pass, Texas. Hatched areas in (A) and (B): daily productivity lost to gamete release; this allowed total reproductive effort to be estimated by integrating the total loss of individual production associated with reduced productivity during spawning periods (see 'Results' for details of computation)

production of the 1993 MP nonreproductive cohort from its settlement through February 1995 to that of the 1992 MP cohort from March 1994 through the cessation of its spawning in December 1994 allowed the mean production of the 1992 cohort from initial settlement to cessation of the first spawning period (~19 mo) to be estimated as 2.19 g. Summing the values for mean individual gamete release and tissue plus shell production yielded total mean individual production estimates from initial settlement of 5.04 and 8.30 g AFDW for the 1993 FP and 1992 MP cohorts, respectively. During spawning periods, release of gametes was estimated to account for 76 and 74% of total indi-

vidual AFDW production in the 1993 FP and 1992 MP cohorts, respectively (Fig. 7A,B). Individual production of the nonreproductive 1993 MP cohort was 0.72 g. When added to that for the reproductive 1992 MP cohort, a total individual production for the MP population of 9.02 g was obtained, of which reproductive effort accounted for 68%.

DISCUSSION

Shell growth rate in tropical pernids is greater than that found in temperate mytilids (Vakily 1989). The SL achieved in the first year in Texan *Perna perna* populations (42 to 53 mm SL) fell within the range reported for endemic *P. perna* populations (25 to 79 mm SL, Table 1), suggesting that the Gulf of Mexico is capable of supporting populations of this species.

More rapid shell growth at MP (53 mm SL in the first year) relative to FP (42 mm SL in the first year) may have been associated with *Perna perna's* lack of spawning in its first year of life. Allocation of 76% of total production to gamete release in the 1993 FP cohort resulted in reduced growth relative to the nonspawning 1993 MP cohort, which presumably allocated all nonrespired assimilation to growth. The basis for lack of reproduction in the 1993 MP cohort is unknown, but may have resulted from nutritional conditions at MP being too limited to support maturation in the first year of life. The relatively poorer condition of the 1993 MP cohort was reflected by reduced tissue mass relative to the 1993 FP cohort during nonspawning periods (Fig. 5B,D). Competition with the 1992 cohort at MP, which did not occur at FP, may have further reduced food resources available to the 1993 MP cohort.

The 2 to 3 yr life span characteristic of the FP and MP populations was similar to that of South African and Algerian populations, in which few individuals survive beyond 2 yr (Berry 1978, Berry & Schleyer 1983, Abada-Boudjema & Dauvin 1995). In contrast, life spans of temperate mytilids vary from 4 to 24 yr (Seed 1976).

Among mytilids, the high growth rates of pernids allow them to sustain higher annual production rates than temperate members of the genus *Mytilus.* The

Table 1. *Perna perna.* Published values of first-year growth rates for populations in relation to latitude and temperature. na: not available

