Field observations on white shrimp, *Litopenaeus setiferus*, during spring spawning season in SC, USA, 1980-2003

Larry B. DeLancey, James E. Jenkins, Mark B. Maddox, J. David Whitaker, and Elizabeth L. Wenner

SEDAR-PW6-RD27

9 May 2014

JOURNAL OF CRUSTACEAN BIOLOGY, 25(2): 212–218, 2005

FIELD OBSERVATIONS ON WHITE SHRIMP, *LITOPENAEUS SETIFERUS*, DURING SPRING SPAWNING SEASON IN SOUTH CAROLINA, U.S.A., 1980–2003

Lawrence B. DeLancey, James E. Jenkins, Mark B. Maddox, J. David Whitaker, and Elizabeth L. Wenner

South Carolina Department of Natural Resources, P.O. Box 12559, Charleston, South Carolina, 29412. U.S.A.
(LBD, corresponding author): delanceyl@mrd.dnr.state.sc.us

ABSTRACT

Fishery dependent trawl samples taken in spring prior to commercial shrimp trawling season in South Carolina were analyzed for annual relative abundance, sex ratios, and ovarian development of white shrimp, *Litopenaeus setiferus*, during 1980–2003. Fishery independent trawl samples were analyzed for relative abundance and ovarian development of female *L. setiferus* during the same period. Relative abundance varied greatly among years, and was thought to be strongly influenced by winter water temperature. The decade of the 1990s was a period of mild winters and high abundance of white shrimp in South Carolina. Biological observations about size and sex ratios of shrimp were consistent with past studies done along the southeastern Atlantic coast. Proportions of male shrimp in fishery dependent collections appeared to increase with advance of maturation of female shrimp. After spawning, numbers of male shrimp declined, suggesting that males are attracted to location of females prior to spawning, as has been postulated in published laboratory studies. Analyses of fishery independent samples indicated a slight delay in time of maturation of female shrimp during cool temperatures in spring; conversely, spring seasons with warm temperatures seemed to speed up maturation. This study should help elucidate the location of spawning areas for *L. setiferus* off South Carolina, in addition to its primary purpose of managing the shrimp fishery on a biological basis.

The white shrimp, *Litopenaeus setiferus* (Linnaeus, 1797), is the most important penaeid species taken in commercial and recreational harvest along the Atlantic coast of the southeastern United States of America (National Marine Fisheries Service[1]). It constitutes about two thirds of the annual commercial harvest in South Carolina, and also supports a large recreational fishery (McKenzie, 1981; Lam *et al*., 1989; Low, 2002). Consequently, it has been a subject of numerous studies; see Lindner and Cook (1970) and Williams (1984) for review.

Litopenaeus setiferus begin spawning in the spring of the year (Lindner and Anderson, 1956) along the southeastern U.S. coast. These sexually mature shrimp produce the progeny that comprise most of the harvest in late summer and autumn (Lam *et al*., 1989). Because of their size and market demand at that time of year, these spring shrimp have a high value (South Carolina Department of Natural Resources (SCDNR), Fisheries Statistics Section). In years of average or greater abundance of these spring shrimp, the commercial shrimp trawling season in South Carolina territorial waters is opened by the SCDNR after spawning of at least a substantial portion of the population, to allow harvest of these valuable shrimp. Opening of the season is largely determined by examining the ovarian development of female shrimp using methods described below.

The timing of spawning in penaeid shrimp may differ, based on whether the female's thelycum, the specialized structure that receives the spermatophore from the male shrimp, is "open" or "closed" (Dall *et al*., 1990). *Litopenaeus setiferus* possess an "open" thelycum, and spawning is thought to occur shortly after mating, whereas spawning in "closed" thelyca penaeids may occur weeks after mating (Browdy, SCDNR, personal communication; Dall *et al.* 1990). Therefore, inferences about spawning location may be made when sampling indicates shrimp spawning activity. Although Misamore and Browdy (1996) described mating of *L. setiferus* in the laboratory, and Weymouth *et al*. (1933) and Lindner and Anderson (1956) described gonadal development by geographic area, long term field observations and relatively recent published data for South Carolina are lacking. More extensive laboratory study on another species with an open thelycum, the Pacific white shrimp, *Litopenaeus vannamei* (Boone, 1902), has been conducted in the Americas because of its success in culture operations (see Ogle, 1992, for review). Field information such as that collected in the present study can be useful in inference about reproductive behavior, besides its primary purpose for management of shrimp season openings. This paper summarizes relative abundance and reproductive data collected over two decades during spring sampling for *L. setiferus* in South Carolina.

MATERIALS AND METHODS

Fishery dependent samples were first collected aboard commercial shrimp trawlers in 1980. Following years of low white shrimp abundance caused by lethal winter water temperatures (McKenzie, 1981), sampling resumed on a consistent basis (at least three trawlers sampled per spring) in 1984, and continues to the present. Trawlers are accompanied by SCDNR personnel into areas closed to trawling (prior to season opening) and allowed to make several tows and retain the catch to cover expenses. Some effort has been made to sample different areas of the state's coastline, with most samples being collected near estuarine inlets that are historically productive for spawning white "roe" shrimp (Fig. 1). All tows are made during daylight, with tow duration ranging from 20 min to 180 min, but generally one hour or less. Fishing gear include twin (four nets) or double rigs (two nets) with head ropes ranging from 12 m to 27 m, and stretched mesh size was usually 4.7 cm. A subsample of at least 2.3 kg (5.0 pounds) is removed from the total catch (which is weighed or estimated by volume after the vessel crew sorts the shrimp from bycatch). Total length (TL, mm)

[1] National Marine Fisheries Service Unpublished Data Website: http://www.st.nmfs.gov/st1/commercial/index.html.

