

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

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Abstract

The temporal pattern of reproduction and recruitment is described from monthly population samples (June, 1989 through November, 1990) of two penaeid shrimp species, *Trachypenaeus similis* (Smith) and *T. constrictus* (Stimpson), from an inshore location (Mississippi Sound near Horn Island) in the Northcentral Gulf of Mexico. The presence or absence of mating plugs (associated with mating and insemination) and ovarian maturity (an indicator of spawning) were used to examine breeding in adult females. Females with mature ovaries occurred in samples from April through October and November in *T. constrictus* and *T. similis*, respectively, with peak values in July to September in both species. The percentage of inseminated females fell to low or zero values in the late fall and winter, indicating a cessation of mating activity. Sexual maturity of males was indicated by fusion of the gonopodal endopods (petasma); mature males were present throughout the year in both species. Recruitment intensity was described as the percentage of juvenile individuals in monthly population samples of each species ("identifiable juveniles"). Very small *Trachypenaeus* juveniles, at a size closer to actual recruitment but too small to be identified to species ("unidentifiable juveniles"), were used in calculating another recruitment index based on combined monthly samples of both species. Both indices indicated that recruitment occurred throughout most of the year with no obvious seasonal pattern. The monthly spawning intensity of each species was highly correlated with water temperature at the month of sampling, indicating the possible importance of temperature as a proximate factor acting on gonadogenesis and spawning pattern. It is hypothesized that larval food supply may be an important ultimate factor or selective pressure acting on spawning seasonality in these penaeid shrimps. There were no statistically significant correlations between monthly estimates of spawn-

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ing intensity and recruitment using lag periods from one to 3 months, indicating a complex stock-recruitment relationship in these species.

Keywords: Gulf of Mexico; Penaeidae; Recruitment; Reproduction; Seasonality; Shrimp

1. Introduction

Proximate factors that both initiate and terminate breeding and spawning periods in marine invertebrates, such as temperature, light, and food availability to reproductive adults (Orton, 1920; Giese & Pearse, 1974; Sastry, 1983), are still inadequately identified and understood in many species. Likewise, the ultimate factors influencing reproductive patterns, i.e. the environmental conditions (selection pressures) which favor successful larval development and survival to recruitment, such as availability of food to planktonic larvae, and to which the timing of spawning periods have been adapted, are still poorly documented in marine invertebrates, including crustaceans (Sastry, 1983). Baker (1938) recognized that detailed basic studies on the temporal pattern of gonadogenesis and breeding were necessary first steps in the identification and explanation of the action of proximate and ultimate factors on reproduction. A similar rationale applies to an understanding of recruitment processes, especially regarding such fundamental issues as stock-recruitment relationships and predictability of recruitment pattern and success.

Although the non-commercial species of penaeid shrimps are abundant and ecologically important members of coastal and shelf habitats in the Gulf of Mexico, basic information on their temporal patterns of breeding and recruitment is virtually absent. Two such species are the shrimps *Trachypenaeus similis* (Smith) and *T. constrictus* (Stimpson). Brusher et al. (1972) reported on the monthly percentage of females of *T. similis* with "ripe" ovaries in a study based on composite samples taken over a 2-yr period from a variety of locations and depths in the Northwestern Gulf. Huff & Cobb (1979) made some limited observations on seasonality of insemination (presence of spermatophores on females) in *T. constrictus* taken from a variety of stations off western Florida. Subrahmanyam (1971) made more extensive observations about reproductive seasonality of "*Trachypenaeus* spp." and other penaeid species off the Mississippi coast, using larval abundances as an indicator of previous spawning. However, no detailed observations have been made on reproduction of and recruitment into populations of either *T. similis* or *T. constrictus*.

The purpose of this study was to determine the seasonal pattern of breeding in *T. similis* and *T. constrictus* from monthly trawl samples taken at a single location off Mississippi, USA. Breeding indices based on insemination and ovarian maturity were calculated for females, whereas sexual maturity in males was followed by observations of gonopodal fusion. In addition, information from size frequency distributions of juvenile and adult males and females from these samples was used to estimate the intensity and timing of juvenile recruitment into these shrimp populations.

2. Materials and methods

Monthly samples were taken from populations of *T. similis* and *T. constrictus* for 18 months (June 1989 through November 1990) in Mississippi Sound at the northwestern end of Horn Island, Mississippi, USA (30° 15' N, 88° 45' W), 9 km from the mainland. Poor weather conditions prevented sampling in July and October 1989. An otter trawl (head rope or mouth width of 5 m, with a bag-end mesh of 4 mm) was used to drag the bottom at a depth of 6–12 m. Sampling began just after sunset. Our goal was to obtain ≈ 300 individuals·species⁻¹ in each monthly population sample. After each trawl, all specimens of *Trachypenaeus* were removed from the trawl catch. When abundances were low, we made 10–15 trawls for 2–3 h in attempting to reach the desired sample size for each species. Sampled shrimp were immediately preserved in a 50% seawater formalin solution or in Davidson's solution (Shaw & Battle, 1957). Samples were later washed in tapwater and stored in 70% ethanol.

Measurement of surface water temperature taken at the time and site of collection concurred closely with surface and bottom temperatures obtained from the Gulf Coast Research Laboratory hydrological station (No. 83, Dog Keys Pass) one mile to the north of the sampling site. Since the sampled shrimp populations inhabit the bottom, we chose to use bottom temperature records from this hydrological station as an estimate of ambient water temperature for each month of sampling. Water temperature at the bottom varied from lows of 12–17 °C in the winter months to highs of 27–30 °C in the summer months.