Locality	Latitude	Mean temp. (°C)	Temp. range (°C)	Shell length at 1 yr (mm)	Source
North America					
Fish Pass, Texas, USA	27° N	22	10–30	42	This study
Mansfield Pass, Texas, USA	26° N	22	10–30	53	This study
South America					
Sucre, Venezuela	10° N	26	22–30	70 (8 mo)	Carvajal (1969)
Ubatuba, Brazil (Site 1)	23° S	23.5	19–28.5	25	Marques et. al. (1991)
Ubatuba, Brazil (Site 2)	23° S	23.3	19.5–28.5	27	Marques et. al. (1991)
Ubatuba, Brazil (Site 3)	23° S	23.5	18–27	25	Marques et. al. (1991)
Asia					
Vizhinjan, India	8° N	na	21–30	55–70	Appukuttan et. al. (1980)
Puttalam Lagoon, Sri Lanka	9.2° S	na	na	72–78	Indrasena & Wanninayake (1994)
Africa					
Algiers, Algeria (Site 1)	36° N	na	10–24	30	Abada-Boudjema & Dauvin (1995)
Algiers, Algeria (Site 2)	36° N	na	12–26	26	Abada-Boudjema & Dauvin (1995)
Temara, Morocco	33° N	na	14–23	33.5	Shafee (1992)
Pointe-Noire Bay, Congo	4° S	na	16–28	63	Cayré (1978)
Zululand, South Africa (Site 1)	27° S	24	na	51	Tomalin (1995)
Zululand, South Africa (Site 2)	27.5° S	24	na	49	Tomalin (1995)
Zululand, South Africa (Site 3)	28° S	23	na	52	Tomalin (1995)
Zululand, South Africa (Site 4)	28° S	23	na	46	Tomalin (1995)
Durban, South Africa (Site 1)	29° S	22	20–25	57.7	Tomalin (1995)
Durban, South Africa (Site 2)	29° S	22	20–25	79	Tomalin (1995)
Durban, South Africa (Site 3)	29° S	22	21–22	57.5	Tomalin (1995)
Durban, South Africa (Site 4)	30° S	21	20–25	52.1	Tomalin (1995)
Umdoni, South Africa	30° S	21	na	46	Tomalin (1995)
Transkei, South Africa	31–33° S	na	na	30–40	Lasiak & Dye (1989)
Saldanha, Bay, South Africa	33° S	15	13–16	52	van Erkom Schurink & Griffiths (1993)
Algoa Bay, South Africa	34° S	18	15–21	59	van Erkom Schurink & Griffiths (1993)
Plettenberg Bay, South Africa	34° S	na	na	30–40	Crawford & Bower (1983)

highest production rate among pernids was for a South African *Perna perna* population ranging from 6.45 to 7.61 kg m^{-2} yr^{-1} (Berry 1978), twice that of the highest rate reported for *M. edulis* (Dare 1976). Other pernid production rate values include 1.31 kg m^{-2} yr^{-1} for a Moroccan *P. perna* population (Shafee 1992), and 1.19 kg m^{-2} yr^{-1} for a pollution-stressed, Hong Kong *P. viridis* population (Cheung 1993). Annual production rates at FP and MP were 2.44 and 1.86 kg m^{-2} yr^{-1}, respectively, falling within the range of values (1.3 to 7.6 kg m^{-2}) reported for *P. perna* (Berry 1978, Shafee 1992). Standing crop flesh plus shell AFDW production values for other mytilaceans include 1.46 to 7.88 kg m^{-2} yr^{-1} for *Choromytilus meridionalis* (Griffiths 1981), 2.12 kg m^{-2} yr^{-1} for *M. edulis* (Deslous-Paoli et al. 1990), and 3.41 kg m^{-2} yr^{-1} for *M. galloprovincialis* (Hosomi 1985). Thus, production values reported for *P. perna*, including our data, fall within the range of 1 to 4 kg m^{-2} yr^{-1} for the majority of other mytilacean species.

The lack of age-related productivity trends in Texan *Perna perna* cohorts suggest that their productivity may be regulated by physical factors. Within their dense beds, population biomass and productivity may be constrained by available space and degree of tolerated aggregation. Lack of available space may have been the basis of the unsuccessful recruitment of the 1994 FP and MP cohorts. Successful recruitment of new cohorts did occur in years subsequent to the sampling period, after the densities of the dominant 1992 and 1993 cohorts had waned at the FP and MP sites.