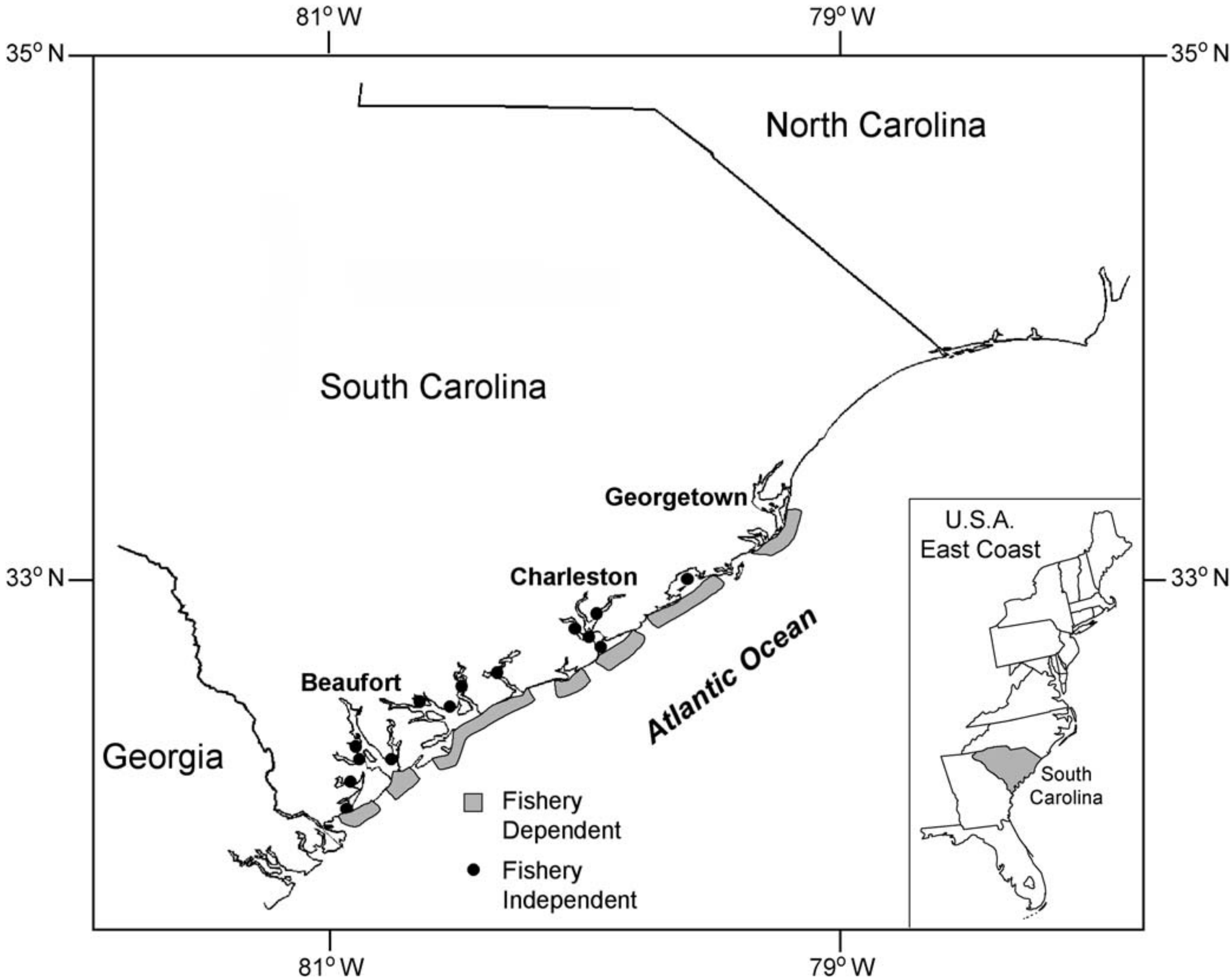

Fig. 1. The east coast of the United States of America (inset), and preseason commercial trawl (fishery dependent) and SCDNR trawl (fishery independent) sampling areas in South Carolina, 1980–2003.

are recorded for 50 individuals. Sex and ovarian development stage of female shrimp are determined by gross visual observation (King, 1948; Lindner and Anderson, 1956) from the subsample. The ovaries are categorized as undeveloped, early development ("pepper"), advancing ("yellow"), ripe, and spent.