Reproductive condition of females was determined by observations of ovarian maturity and insemination in preserved specimens. To make observations on the stage of ovarian development, the posterior lobes of the ovary were exposed by dissection into the first two abdominal segments (Cobb et al., 1973; Bauer & Rivera Vega, 1992) and examined with a stereomicroscope using 25× magnification. Ovaries were subjectively scored as in Cobb et al. (1973) on the basis of relative size, color, and size of oocytes as *undeveloped* (posterior ovarian lobes thin strands, transparent to opaque), *early developing* (ovarian lobes thickened cords, cream to light yellow in color), *late developing* (lobes medium-sized irregular cylinders, yellow to orange in color, oocytes clearly visible at 25×), and *ripe* (lobes large irregular cylinders, orange to brown-orange in color, oocytes clearly visible at 25×). Frequency distributions of different developmental stages of oocytes in the four ovarian stages were made by sampling pieces of ovaries visually scored to each of four stages from 10 females·stage⁻¹. A smear of each ovarian sample was made on a slide with a grid, and oocytes on grid sections (chosen at random until total oocytes observed > 100) were classified into developmental stages ($n = 80$ ovarian smears; overall mean No. oocytes observed·sample⁻¹ = 160; range of mean No. oocytes·sample⁻¹ = 140–172; total range of number of oocytes·individual·sample⁻¹ = 104–235). The developmental stages of oocytes were characterized and defined according to cytological characteristics and degree of vitellogenesis similar to those used by Cobb et al. (1973) and Bauer & Rivera Vega (1992) and from size (maximum diameter) taken from measurements of oocytes from preliminary samples of ovaries: *undeveloped* [mean diameter = 32.7 $\mu\text{m} \pm 15.3$ (SD) for *T. similis*, $n = 200$; 34.6 $\mu\text{m} \pm 16.3$ for *T. constrictus*, $n = 200$]; *early developing* (mean = 75.1 $\mu\text{m} \pm 12.9$ for *T. similis*, $n = 200$;

95.4 $\mu\text{m} \pm 19.7$ for *T. constrictus*, $n = 161$); late developing (mean = 134.4 $\mu\text{m} \pm 25.7$ for *T. similis*, $n = 102$; 176.8 $\mu\text{m} \pm 21.7$ for *T. constrictus*, $n = 100$), and ripe (mean = 220.3 $\mu\text{m} \pm 32.0$ for *T. similis*, $n = 100$; 227.8 $\mu\text{m} \pm 25.4$ for *T. constrictus*, $n = 67$).

Two measures of female breeding activity were calculated in each species for each month: (a) percentage of adult females with *mature* ovaries and (b) percentage of adult females that were inseminated. We followed Cobb et al. (1973), Kennedy et al. (1977) and Bauer & Rivera Vega (1992) in grouping *undeveloped* and *early developing* ovaries as *immature*, with *late developing* and *ripe* ovaries grouped as *mature* (approaching or imminent spawning). In order to calculate the percentage of *adult* females with a *mature* ovary or which were inseminated in monthly samples, we had to select a minimum size above which females were considered to be *adult*, i.e. capable of breeding. To do so, we chose the smallest size class which contained a female with a *mature* ovary as the lower size limit for adult females (10.5 mm C.L. for *T. similis* and 7.5 mm C.L. for *T. constrictus*). The size of the smallest inseminated female was very close to that of the smallest female with a mature ovary in both species. Therefore we used the same minimum size to define "*adult female*" in making calculations of percentage of adult females inseminated.

Observations were taken on all females for insemination, recognized by the presence of a mating plug protruding from the genital area, the thelycum (Bauer & Lin, 1993). Sexual maturity of males in penaeids is indicated by fusion of petasmas (gonopodal endopods) (Pérez Farfante, 1969), and accordingly all males were checked for presence or absence of petasma fusion.

Size of all individuals was measured as carapace length (C.L.), defined as the chordal distance from the posterior edge of the eye orbit to the posterior mid-dorsal edge of the carapace. Size frequency distributions were constructed separately for males and females using 0.50 mm C.L. size intervals.

The intensity of recruitment of juveniles was estimated by calculating the percentage of juvenile individuals in each monthly sample. Two categories of juveniles were recognized in making two different estimates of recruitment. In the first, recruitment was defined as the percentage of juveniles that could be identified to species ("*identifiable juveniles*") of the total number of individuals in each monthly sample for each species. In each species, juvenile size classes were defined separately for males and females because of sexual dimorphism at size of sexual maturity. For females, the size classes smaller than that containing the smallest female with a mature ovary were considered juvenile size classes (< 10.5 mm C.L. for *T. similis*, < 7.5 mm C.L. for *T. constrictus*). In males, size classes smaller than that containing the smallest male with a fused petasma (gonopod) were classified as juvenile for the purpose of recruitment estimates (< 7.5 mm C.L. in *T. similis* and < 5.0 mm C.L. in *T. constrictus*).

In some months, samples included smaller individuals (3–6 mm C.L.) of *Trachypena* that could not be identified reliably to species because genital characters (Pérez Farfante, 1971, 1988) were not sufficiently developed. These "*unidentifiable*" juveniles were used to make an estimate of "*generic*" recruitment, calculated as the percentage of "*unidentifiable Trachypena juveniles*" in total population samples of *Trachypena* (individuals identified as *T. similis* and *T. constrictus* plus the unidentifiable juveniles).

Spearman pairwise rank correlation coefficients were calculated to test the hypotheses (a) "There is no correlation between water temperature (at the same months n of sampling; at months $n-1$, $n-2$, and $n-3$) and percentage of adult females with mature ovaries at months n " and (b) "Recruitment values for "identifiable juveniles" at months $n+1$ ($n+2$; $n+3$) are not correlated with values for percentage of females with ripe ovaries at months n ." Our use of lag periods of one to 3 months for testing of possible correlations between spawning (incidence of females with mature ovaries) and recruitment of "identifiable juveniles" was based on approximations for the periods (a) from appearance of mature ovary to spawning (one month or less in a penaeid; Linder & Anderson, 1956) and (b) for completion of larval development to recruitment (one month, based on Pearson, 1939 and Dall et al., 1990).

3. Results

3.1. Oocyte composition of visually scored ovarian stages

The size frequency distributions of different developmental stages of oocytes from samples of visually scored ovarian stages are given in Fig. 1 for *T. similis* and *T. constrictus*. In undeveloped ovaries, principally undeveloped and also some early developing oocytes were found. In early developing ovaries, the proportion of early developing oo-