Of the standing crop production, 42 to 54 % was allocated to organic shell production in the FP and MP populations, respectively. Similar values have been reported for other *Perna perna* populations, ranging from 32.9 to 47.1 % (Berry 1978, Shafee 1992), while a value of 55.5 % was recorded for a *P. viridis* population (Cheung 1993). In contrast, standing crop organic production allocated to shell in *Mytilus edulis* ranged from 15.8 to 41.6 % (Dare 1976, Deslous-Paoli et al. 1990), was 26 % in *Aulacomya ater* (Griffths & King 1979a), and was only 11.8 % in *M. galloprovincialis* (Hosomi 1985). Thus, pernid shell growth takes up a greater proportion of organic standing crop production (mean of published values = 45.5 ± 3.5 %, n = 6, range = 32.9 to 55.5 %, see above) compared to other mytilid species (mean of published values = 23.9 ± 3.6 %, n = 7, range = 11.8 to 41.68 %, see above), suggesting that pernids either have a greater proportion of shell mass as organic periostracum and matrix or have a proportionately more massive shell relative to tissue biomass. The adaptive value of this fundamental difference in pernid shell architecture warrants further study.

Reproduction makes up 17 to 98 % of total production (tissue + shell + gamete production) in marine bivalves (for reviews see Griffiths & Griffiths 1987, Dame 1996). Thus, in gravid *Perna perna*, gonads account for >50 % of body mass (Berry 1978, van Erkom Schurink & Griffiths 1991), and laboratory spawning resulted in a 60 % reduction in tissue AFDW. These values correspond to post-spawning tissue biomass losses of 40 to 50 % in the 1993 FP and 1992 MP cohorts and post-spawning individual tissue biomass reductions of 50 to 60 % in *Choromytilus meridionalis* (Griffiths 1977) and 29 to 47 % in *Mytilus edulis* (Thompson 1979).

Based on loss of standing crop AFDW production during spawning periods, individual reproductive effort was 76 and 74 % of production in the 1993 FP and 1992 MP cohorts, respectively. When computed from summed negative production values, gamete production in South African *Perna perna* populations increased from 8–11 to 39–41 % of total production in the first and second years of life, respectively (Berry 1978). Based on adult biomass loss during reproductive periods, reproductive efforts were estimated to be 10.4 to 17.4, 38.9 and 63.6 % of total production in the first, second, and third year of life in a Moroccan *P. perna* population (Shafee 1992). Our laboratory-estimated value of a spawning biomass loss of 60 % was consistent with estimated reproductive efforts of field populations at 74 to 76 % of total AFDW production at FP and MP, suggesting that summation of negative production rates (Berry 1978) may underestimate reproductive effort in this species. Indeed, when computed from negative production rates, reproductive efforts for FP and MP were only 31.3 and 12.6 % of total production, respectively. Among other mytilaceans, gamete production expressed as a percentage of total production was 18.8 % in *Geukensia demissa* (Kuenzler 1961), 35.0 %, in *Mytilus edulis* (Bayne & Newell 1983), 35.6 to 88.8 % in *Aulacomya ater* (Griffiths & King 1979a,b), and up to 75 % in *Choromytilus meridionalis* (Griffiths 1981). As the total annual productions and reproductive efforts of the FP and MP populations fell within those reported for other mytilids, Gulf of Mexico habitats appear to be able to support typical populations of *P. perna*.

Reported spawning periods for *Perna perna* are highly variable (for review see Vakily 1989). Spawning ceases below the lower spawning limit of 18°C (Shafee 1989), accounting for the winter cessation of spawning at FP and MP at water temperatures <18 to 20°C, as has also been reported for Moroccan (Shafee 1989) and Algerian (Abada-Boudjema & Dauvin 1995) *P. perna* populations. In contrast, tropical and subtropical *P. perna* populations inhabiting waters which do not fall below 18°C tend to spawn sporadically throughout the year (Vélez & Martinez 1967, Carvajal 1969, Lunetta 1969, Benítez & Okuda 1971, Vélez 1971, Acuña 1977, Berry 1978, Lasiak 1986, van Erkom Schurink & Griffiths

1991), with spawning suppressed during summer (Carvajal 1969, Lunetta 1969, Vélez 1971) when water temperatures exceed this species' 28°C upper limit for gametogensis (Vélez & Epifanio 1981). Water temperatures approaching 28°C may have been the basis for the mid-summer interruption of spawning at FP (Fig. 5).