Fishery independent samples have been collected aboard SCDNR research vessels since 1976, although for consistency, in this study only samples taken after 1979 were used for analyses in combination with fishery dependent samples. Trawl nets measuring 6.2 m (headrope length) with 2.5-cm stretch mesh are used to assess commercially important shrimp stocks in South Carolina. Although vessels and tow times have changed, general trawling methods and locations have remained consistent. These locations are primarily in estuaries inshore of legal commercial trawling areas, and have been used to assess the potential success of subsequent commercial and recreational harvests. Samples are collected at fixed stations around Charleston Harbor on at least a monthly (often weekly or biweekly) basis, while stations south of Charleston are sampled in March, April, June, August, October, and December. Some limited sampling occurs north of Charleston. Previous analyses determined that catches made in April are most reliable in assessing potential spawning class strength. Catches of shrimp are subsampled ($n = 50$) for size (TL) and gross disease (data not included in present analyses), and total catch is enumerated or estimated with weight. When female white shrimp in advanced ovarian development appear in samples, sex composition and ovarian developmental stage of females are determined for those samples.

Daily water temperature data collected by stem thermometer (± 0.1°C) in Charleston Harbor at the U.S. Customs House[2] and at Fort Johnson (SCDNR unpublished data) were used to examine the effect of spring temperatures on ovarian development of shrimp.

Catch rates of white shrimp were standardized to 50-m total headrope length for trawls and 1-hr tow times for samples taken on commercial vessels (fishery dependent). Fishery independent catch rates were standardized to 15-min tow times and double-rigged 6.2-m headrope trawls.

Examination of data from commercial landings revealed nonnormal distribution (uncorrected by transformation); therefore, the nonparametric Spearman correlation coefficient was calculated for ranks of catch rates and subsequent landings and potential effect of winter water temperature on catch rates and landings ($P \leq 0.05$; Sokal and Rohlf, 1981; SPSS, 1997). Assuming nonnormality for distribution of classes of female ovarian stage, proportions of male shrimp collected by class of advanced ovarian stage of females (in collections where total $n = 10$ or greater shrimp) were compared using the nonparametric Kruskal Wallis test ($P \leq 0.05$).

[2] National Oceanic and Atmospheric Administration, National Oceanographic Data Center, Silver Spring, Md.

Table 1. Catch rates of white shrimp, *Litopenaaeus setiferus*, obtained aboard commercial shrimp trawlers during spring preseason sampling in South Carolina and subsequent commercial landings, 1980–2003. Number of shrimp per tow standardized to one hour tow time, 50-m length (headrope) trawl.

Year	Range of sampling dates	Number of trawls	Number shrimp per tow	Commercial landings (1000 kg)
1980	25 Apr.–20 May	47	995.7	110.5
1981	15 May	4	6.1	0.9
1984	11 June	1	55.8	0.5
1985	10–11 June	18	5.6	1.4
1986	10–11 June	22	43.1	9.5
1987	19–21 May	36	1950.1	138.2
1988	6–16 June	25	58.3	2.3
1989	9–18 May	36	2476.8	180.9
1990	27 Apr.–22 May	31	221.8	11.4
1991	2–8 May	23	4004.5	380.5
1992	4–6 May	14	3046.4	280.9
1993	10–24 May	26	1253.5	375.5
1994	17–18 May	20	1074.3	41.8
1995	3–8 May	19	4600.2	404.5
1996	20–30 May	27	1434.5	28.2
1997	30 Apr.–9 May	25	1412.6	210.0
1998	30 Apr.–19 May	32	2090.2	363.6
1999	3–12 May	14	1537.1	272.7
2000	27 Apr.–17 May	35	2801.7	397.7
2001	31 May–14 June	19	34.9	0.5
2002	2–8 May	18	2221.3	134.5
2003	1–15 May	18	285.9	47.7

RESULTS

Numbers of white shrimp per tow varied greatly, ranging from a few individuals to several thousand, sometimes in collections made during the same day in the same general area. Average annual numbers also varied substantially (Table 1; Fig. 2). The decade from 1991 through 2000 was characterized by mild winters and relatively large numbers of spring spawners and subsequent commercial landings (Table 1; Fig. 3). Significant ($P \leq 0.05$) correlations were found for both fishery dependent catch rates ($\rho = 0.79$) and fishery independent catch rates from April samples ($\rho = 0.95$) and subsequent commercial spring harvest. Correlations were also significant for January water temperature and fishery dependent catch rates ($\rho = 0.69$), fishery independent catch rates ($\rho = 0.83$), and spring commercial landings ($\rho = 0.86$).

A total of 18,166 *L. setiferus* was measured in 527 fishery dependent trawl samples (Fig. 4). Average TL of male shrimp was 146.4 mm (±8.52 std. dev.) and of female shrimp was 156.3 mm TL (±10.82 std. dev). An average of 27.5 male and 26.8 female shrimp per tow was observed in subsampled catches. Percentages of male shrimp in fishery dependent samples containing at least ten individuals ranged from six to ninety percent, whereas percentages of females ranged from ten to ninety-four percent.