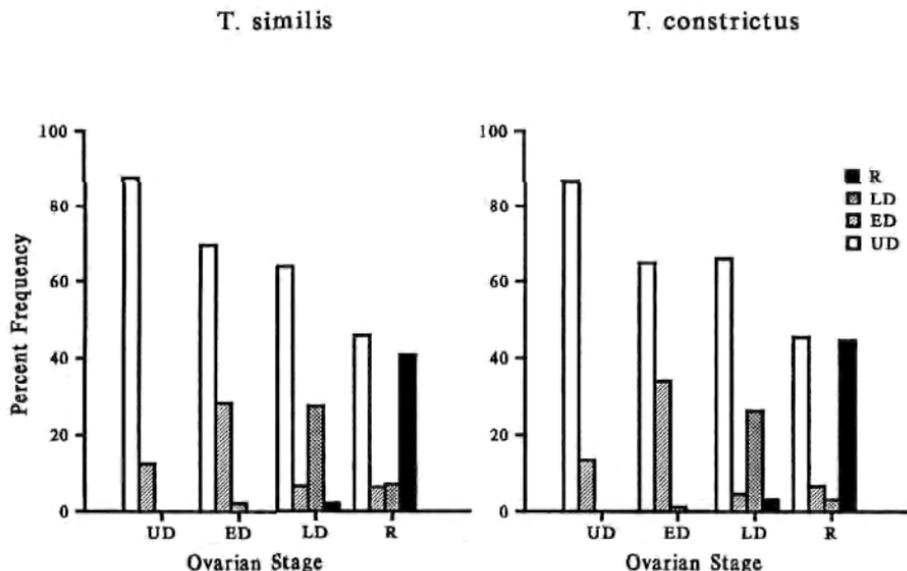


Fig. 1. Size frequency distributions of different developmental stages of oocytes made from samples of ovaries scored visually into different stages of ovarian maturity in *T. similis* and *T. constrictus*. Histogram bars represent mean percent frequency of oocyte stages based on samples from 10 females for each ovarian stage. For oocyte and ovarian stages, UD = undeveloped, ED = early developing, LD = late developing, and R = ripe. Histogram bars for UD, ED, LD, and R oocyte stages are unfilled, hatched, crosshatched, and filled, respectively.

cytes increased, and a few *late developing* (vitellogenic) oocytes were encountered. In *late developing* and *ripe* ovaries, *late developing* and *ripe* (vitellogenic oocytes with cortical granules) were the dominant oocyte types, respectively, other than *undeveloped* oocytes, which were well represented in all ovarian stages.

Trachypenaeus similis

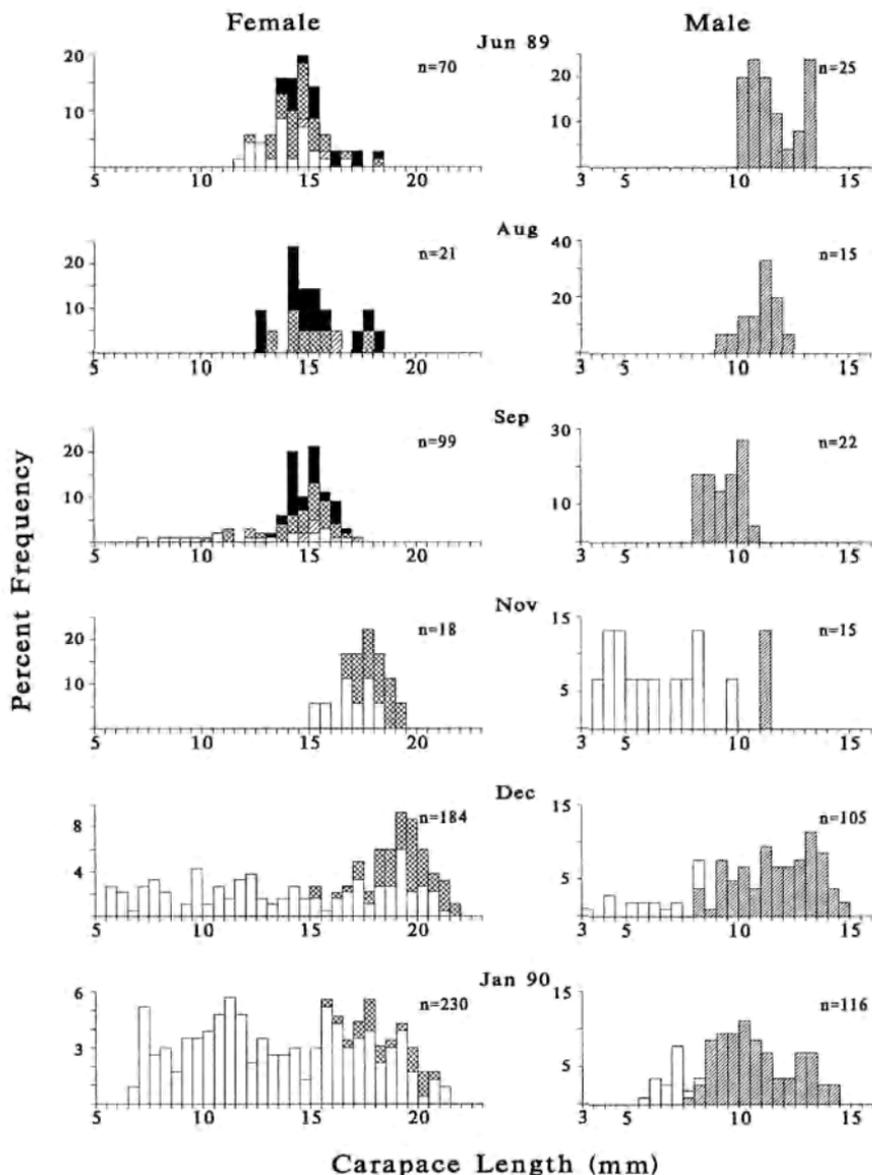
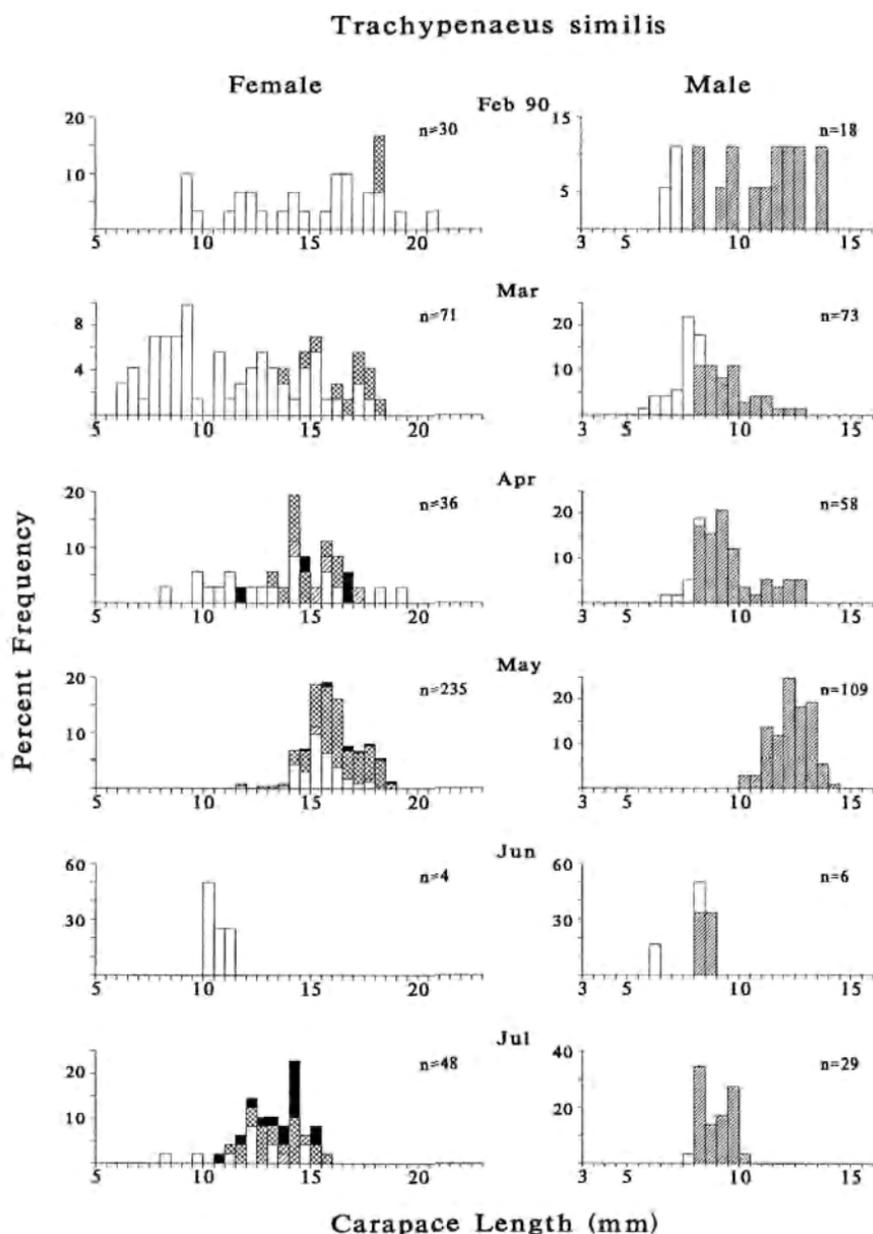


