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Density Dependent Sex-reversal in Pink Shrimp, *Pandalus Borealis*, on the Scotian Shelf

by

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ABSTRACT

On the Scotian Shelf, transition of *P. borealis* from male to female occurred at different sizes and ages, and could not be related to a minimum size, age, or number of instars. Our data do not show the positive relationship between density of older females and size at sex transition predicted by sex allocation theory. Size at transition was inversely related to density, which was attributed to density dependent growth affecting all stages. Density appears to become increasingly important as a factor determining growth as densities increase, while at low densities, other factors, including temperature, are also involved. We concluded that males have a growth related physiological threshold at which they are obligated to enter the transitional phase and that final maturation to the female is associated with a separate size related threshold. Transition is a growth phase that is extended in areas of early male maturation until the female threshold is attained. In warmer areas where the difference between male and female thresholds are great the benefits of protandry are decreased and the population may regress to the dioecious state, resulting in more Primary Females.

INTRODUCTION

Pandalus borealis is a protandric hermaphrodite, changing to the female after 1-4 years as a male, depending on geographic location and local conditions (Shumway *et al.* 1986). Pandalid shrimp have been used as a “model” in theories about the environmental, genetic and evolutionary mechanisms determining sex allocation in organisms. Theories on the adaptive value of protandry range from the increased reproductive efficiency of small males and large females (Warner 1975) to no adaptive value, or even negative effects in some situations (Carpenter 1978). The species is the target of an important fishery in the North Atlantic and North Pacific. Despite the important role that protandry must play in the population dynamics of the species, the factors which determine size and age of sex change are not considered in stock assessments except implicitly e.g. egg per recruit analysis.

Charnov *et al.* (1978) offered empirical evidence that *P. jordani* off Oregon and Northern California actively alters the age at which it changes sex in response to changes in age composition of the population, in accordance with sex allocation theory and genetic models. They found a negative correlation between the female proportion of *Pandalus jordani* first time breeders (also called primary females) and the ratio of older breeders (both males and females) to first breeders. In other words, as the proportion of older breeders decreased, the population compensated for the decrease in reproductive capacity by lowering the age at sex change. Charnov (1981) argued that the increased numbers of primary females (i.e. decrease in age at sex change) of *P. borealis* in the Skagerak observed by Jensen (1967) were caused by a decrease, through

fishing, in older breeders according to sex allocation theory. Charnov and Anderson (1989) proposed that, at a single location, shrimp have neither a fixed size or age at sex change and, as further evidence to the aged-based analysis presented in Charnov (1978) showed that annual fluctuations in population *size* distribution (as measured by the mean size of breeding individuals) was *positively* correlated to the size at sex change. In other words, as the mean size of breeding animals decreased, due to increased mortality of older, larger breeders through fishing or environmental factors, the size at sex change also decreased. On the other hand, Bergstrom (1997) found no evidence that annual variation in age/size structure affected the time at sex change in *P. borealis* from enclosed fjordic populations, however, his study encompassed a short time series. In view of the controversy surrounding size/age of sex change in Pandalid shrimp and its potential importance in population dynamics, we examined possible factors influencing sex change in Scotian Shelf shrimp and discuss their implications to stock assessments and management in the area. The Scotian Shelf is an excellent area for such a study as it harbours a small, isolated stock that has shown relatively high, year-classical fluctuations in abundance. In addition, exploitation rates are low (<10% Koeller et al 1997).

MATERIALS AND METHODS

Shrimp surveys were conducted on the eastern Scotian Shelf shrimp holes (Figure 1) by the Department of Fisheries and Oceans' Research vessel *E.E. Prince* in spring (April-May) and fall (October-November) of 1982-88 inclusive, and in June 1995-97 by commercial vessels. For all surveys, at least 45 thirty minute trawl sets were conducted during daylight hours, allocated approximately equally among the main shrimp holes (Canso, Louisbourg and Misaine). In 1995-97 additional coverage (approx 15 sets annually) was obtained for the inshore shrimp grounds (The Noodles). Stations were allocated randomly within each of the four areas except in Misaine Hole, where the same stations were fished due to difficulties finding trawlable bottom. *E.E. Prince* used the same trawl (Yankee 36 shrimp trawl, 40 mm codend mesh) throughout its series, however, three different commercial vessel/trawl combinations were used from 1995-97, requiring comparative fishing experiments in 1996 and 1997 to allow comparison with the 1995 vessel in terms of catch rates and size selectivities (Koeller *et al.* 1996, 1997). Since there is no comparative fishing data between vessels/gears used in 1982-88 and 1995-97 it is not possible to directly compare these two series in terms of densities, but because the same codend mesh size (40mm) was used for both series, selectivities were assumed to be reasonably similar.