Examination of frequency of ovarian development in female shrimp in fishery dependent tows revealed most were in advanced ovarian development, while proportionately more shrimp collected in fishery independent trawl samples ($n = 607$) were in early development. Many of the latter samples were collected earlier in the year and further up the estuary than fishery dependent samples (Figs. 5, 6). Despite this, female white shrimp collected in fishery independent

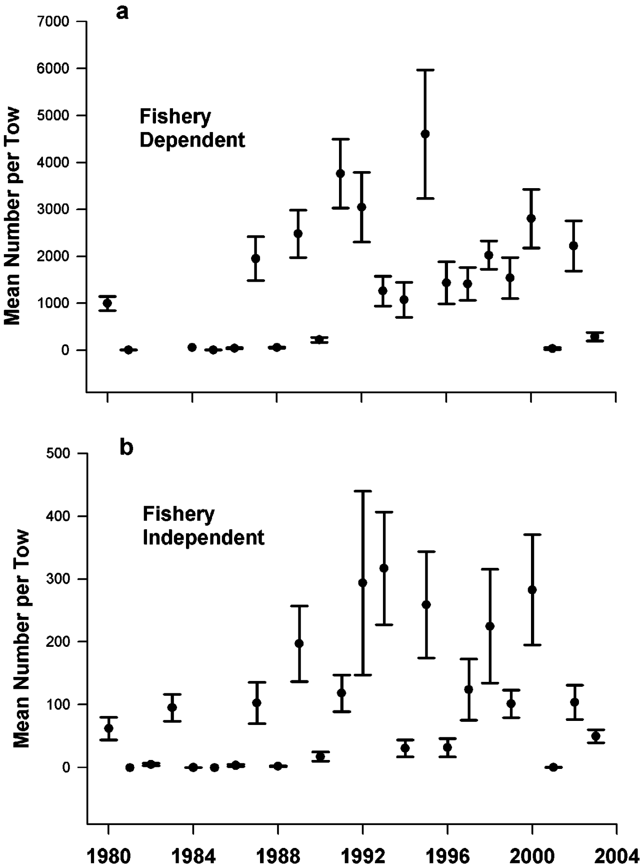

Fig. 2. Annual mean number per tow and standard error of white shrimp, *Litopenaeus setiferus*, collected in South Carolina in: (a) fishery dependent sampling aboard commercial trawlers, and (b) fishery independent sampling aboard SCDNR trawlers, 1980–2003.

samples showed a relatively high proportion of spent individuals. A small number of females carrying at least portions of spermatophores was collected during this study.

Tabulation of numbers of male shrimp to average female ovarian stage in fishery dependent samples revealed that the highest percentage of males occurred with females approaching spawning (ripe or near ripe), then declined after

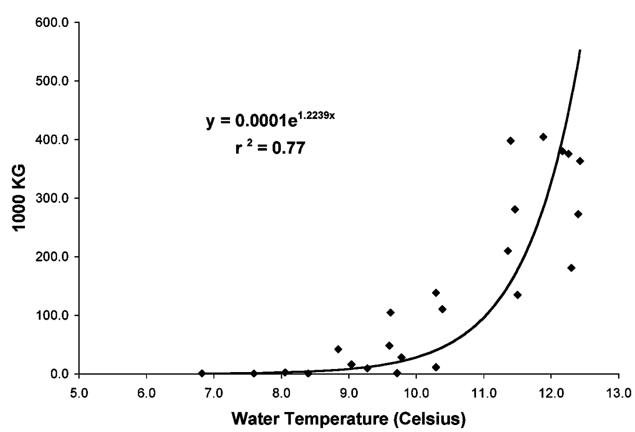

Fig. 3. Average January water temperature in Charleston Harbor, South Carolina, *versus* spring commercial trawl landings of white shrimp, *Litopenaeus setiferus*, in South Carolina, 1980–2003.

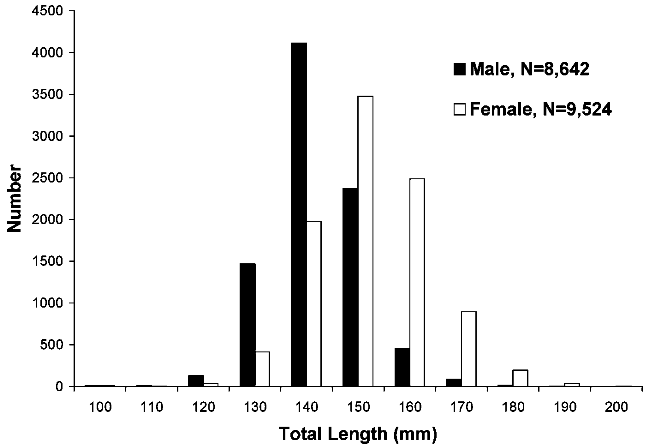

Fig. 4. Total length of white shrimp, *Litopenaeus setiferus*, collected in fishery dependent trawls in South Carolina, 1980–2003.