Fig. 2.

3.2. Breeding patterns

Reproductive condition of males and females is illustrated in size frequency distributions made from monthly collections of *T. similis* (Fig. 2) and *T. constrictus*



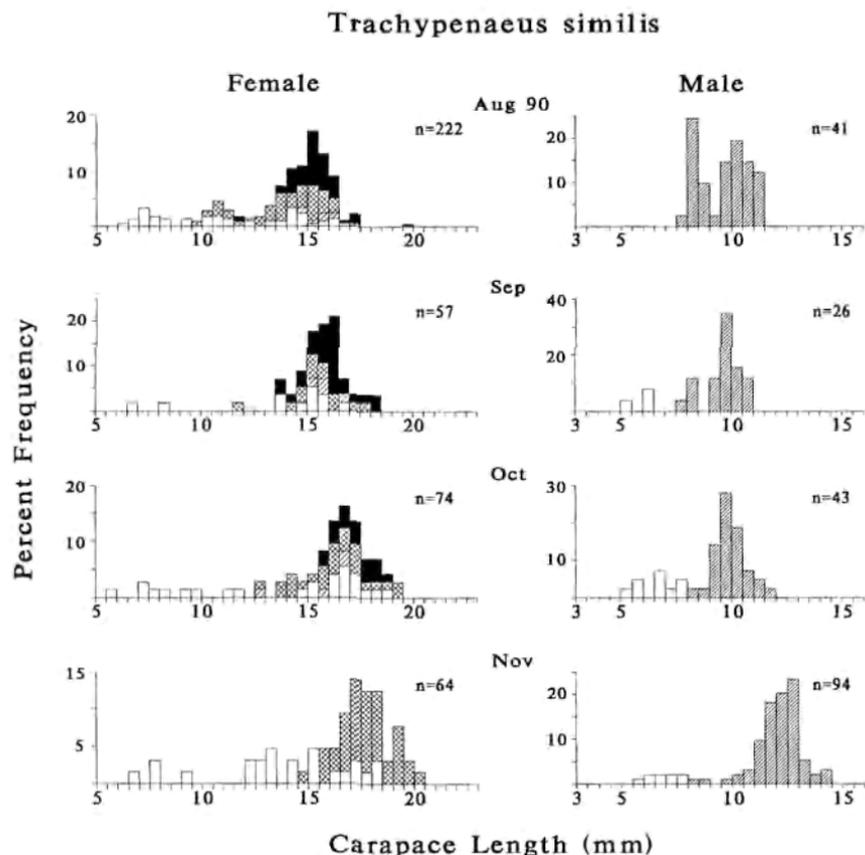


Fig. 2. Monthly size frequency distributions of females and males of *T. similis* showing reproductive condition for June 1989 through November 1990 except for July and October 1989, months in which a sample could not be taken. For females, unfilled bar = uninseminated with immature ovary; hatched bar = uninseminated with mature ovary; crosshatched bar = inseminated with immature ovary; filled bar = inseminated with mature ovary. For males, unfilled bar = petasma unfused; hatched bar = petasma fused.