Samples of approximately 500 animals were collected from each station and frozen for determinations of length, individual weights and sex/developmental stage. Carapaces were measured to the 0.1mm and aggregated into 1mm cells. Shrimp were identified as immature, male, transitional, primiparous or multiparous females, with transitional and primiparous animals representing the new females of that year. Transitional animals were rare in fall surveys, and only spring surveys were used in analyses requiring summarized data on transitionals. Densities in numbers/square meter from each set were calculated from the total weight caught, mean individual shrimp weights from a subsample, and the area swept by the trawl. Swept area was calculated from distance traveled during the tow and the wingspread of the trawl determined from trawl design specifications (1982-88) or actual measurements during the set using SCANMAR (1995-97). Bottom temperatures on the shrimp grounds during the study period were collected on shrimp and groundfish surveys using a variety of instrumentation including reversing thermometers, CTDs and continuous temperature recorders. Observations during the 1982-88 period were only taken sporadically during some surveys, so analysis involving temperature were limited to a subset of those observations where temperatures were available.

RESULTS

In general, water temperatures on the eastern Scotian Shelf shrimp grounds decreased throughout the 17 yr study period (1982-98), particularly during the *E.E. Prince* survey series (1982-88). Except for Louisbourg Hole water temperatures during the recent commercial survey series (1995-97) were among the coldest recorded (Figure 2). Louisbourg Hole generally has the warmest water of the 4 surveyed shrimp areas, probably due to the close proximity of this area to the warm deep water of the Laurentian Channel.

Biomass trends from shrimp surveys are in general agreement with the commercial CPUE index from Gulf commercial trawlers, the only continuous index of abundance throughout the study period (Figure 3). Abundance decreased during the early 1980's, bottomed out in the mid 80's, and increased thereafter, a pattern which has been attributed to opposite trends in groundfish predator abundance, especially cod (Koeller, in press). In summary, the 1982-88 period is one of both decreasing temperatures and abundance, while the later period is characterized by high abundance and continuing low temperatures. Falling temperatures in 1982-88 would tend to decrease growth rates, while decreasing densities would have the opposite effect. In 1995-97, both high densities and low temperatures would tend to decrease growth rates.

Since primary females are rare on the Scotian Shelf, changes in their abundance relative to females which have changed sex cannot be determined as in Charnov (1978), so the size based analysis presented in Charnov and Anderson (1989) was used. Because transitional animals were identified in our samples we were able to use actual mean size at transition rather than size at 50% female (spring surveys only). As in Charnov and Anderson (1989) we found a highly significant correlation between size at transition and the mean size of breeding adults (males and females, Figure 4A) which they presented as evidence that the size at transition "tracks" annual changes in the population size distribution according to sex allocation theory. However, Figure 4B-D also show highly a significant correlation between these parameters within years. Most observations from Louisbourg Hole are in the upper right quadrant, consistent with the warmer temperatures and expected faster growth rates in this area. Consistently larger overall mean carapace length in Louisbourg Hole throughout the study period is further evidence of faster growth rates here (Figure 5A). Increasing overall mean length during 1982-88 suggests that growth rates were increasing, possibly in response to decreasing densities. Separate mean lengths for males, transitionals and females show similar patterns, indicating that all stages were affected by a common influence (Figure 5B-D). Note however, that transitionals increased in size much more rapidly than either males or females (Figure 5E). Mean carapace lengths for the population and each stage remained high during the latter period (95-97) suggesting continuing high growth rates despite very high densities. However, examination of modes shows 3-5 modes during the first, and only 2-3 modes during the second period, indicating that males, transitionals and females in the recent period while as large or larger than in the mid 1980's, were a year older. This was confirmed by modal analysis of 1988 and 1995 data (Figure 6).