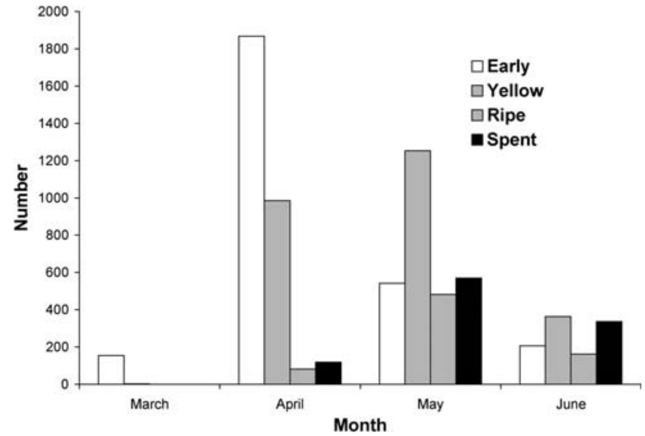

Fig. 6. Number of female white shrimp, *Litopenaeus setiferus*, categorized by ovarian development by month, collected in fishery independent trawls in South Carolina, 1980–2003.

spawning (Fig. 7). Analysis using the Kruskal Wallis test revealed significant differences ($P \leq 0.05$) among percentage of male shrimp averaged by female ovarian stage.

Effect of Spring Temperature and Use in Management

Although some sexual composition and ovarian development data were collected as early as March in fishery independent trawls, most maturing animals were found in April through June, with the majority in May. A scatterplot of spring water temperature *versus* date of first appearance of "yellow" stage female shrimp in fishery independent trawls serves to illustrate the apparent effect of relatively cool springs delaying development, and warmer springs accelerating development (Fig. 8). Plots of water temperature in two extreme springs (Fig. 9), and examination of frequency of ovarian development in those years (Fig. 10), illustrates that the difference in timing of maturation between cool and warm spring seasons is relatively small (about two weeks). The examination of frequency of advanced stages of female ovarian development has been used to estimate when at least one-half of the female shrimp would spawn, assuming ripe individuals would spawn within a matter of days. From this information, SCDNR fisheries managers decide on a date for opening the commercial trawling season (Fig. 10).

Discussion

Large variation in catches of nektonic species (as seen in this study) on both a daily and annual time period is typical of trawl samples (Taylor, 1953) and for *L. setiferus* (Bishop and Shealy, 1977; Music, 1994). Commercial shrimp trawling operations target "concentrations" of shrimp when possible (Anderson *et al.*, 1949). Annual variation in the present study was primarily due to winter water temperature, with poor survival of overwintering white shrimp in colder winters (Williams, 1969; McKenzie, 1981; Lam *et al.*, 1989; SCDNR, unpublished data).

Results of statistical analyses revealed that both fishery dependent and fishery independent catch rates were significantly correlated with subsequent commercial landings, and January water temperature was significantly

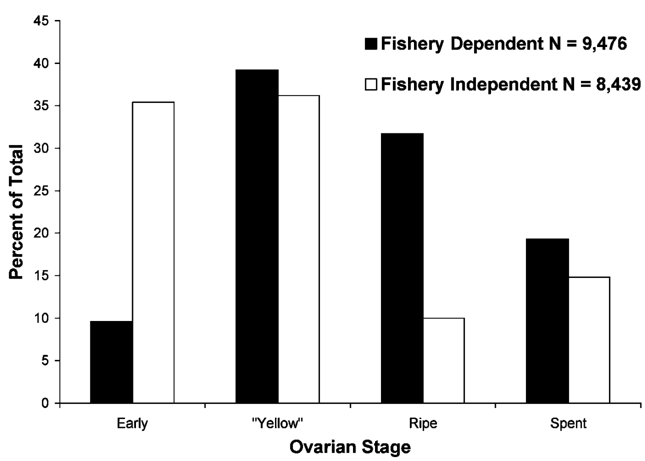

Fig. 5. Frequency of stages of ovarian development for female white shrimp, *Litopenaeus setiferus*, in fishery dependent and fishery independent trawls in South Carolina, 1980–2003.

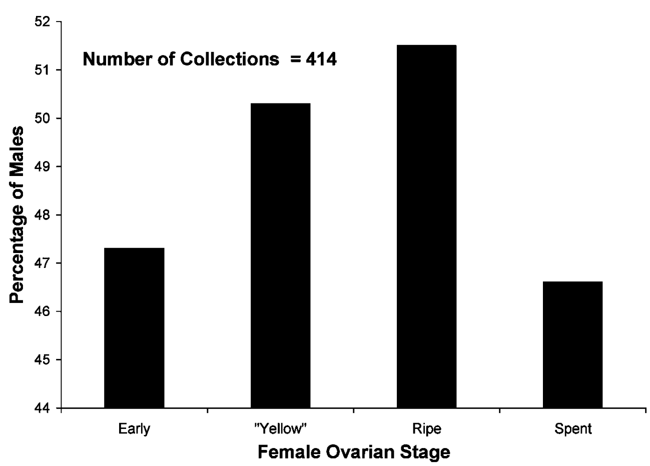

Fig. 7. Percentage of male white shrimp, *Litopenaeus setiferus*, averaged by female ovarian stage in fishery dependent trawls taken in South Carolina, 1980–2003.