(Fig. 3). Males with fused petasmata (gonopods) were found throughout the year in both species (Figs. 2–3). The temporal pattern of ovarian maturity is summarized for both species in Fig. 4, with more detailed information in Figs. 2–3. No *T. similis* females with mature ovaries were found from November 1989 through March 1990 nor again in November 1990, the last month of sampling. The period of low ovarian activity in *T. constrictus* was similar, from November 1989 through March 1990, and including October and November in 1990. Females with mature ovaries began to appear in April 1990 for *T. similis* and, less abundantly, in April and June 1990 for *T. constrictus* (Figs. 2–4). Both the June 1989 and May 1990 samples for the latter species showed no females with mature ovaries, but the sample sizes were quite small (Fig. 3). The June 1989 sample of *T. similis* (Fig. 2) showed a value for percentage of adult females with mature ovaries nearing 30% (Fig. 4), but no comparison can be made with the June

Trachypenaeus constrictus

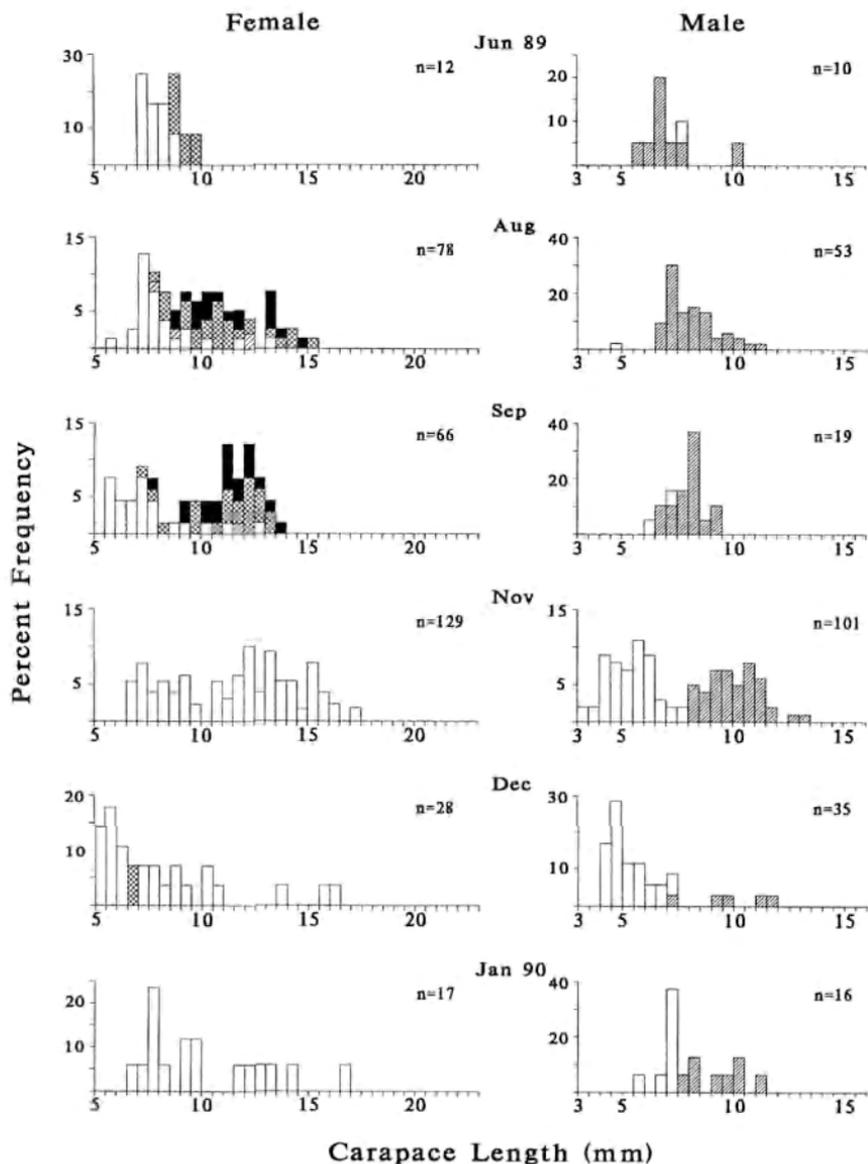


Fig. 3.

1990 sample which was quite small (Fig. 2). In both species, July to September 1990 were peak months in which >30% of adult females had mature ovaries. Values for August and September showed similar highs in 1989 and 1990. In October 1990, a high percentage of *T. similis* females still had ovaries with abundant postvitellogenic oocytes

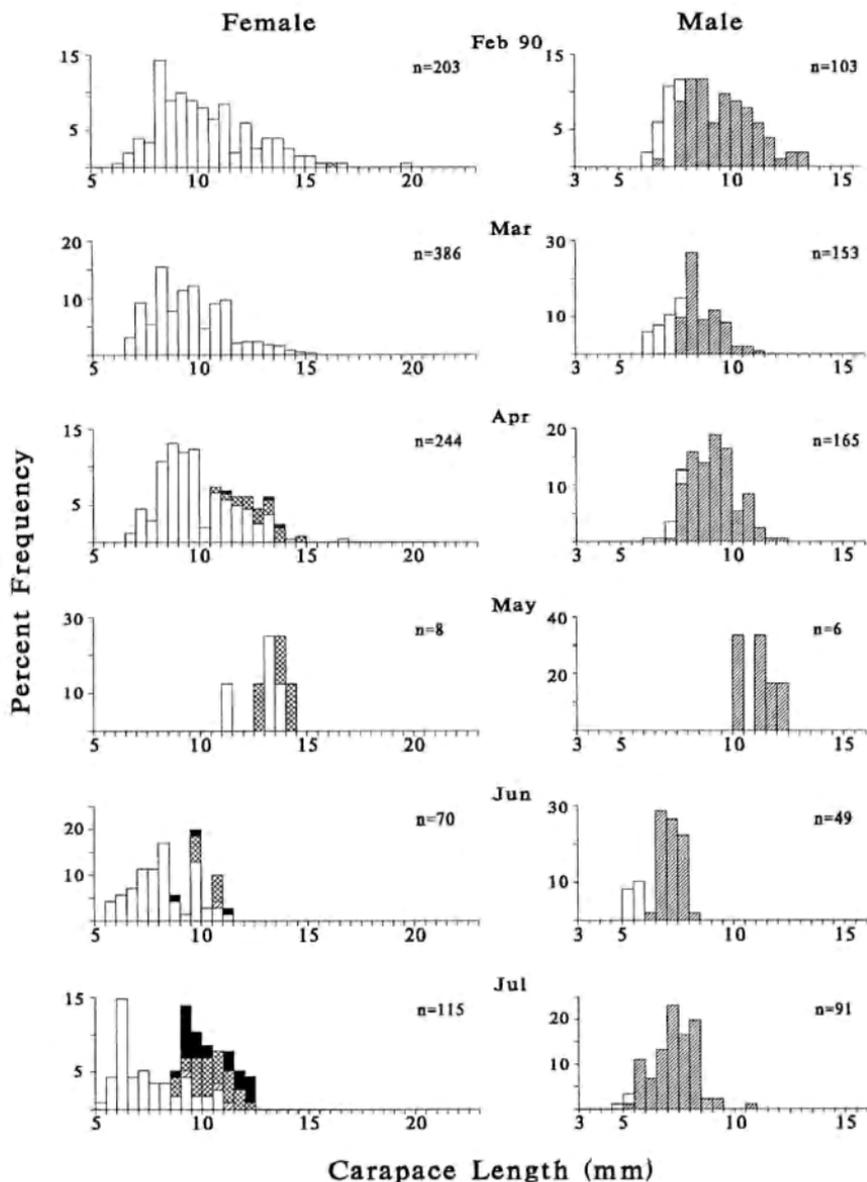
Trachypenaeus constrictus

Fig. 3.