In order to determine if the density of older (multiparous) females was related to the size at transition we regressed the mean size of transitional animals in each area against the abundance of multiparous females for the 1982-88 spring survey data (annual means for each area, Figure 7A). The relationship is significant at $p < 0.05$, but with a negative slope. In other words, as the abundance of older females decreases, the size at transition increases, a result which is opposite to that predicted by sex allocation theory. The relationship between overall mean carapace length (i.e. all stages) and total density for both spring and fall surveys (annual means for each area, Figure 7B) was also highly significant, indicating that the relationship between size at transition and multiparous female density is probably due to density dependent growth of the entire population. A highly significant correlation between carapace length and density for each fishing set of the 1982-88 and 1995-97 survey series shows that the density dependent effect has a small scale spatial component. R-squared increases when the shrimp holes are included in a multiple regression, with density, temperature and area explaining nearly 50% of the variance in the model in the 1995-97 series. The 1982-88 series also showed that cruises contributed significantly to the variance, presumably because some cruises showed stronger relationship between carapace length and density. Note that in both periods density was more important than temperature in explaining the variance around the model when all densities are included in the analysis. However at low densities (< 1 animal per square meter, 1995-97 data) temperature was more important, and the correlation is positive as expected. The characteristic decreasing pattern of residuals for the length *versus* density scatter diagram (Figure 7C & D) also indicates that density becomes increasingly important as a determinant of carapace length (i.e. growth) as density increases, while other factors, including temperature, become more important as densities decrease.

Deviation analysis (Skuladotir 1981) on the 1982-88 data series in combination with sex determination (Figure 8) provides additional information on the relationship between growth rates, density, and size/age at sex change. The 1980 year-class (born in the spring) was the largest during the period. In the spring of 1984 most of this year-class was still immature, but by fall it had matured into males. It remained male during 1984. In spring 1985 a portion of this year-class changed to females, but as much as half remained male until the

following spring. Consequently, some of this year-class changed sex at age 5, after 2+ years in the male phase, while the remainder changed sex at age 6, after 3+ years in the male phase. The preceding year-class (1979) was relatively small and changed sex in the springs of 1983 and 1984, at age 4 and 5. In the spring of 1987 males, were distributed among three year-classes, including the relatively large 1982 and 1984 year-class, and the small 1983 year-class. Both the 1982 year-class and 1983 year-class changed sex in spring 1987 and 1988 at ages 5-6 and 4-5, respectively leaving only one year-class of males (1984). Growth rates of the 1979, 1980 and 1982 year-classes are given in Figure 9A, and of the 1982 year-class in the three shrimp holes in Figure 9B. Although the higher temperatures in Louisbourg Hole resulted in slightly higher growth rates, this increase was small relative to the density effect between year-classes.

DISCUSSION

The present study indicates that the results presented by Charnov and Anderson (1989) as evidence that Pandalid shrimp actively change the size of sex reversal according to sex allocation theory can simply be explained as interannual and local differences in growth rates. Bergstrom (1997) also rejected Charnov's proposal, however, his conclusions were based on negative results from a short (4yr) time series with limited spatial coverage.

Our results also show that the size at sex reversal is inversely related to the density of older females, opposite to that predicted by sex allocation theory, and that this relationship is a density dependent growth effect that applies to all sizes and stages, not just transitionals. The adaptive advantage to Pandalids of actively changing size at sex reversal as described by Charnov (1978) is that the loss of egg production from increasing mortality of females is offset by decreasing size at sex change. The negative correlation with density we observed has the same result in terms of egg production, without the need to assume that males actively regulate their length at sex change to the density of females in their vicinity, perhaps by detecting the concentration of female chemical signatures in the surrounding water. Since the average size of females increases as their density decreases and fecundity is positively correlated to size (Shumway *et al.* 1986), average egg production per female still increases with decreasing female densities. Our results do not, of course, refute sex allocation theory itself as described by Charnov (1978), but they do indicate that Pandalids are in inappropriate model for demonstrating its principles.

The advantage of protandry as proposed by Warner (1974) is that less energetically demanding sperm are produced by small animals, while the more energetically demanding eggs are produced by the largest members of the population. In addition, egg production is directly related to size of females, so a larger female has a selective advantage. The observed "growth spurt" of transitionals on the Scotian Shelf suggests that this stage furthers the advantages of protandry by producing the largest females possible under the prevailing environmental constraints. It is reasonable to assume that a species which has evolved to make the largest individual of the population female would also have physiological/ecological mechanisms that ensured the current population of females was as large as possible.