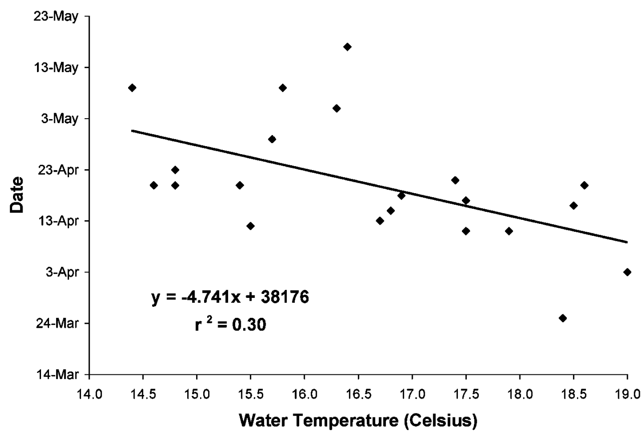

Fig. 8. Scatterplot of average water temperature from March 15 to April 15 in Charleston Harbor, South Carolina, *versus* date of first collection of female white shrimp, *Litopenaeus setiferus*, in "yellow" ovarian stage in fishery independent trawls in South Carolina, 1980–2003.

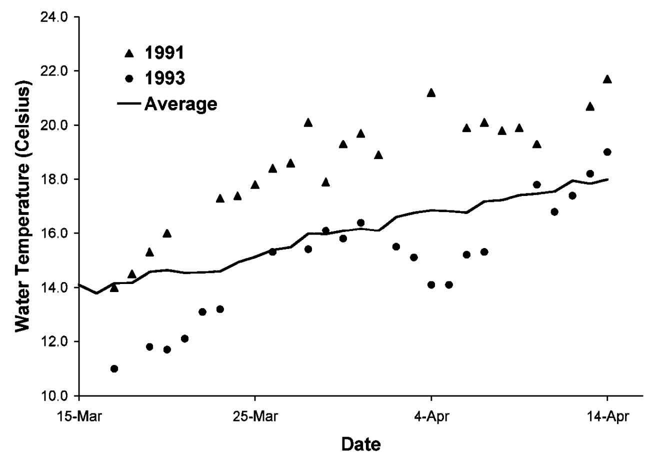

Fig. 9. Scatterplot of water temperature collected in Charleston Harbor, South Carolina, March 15–April 15 in 1991, 1993, and averaged for 1959–2003.

correlated with both catch indices and landings. Such data are important for managing fisheries by setting opening dates and prediction of harvest for fishermen, and was used for closure of the U.S. Exclusive Economic Zone to shrimp trawling following winter mortality of *L. setiferus* (South Atlantic Fisheries Management Council, 1993). These data demonstrate the importance of maintaining long term resource monitoring programs, an issue during times of budget constraints.

Biological observations on *L. setiferus* in this study are consistent with previous studies conducted on the species. Weymouth *et al.* (1933) and Pérez Farfante (1969), for example, observed that females grow larger than males, and the overall approximate 1:1 ratio of males to females is consistent, although it can be temporally quite variable (Bishop and Shealy, 1977; Lindner and Cook, 1970; Pérez Farfante, 1969). Relatively smaller male *L. setiferus* may be subjected to more predation than larger females; thus, the ratio of adult shrimp may be skewed toward females (Pauly *et al.*, 1984). In the study most similar to the current one, Weymouth *et al.* (1933) found that the proportion of female white shrimp to male white shrimp increased during the spring spawning season in Georgia offshore waters, then declined dramatically in summer. Weymouth *et al.* (1933) concluded that this was due to differential behavior associated with spawning. The apparent increase in the number of males with females nearing spawning as noted in the present study may be caused by attraction with pheromones, as suggested by Wyban and Sweeney (1991). If some of the collections in this study represented portions of spawning aggregations, then it raises the question of the fate of male shrimp after spawning. Perhaps they passively disperse while undergoing spermatophore regeneration before reseeking ripening females (Leung-Trujillo and Lawrence, 1987).

Fishery independent samples yielded many spent female shrimp inshore of commercial trawling areas. This may indicate spawning in estuaries but also suggests a postspawning movement inshore by some individuals to feed and escape predation (Boesch and Turner, 1984; Williams, 1955).

Lindner and Anderson (1956) suggested that the general rise in spring water temperature, as opposed to a specific temperature, triggered the onset of sexual maturation in *L. setiferus*. In this study, extremely cool spring temperature seemed to delay maturation slightly while warmer temperatures promoted more rapid development, although the difference was only a few weeks.

The collection of mated female shrimp serves as further corroboration of some fairly specific spawning areas. Only a few hours are thought to occur between mating and spawning of eggs (C. Browdy, SCDNR, personal communication), therefore the distance traveled would likely be fairly short. The majority of these shrimp are probably not undergoing extensive migration, unlike in the fall or early spring (Lindner and Anderson, 1956; McCoy and Brown, 1967; Whitaker *et al.*, 1989; SCDNR, unpublished data). Most of these spawning areas are either closed to bottom trawling or generally not trawled heavily until spawning has progressed, and other potentially disruptive activities, such as extensive dredging and disposal of dredged material, and beach renourishment, should be carefully monitored.

Our study did not attempt to address spawning of white shrimp that occurs later in the summer, although summer spawning can be important in producing progeny that recruit to estuaries in late fall and constitute a portion of the overwintering class (Lindner and Anderson, 1956; SCDNR, unpublished data). To further elucidate movements during spawning, some combination of laboratory spawning and increased field tracking should be considered in the future. Night sampling during peak spawning periods could yield more precise estimates of the proportion of shrimp actively spawning, as most penaeids studied in the laboratory appear to spawn at night (Dall *et al.*, 1990; Misamore and Browdy, 1996).