(Fig. 4), but in *T. constrictus* there were no pre-spawning females (Figs. 3–4). In November 1990, as in November 1989, all adult females of both species had immature (non-vitellogenic) ovaries (Figs. 2–4).

Insemination (presence or absence of mating plugs) in adult females followed a

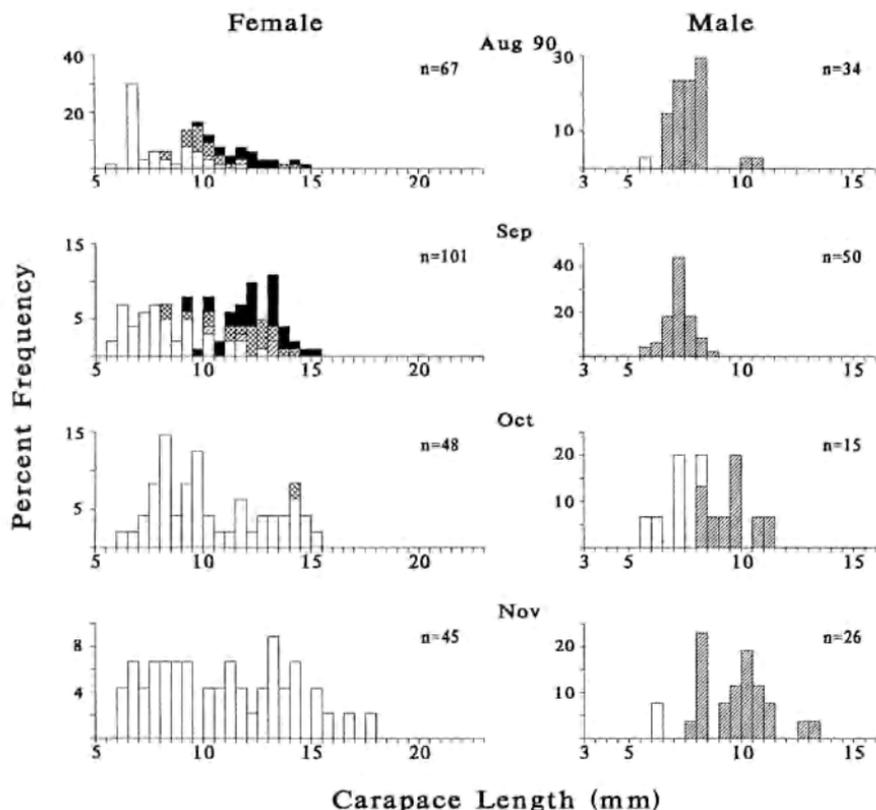
Trachypenaeus constrictus

Fig. 3. Monthly size frequency distributions of females and males of *T. constrictus* showing reproductive condition for June 1989 through November 1990 except for July and October 1989, months in which samples could not be taken. Histogram legend same as for Fig. 2.

pattern similar to that for ovarian maturity but it was more expanded in time (Fig. 5). In *T. similis*, inseminated adult females were found in all monthly samples, but the lowest proportion of inseminated females took place in the winter months when females lacked mature ovaries, with an increase in the spring to highs in the summer and autumn months. In *T. constrictus*, there were several months (November 89 through March 1990, October and November 1990) in which adult females lacked mating plugs (Fig. 5). Inseminated females of *T. constrictus* began to show up in samples in April 1990. Values for percentage of inseminated females were highest in *T. constrictus*, as in *T. similis*, in the summer and early fall, but fell to nearly zero in October 1990. No inseminated females were taken in November 1989 nor November 1990 (Fig. 5).

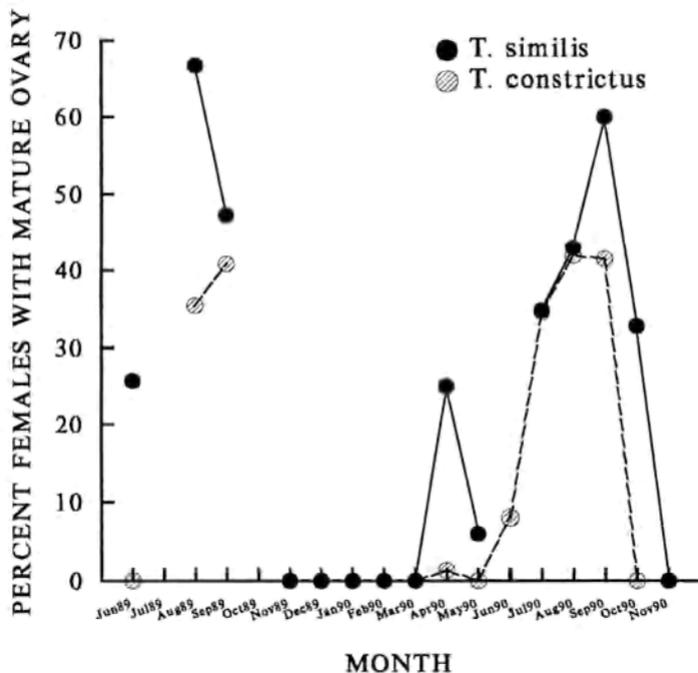


Fig. 4. Temporal pattern of ovarian maturity in *T. similis* (solid lines and filled circles) and *T. constrictus* (dotted lines and hatched circles), showing the percentage of adult females with mature ovaries in each month. Zero values for *T. similis* are placed on the zero line while those for *T. constrictus* rest just above it (the April value is 1.3%). No samples were taken in July and October 1989. The June 1990 sample for *T. similis* contained only two females of reproductive size and is not included.