Biotic and abiotic factors other than temperature may initiate periodic spawning episodes in asynchronously spawning populations (Romero & Moreira 1980, Salomão et al. 1980, Vélez & Epifanio 1981). Like *Perna perna*, other tropical and subtropical mytilids, including *P. viridis* (Walter 1982, Cheung 1993), *P. canaliculus* (Greenway 1975, Hickman & Illingworth 1980), *Choromytilus meridionalis* (Griffiths 1981), *Aulacomya maorina* (Kennedy 1977) and *A. ater* (Griffiths & King 1979a, van Erkom Schurink & Griffiths 1991), spawn sporadically during all but winter months, while those of temperate mytilids are generally restricted to 1–3 mo during spring and summer (for reviews see Seed 1976, Griffiths & Griffiths 1987, Dame 1996). Indeed, spawning was more temporally restricted and seasonally synchronous in populations of *Mytilus galloprovincialis* than in sympatric populations of the tropical/subtropical species *A. ater*, *C. meridionalis*, and *P. perna* (van Erkom Schurink & Griffiths 1991, Abada-Boudjema & Dauvin 1995). Temporally restricted spring/summer spawning periods of temperate mytilid species appear to allow synchronization with spring/summer bursts of phytoplankton production that support their planktotrophic larval development (Seed 1976). In contrast, tropical/subtropical mytilids may be stimulated to spawn during unpredictable phytoplankton blooms or periods of elevated temperatures (for review see Griffiths & Griffiths 1987), leading to their characteristic asynchronous reproductive patterns. Thus, the subtropical species *C. meridionalis* and *A. ater* have multiple, asynchronous spawning events associated with phytoplankton availability (Griffiths 1977). In these 2 species, mature gametes were continuously present in the gonads, suggesting that gametes were being released over prolonged periods (Griffiths 1977). In contrast, temperate mytilids have a single, major, abbreviated, annual reproductive effort (Baird 1966, Dare 1976, Thompson 1979, Dix & Ferguson 1984) marked by complete loss of mature gametes from the gonad (Thompson 1979).

Protracted reproductive periods during which assimilated energy is continuously allocated to gamete production (i.e., 'direct costing', Sibly & Calow 1986) should result in allocation of a greater proportion of nonrespired energy to reproduction than would occur on discharge of accumulated gametes in a single, major, abbreviated, annual spawning event characteristic of temperate mytilids (i.e., 'absorptive costing', Sibly & Calow 1986). Thus, estimates of relative reproductive effort in subtropical/tropical mytilid populations at 74–76% (this study), 39–41% (Berry 1978), and 10.4–63.6% (Shafee 1992) for *Perna perna*, 35.6–88.8% for *Aulacomya ater* (Griffiths & King 1979a,b) and 75% for *Choromytilus meridionalis* (Griffiths 1981) are considerably elevated compared to those of temperate mytilids at 35% for *Mytilus edulis* (Bayne & Newell 1983) and 18.8% for *Guekensia demissus* (Kuenzler 1961).

The results of our study indicate that growth rate, recruitment, reproductive effort and productivity in 2 Texan *Perna perna* populations fell well within the limits of these parameters recorded for endemic populations of this species throughout its world-wide geographic range. Even though recruitment of the 1994 cohorts to both Texan populations was poor, massive recruitments of new cohorts have been observed in both these populations subsequent to the study period. Thus, Gulf of Mexico shores are capable of supporting *P. perna* populations whose dynamics are similar to those of endemic populations on other continents. Our data suggest that populations of *P. perna* could spread beyond the species' present Texas/Mexico range (Hicks & Tunnell 1993, 1995) under the prevalent environmental conditions of the Gulf of Mexico; thus, the distribution, dispersal, and colonization success of *P. perna* should continue to be monitored in North America.

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