Finally, the results of this and previous studies on *L. setiferus* can be contrasted with inferences about spawning of the two other major wild harvested penaeid species in the U. S. The pink shrimp, *Farfantepenaeus duorarum* (Burkenroad, 1939) and the brown shrimp, *Farfantepenaeus aztecus* (Ives, 1891) are both "closed" thelycum species,

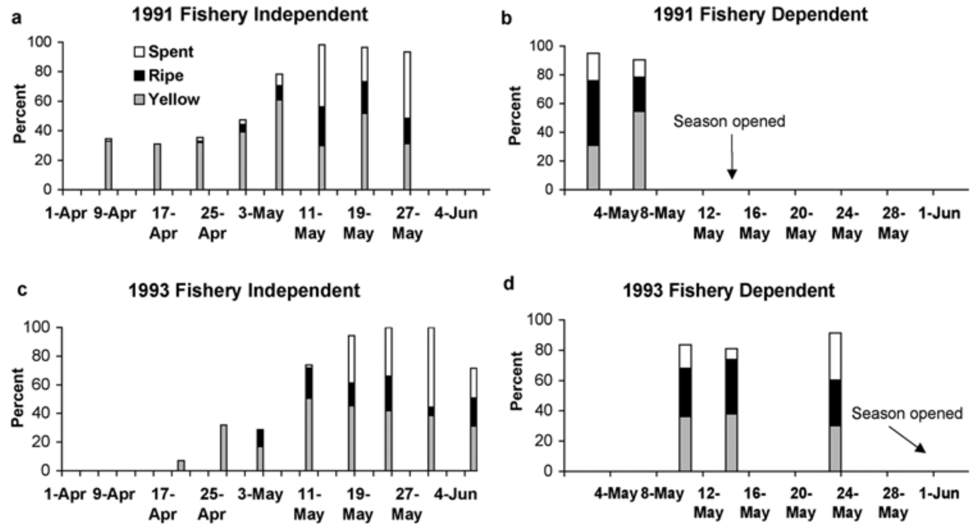

Fig. 10. Percentage of "yellow," ripe, and spent female white shrimp, *Litopenaeus setiferus*, taken in fishery independent trawls in South Carolina in (a) 1991 and (c) 1993, and in fishery dependent trawls in (b) 1991 and (d) 1993.

therefore egg laying may occur some time after mating, and at much greater depths than *L. setiferus* (Dall *et al*., 1990; Renfro and Brusher, 1982; Williams, 1984). *Farfantepenaeus duorarum* probably shares a similar spring-summer pattern of reproduction with *L. setiferus*, whereas *F. aztecus* appears to have peaks of spawning in spring and fall, at least in the Gulf of Mexico (Renfro and Brusher, 1982; Williams, 1955). Some annual patterns of reproduction in smaller penaeids have been recently examined by Bauer and Lin (1994) for *Trachypenaeus spp*. in the Gulf of Mexico and Sakaji (2001) for *Metapenaeopsis dalei* (Rathbun, 1902) in Japan, revealing that these species, unlike *L. setiferus* off the southeastern U.S. coast, have more protracted spawning activity throughout much of the year. Further research on this important aspect of the life history of penaeid shrimp will hopefully be forthcoming to enhance our understanding and ensure the sustainability of this ecologically important and heavily utilized group.

Acknowledgements

We thank the commercial shrimp trawler captains and crews that participated in this study. We also thank the captains of research vessels: J. LaRoche, P. Richards, G. Miller, and P. Tucker. The figures were prepared by K. Swanson. This paper was part of a penaeid shrimp symposium held at the spring meeting of the Crustacean Society in Williamsburg, Virginia, June 2, 2003. The symposium was partially sponsored by the Atlantic States Marine Fisheries Commission and the Southeast Area Monitoring and Assessment Program. This paper is contribution number 553 from the South Carolina Marine Resources Center.

Literature Cited

Anderson, W. W., M. J. Lindner, and J. E. King. 1949. The shrimp fishery of the southern United States.—Fish and Wildlife Service (U.S.), Commercial Fisheries Review 11: 1–17.

Bauer, R., and J. Lin. 1994. Temporal patterns of reproduction and recruitment in populations of the penaeid shrimps *Trachypenaeus similis* (Smith) and *T. constrictus* (Stimpson) (Crustacea: Decapoda) from the Northcentral Gulf of Mexico.—Journal of Experimental Marine Biology and Ecology 182: 205–222.

Bishop, J. M., and M. H. Shealy, Jr. 1977. Biological observations on commercial penaeid shrimps caught by bottom trawl in South Carolina estuaries, February 1973–January 1975. South Carolina Marine Resources Center, Technical Report 25. 97 pp.

Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes, the role of food and refuge.—Estuaries 7: 460–468.

Dall, W., B. J. Hill, P. C. Rothisberg, and D. J. Sharples. 1990. The Biology of the Penaeidae. Advances in Marine Biology 27 (J. H. S. Blaxter and A. J. Southward, series editors). Academic Press, Harcourt Brace Jovanovich, London.