3.3. Recruitment

Recruitment estimates for *T. similis* and *T. constrictus* based on “identifiable” juveniles showed no evident seasonal patterns, with some recruitment throughout the year except for June and August 1989 in *T. similis* and May 1990 for both species (Fig. 6). Highest recruitment occurred in December 1989 for *T. constrictus*, and there were peaks in November 1989, March 1990 and June 1990 for *T. similis*.

Using the recruitment index based on generally smaller *Trachypenaeus* juveniles which could not be identified to species (“unidentifiable juveniles”), recruitment peaks can be identified in August 1989 and November 1989 through January, perhaps February 1990 (Fig. 6). However, the highs of August and November 1989 were not repeated in August and November 1990, when there was no or very low recruitment as measured by this index. Other months of no recruitment of the small “unidentifiable” juveniles were June 1989 and April, May, and September 1990.

3.4. Tests of possible correlations among temperature, breeding, and recruitment values

In both species, the highest correlation between values of temperature and ovarian maturity were those taken at the month of sampling ($r_s = 0.79$ for *T. similis*, $= 0.78$ for

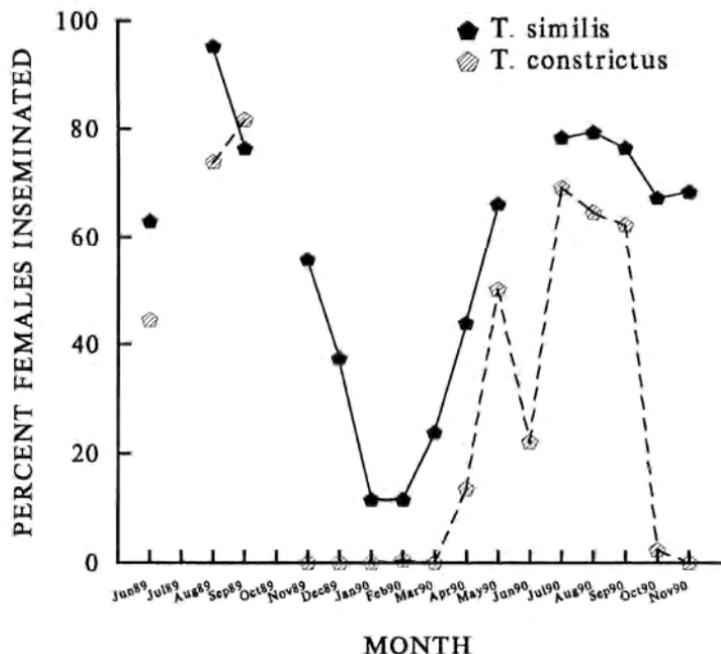


Fig. 5. Temporal pattern of insemination in *T. similis* (solid lines and filled pentagons) and *T. constrictus* (dotted lines and hatched pentagons), showing the percentage of adult females with mating plugs for each month. No samples were taken in July and October 1989. The June 1990 sample for *T. similis* contained only two females of reproductive size and is not included.

T. constrictus, $n = 16$, $p < 0.001$ in both cases). Using temperature values for the month prior to the month of sampling, correlations were lower but still statistically significant ($r_s = 0.76$ for *T. similis*, $n = 13$, $0.001 < p < 0.005$; $r_s = 0.55$ for *T. constrictus*, $n = 13$, $p = 0.05$). Correlations calculated with temperature values from 2 and 3 months previous to sampling dates were not statistically significant in either species ($p > 0.10$, $n = 13$).

A possible relationship between spawning (as approximated by percentage of females with mature ovaries) and subsequent recruitment of "identifiable juveniles" into the shrimp populations sampled was examined, using 1, 2, and 3 month lag periods between spawning intensity for a given month and subsequent recruitment. The null hypothesis of no correlation was accepted ($p \geq 0.10$) in all cases for both species.

4. Discussion

The spawning pattern of these nearshore (9 km from the mainland) populations of *T. similis* and *T. constrictus* at a subtropical-temperate latitude (30°N), approximated by the presence of females with mature (near spawning) ovaries, was decidedly seasonal. The major peak in occurrence of pre-spawning females took place in the summer (July to September), beginning in April and terminating by October in *T. constrictus*

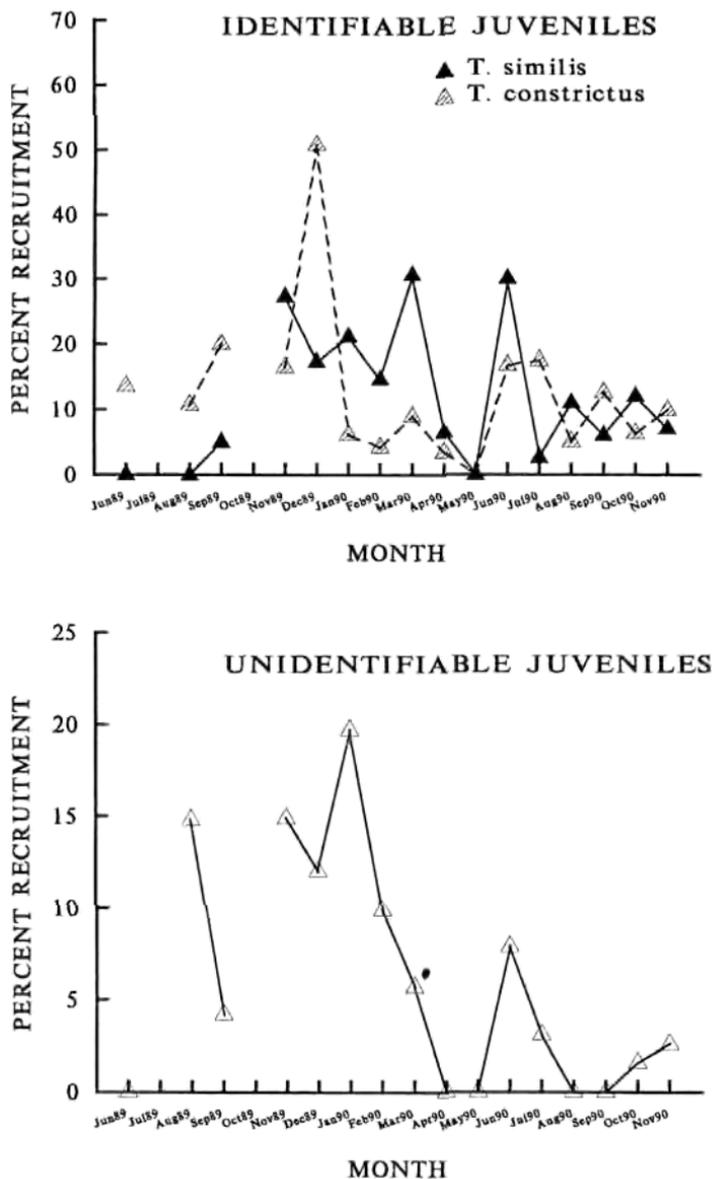


Fig. 6. Temporal pattern of recruitment in *T. similis* (solid lines and filled triangles) and *T. constrictus* (dotted lines and hatched triangles) (upper graph), showing percentage of identifiable juveniles in monthly samples of each species, as well as the percentage of unidentifiable *Trachypenaeus* juveniles (lower graph) in the combined sample of both species for each month. No samples were taken in July and October 1989.

and in November in *T. similis*. Subrahmanyam (1971) used abundances of planktonic eggs and larvae as an indicator of spawning in several species of penaeid shrimps off the Mississippi coast, including "*Trachypenaeus* spp." His results indicated a spawn-

ing period for *Trachypenaeus* spp. from April to November, concordant with our observations, in which ovarian maturity was used as an indicator of spawning. Our results indicate a single strong summer peak in spawning for both species at this inshore location.

Brusher et al. (1972) looked at the temporal distribution of females of *T. similis* with "ripe" ovaries in samples integrated from various locations and depths (all greater than those sampled in our study) throughout the Northwestern Gulf of Mexico. His results indicated low level spawning throughout the year, without any major peaks. Studies on a variety of *Penaeus* species in the Gulf and along the eastern US coast have indicated that breeding seasons within a species are more extended in populations (a) from deeper water at the same latitude where bottom water temperatures in winter are higher than those inshore and (b) from more southerly locations (reviews in Pérez Farfante, 1969; Williams, 1984; Dall et al., 1990).

Seasonal patterns of frequency of inseminated females followed the pattern of frequency of females with mature ovaries. In both species, the absence (*T. constrictus*) or reduction (*T. similis*) of insemination in females during the fall and especially winter months probably reflects a period of molting, after which the mating plug and stored sperm are lost (Bauer & Lin, 1993), without a mating until the following spring. The spring mating would have to be preceded by another molt, since mating occurs just after molting of the female in these "closed thelycum" species (Bauer, 1991, 1992a, pers. obs.). The inseminated females of *T. similis* captured in the winter may be individuals that molted and mated in the late summer or in the fall which then went through the winter without molting (and loss of mating plug), although a winter molt followed by mating and insemination cannot be ruled out by the information available.

Several studies on penaeid reproduction have indicated that variation in water temperature is an important proximate factor acting on spawning (Linder & Anderson, 1956; Pérez Farfante, 1969; Williams, 1984). In both *Trachypenaeus* spp. in this study, the incidence of females with mature ovaries was highly and positively correlated with bottom temperatures of the month of sampling. Correlations between incidence of reproductive females and water temperatures of one or more months preceding sampling were lower or statistically non-significant. These results indicate that if water temperature is indeed the proximate factor stimulating ovarian maturation (and not some other environmental factor that is correlated with it), increases or decreases in water temperature may act relatively quickly (one month or less) in promoting or inhibiting ovarian development in these *Trachypenaeus* spp., as suggested by Linder & Anderson (1956) in their study of spawning in *Penaeus setiferus*.

The hypothesis that food availability for larvae is a major ultimate factor selecting for seasonality in reproduction has been addressed by a variety of studies and reviews dealing with reproductive periodicity in invertebrates with planktotrophic larvae (e.g. Thorson, 1950; Giese & Pearse, 1974; Sastry, 1983; Bauer, 1989, 1992b; Pearse et al., 1991; Bauer & Rivera Vega, 1992). There is a dearth of information on the seasonality of phyto- and zooplankton abundance in Mississippi Sound. However, Moncreiff et al. (1992) described phytoplankton production for one year in 1989–1990 from shallow water near (50–200 m) our sampling site. They found phytoplankton production was greatest from June to September (highest values in August) with low produc-

tion from October through April (lowest in January). This pattern is similar to that of the highs and lows in ovarian maturity, our indicator of spawning, in the *Trachypenaeus* spp. in this study, suggesting that seasonality of larval food supply (as indicated by phytoplankton production) may be an important selective pressure that has acted in the temporal pattern of spawning in *Trachypenaeus* and other penaeid species.

Two indices were used to estimate recruitment, one based on very small *Trachypenaeus* juveniles whose genital structures were not sufficiently developed to permit species identification and another based on juveniles large enough to be identified to species. The index based on “unidentifiable juveniles” is a truer measure of recruitment in the sense that these very small juveniles had entered the benthic populations more recently from the plankton, but since specific identification was not possible, species-specific trends, if any, are obscured. However, no striking seasonal trends in recruitment were evident either in “identifiable juveniles” of *T. similis* or *T. constrictus* or in the smaller “unidentifiable juveniles.” The highest values in both indices tended to occur in the winter and early spring; however, there was a major recruitment of “unidentifiable” juveniles in August 1989.

We attempted to correlate the pattern of spawning (as indicated by ovarian condition of females) with recruitment using an appropriate lag period between “spawning” and subsequent recruitment. However, there were no correlations between “stock” and “recruitment” using lag periods from one to three months. Stock-recruitment relationships are notoriously variable, given the number of life stages between spawning and recruitment and the number of environmental factors acting on them (Yoshioka, 1986). Even if the populations sampled (or nearby populations with similar spawning patterns) are the spawning stock for their own recruits, which is not at all certain, the episodic recruitment of these seasonally spawning *Trachypenaeus* populations indicates a complex and variable stock-recruitment relationship, as many studies on penaeid shrimps have indicated (e.g. Crocos & Kerr, 1983; Potter et al., 1989; Dall et al., 1990).

Dall et al. (1990) cited *Trachypenaeus* as one of several penaeid genera with a “Type 3 life cycle” in which recruitment and juvenile stages occur in inshore waters while adults move offshore for spawning. However, it is apparent from this study from an inshore location that recruitment, growth to maturity, mating, and spawning may all take place in nearshore waters in both *T. constrictus* and *T. similis* without an offshore spawning migration.

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