King, J. E. 1948. A study of the reproductive organs of the common marine shrimp, *Penaeus setiferus* (Linnaeus).—Biological Bulletin 94: 244–262.

Lam, C. F., J. D. Whitaker, and F. S. Lee. 1989. Model for white shrimp landings for the central coast of South Carolina.—North American Journal of Fisheries Management 9: 12–22.

Leung-Trujillo, J. R., and A. L. Lawrence. 1987. Spermatophore regeneration times for three commercially important penaeid species: *Penaeus stylirostris*, *Penaeus vannamei*, and *Penaeus setiferus*.—Journal of the World Aquaculture Society 18: 32A.

Lindner, M. J., and W. W. Anderson. 1956. Growth, migrations, spawning and size distribution of shrimp *Penaeus setiferus*.—Fishery Bulletin (U.S.) 56: 555–645.

———, and H. L. Cook. 1970. Synopsis of biological data on the white shrimp *Penaeus setiferus* (Linnaeus) 1767.—Food and Agricultural Organization Fisheries Reports 57: 1439–1469.

Low, R. A. 2002. Survey of the South Carolina shrimp baiting fishery, 2001. South Carolina Department of Natural Resources, Marine Resources Division Data Report 39. 16 pp.

McCoy, E. G., and J. T. Brown. 1967. Migration and growth of commercial penaeid shrimps in North Carolina. North Carolina Department of Conservation and Development, Division of Commercial and Sports Fisheries, Special Scientific Report 11. 21 pp.

McKenzie, M. D., editor. 1981. Profile of the penaeid shrimp fishery in the south Atlantic. South Atlantic Fishery Management Council, Charleston, South Carolina.

Misamore, M. J., and C. L. Browdy. 1996. Mating behavior in the white shrimps *Penaeus setiferus* and *P. vannamei*: a generalized model for mating in *Penaeus*.—Journal of Crustacean Biology 16: 61–70.

Music, J. L. 1994. Assessment of Georgia's marine fishery resources. Completion Report for Award No. NA16F10020-03. Georgia Department of Natural Resources. 152 pp.

Ogle, J. T. 1992. A review of the current (1992) state of our knowledge concerning reproduction in open thelycum Penaeid shrimp with emphasis on *Penaeus vannamei*.—Invertebrate Reproduction and Development 22: 267–274.

Pauly, D., J. Ingles, and R. Neal. 1984. Application to shrimp stocks of objective methods for the estimation of growth, mortality and recruitment-related parameters from length-frequency data (ELEFAN I and ELEFAN II). Pp. 220–234 *in* J. A. Gulland and B. J. Rothschild, eds. Penaeid Shrimps—Their Biology and Management. Fishing News Books, Farnham.

Pérez Farfante, I. 1969. Western Atlantic shrimps of the genus *Penaeus*.—Fishery Bulletin (U.S.) 67: 461–591.

Renfro, W. C., and H. A. Brusher. 1982. Seasonal abundance, size distribution, and spawning of three shrimps (*Penaeus aztecus*, *P. setiferus*, and *P. duorarum* in the Northwestern Gulf of Mexico, 1961–1962. National Oceanographic and Atmospheric Administration Technical Memorandum. NMFS-SEFC-94. 37 p.

Sakaji, H. 2001. Maturation and spawning of the small penaeid shrimp *Metapenaeopsis dalei* in Tosa Bay, Pacific coast of southern Japan.—Fisheries Science 67: 444–448.

South Atlantic Fisheries Management Council. 1993. Fishery Management Plan for the Shrimp Fishery in the South Atlantic Region. S.A.F.M.C. Charleston, S.C. 84 p.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. The Principles and Practice of Statistics in Biological Research. W. H. Freeman and Company, San Francisco.

SPSS. 1997. SPSS Advanced Statistics 7.5. SPSS, Inc. 444 N. Michigan Ave. Chicago, Ill.

Taylor, C. C. 1953. Nature of variability in trawl catches.—Fishery Bulletin (U.S.) 54: 145–166.

Weymouth, F. W., M. L. Lindner, and W. W. Anderson. 1933. Preliminary report on the life history of the common shrimp *Penaeus setiferus* (Linn.).—Fishery Bulletin (U.S.) 48: 1–26.

Whitaker, J. D., L. B. DeLancey, and J. E. Jenkins. 1989. A study of the experimental closure of South Carolina's sounds and bays to commercial trawling. South Carolina Wildlife Department, Marine Resources Division, Technical Report 72. 54 pp.

Williams, A. B. 1955. A contribution to the life histories of commercial shrimps (Penaeidae) in North Carolina.—Bulletin of Marine Science of the Gulf and Caribbean 5: 116–146.

———. 1969. Penaeid shrimp catch and heat summation, an apparent relationship. FAO World Scientific Conference on the Biology and Culture of Shrimps and Prawns.—Food and Agricultural Organization Fisheries Reports 57: 643–656.

———. 1984. Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States. Smithsonian Institution Press, Washington, D.C.

Wyban, J. A., and J. N. Sweeney. 1991. Intensive Shrimp Production Technology: The Oceanic Institute Shrimp Manual. The Oceanic Institute, Honolulu, Hawaii. 158 pp.

RECEIVED: 19 July 2004.
ACCEPTED: 7 December 2004.