Our results support Charnov and Anderson's (1989) conclusion that Pandalids have neither a fixed size or age at sex reversal. On the Scotian Shelf size at transition increased during a period of increasing growth rates, yet it remained high during a period of slower growth because shrimp remained male for an additional year's growth. Since growth to a larger size in crustaceans implies more molts, transition also cannot be related to a fixed number of instars. If not environmental cues, size, age, or instars, what determines sex change in Pandalid? Our data does not provide a definitive answer, but in view of the evidence and argument above, the question of what triggers sex change should be framed as follows: when does a male *have* to change sex, and what is the minimum size that a female must be? *P. borealis* is a cold water species. In northern areas growth is slow and females are large at transition simply because they are older. In warmer waters such as the Scotian Shelf and Gulf of Maine growth is unusually rapid and males would reach some hypothetical physiological threshold much earlier and at a smaller size, too small to function as females, hence a "growth spurt" to achieve the minimum female size. From an evolutionary perspective, if we assume that protandry evolved from separate sexes each with their own physiological thresholds for maturation, it is quite plausible that females would retain such a threshold after evolution to

protandry. In this context, the appearance of primary females (ie. animals which skip the male phase) in some southern areas (reference) can be viewed as regressive evolution to the original dioecious state because obligative early transition of males negates the benefits of protandry.

The implications of density dependent growth and sex reversal on stock assessment and management of shrimp fisheries are beyond the scope of this paper, but they clearly need to be considered. What about it, Bob? leave it out?

REFERENCES

- Bergstrom, B. I. (1997) Do protandric pandalid shrimp have environmental sex determination. *Marine Biology* 128: 397-407.
- Charnov, E.L. and P.J. Anderson. (1989) Sex change and population fluctuations in pandalid shrimp. *Am. Nat.* 134: 824-827.
- Charnov, E.L. (1979). Natural selection in pandalid shrimp: a test of a life history theory. *Am. Nat.* 113: 515-734
- Charnov, E.L., D. Gotschall and J. Robinson. (1978). Sex ratio: adaptive response to population fluctuations in pandalid shrimp. *Science* 200:204-206.
- Charnov, E.L. (1981). Sex reversal in *Pandalus borealis*: effect of a shrimp fishery. *Mar. Biol. Lett.* 2: 53-57.
- Carpenter, A. (1978). Protandry in the freshwater shrimp *Pararya curvirostris* (Heller, 1862) (Decapoda: Atyidae) with a review of the phenomenon and its significance in decapods. *J. R. Soc. N.Z.* 3(4): 343-358
- Jenson, A.J.C. (1967) The *Pandalus borealis* in the North Sea and Skagerak. *Mar. Biol. Assoc. India, Proc. Symp. on Crustacea, Part IV*, 1317-1319.
- Koeller, P., M. Covey, M. King. (1997). The Scotian Shelf shrimp (*Pandalus borealis*) fishery in 1997. *Can Stock Ass. Res. Doc 97/125*: 51pp.
- Koeller, P. and K. Drinkwater. (in prep). Environmental *versus* ecological influences on the population dynamics of northern shrimp (*Pandalus borealis*). *Proceedings of the International Pandalid Workshop*.
- Skuladottir, U. The deviation method. A simple method for detecting year-classes of a population of *Pandalus borealis* from length distributions. IN *Proceedings of the international pandalid shrimp symposium, February 13-15, 1979*. Frady (ed). Sea Grant Report 81-3. p 283-306.
- Shumway, E. S., H.C. Perkins, D.F. Schick, and A.P. Stickney. 1985. Synopsis of biological data on the pink shrimp, *Pandalus borealis* Kroyer. NOAA Tech. Rep. NMFS 30/FAO Fisheries Synopsis No. 144. 57. PP
- Warner, R.R. (1974). The adaptive significance of sequential hermaphroditism in animals. *Am. Nat.* 109: 61-82.

TABLE 1. Multiple regression analysis of mean carapace length *versus* density, temperature, area and cruise for each fish set of the 1982-88 and 1995-97 survey series.

		df	SS	Mean Sq	F Value	Pr(F)
1982-88 all data	density	1	43.57	43.57	28.33	0.00000027
	temperature	1	7.57	7.57	4.92	0.27590600
	area	3	29.59	9.86	6.41	0.00035990
	cruise	12	45.19	3.77	2.45	0.00535688
	Residuals	202	310.70	1.54		
	R-Square		0.29			
1995-97 all data	density	1	79.83	79.83	57.32	0.00000000
	temperature	1	14.89	14.89	10.69	0.00133559
	area	3	78.72	26.24	18.84	0.00000000
	cruise	2	7.71	3.85	2.77	0.06607837
	Residuals	151	210.30	1.39		
	R-Square		0.46			
1995-97 densities <1	density	1	14.76	14.76	10.82	0.00143310
	temperature	1	36.38	36.39	26.68	0.00000140
	area	3	62.13	20.71	15.19	0.00000000
	cruise	2	5.00	2.50	1.83	0.16594700
	Residuals	90	122.74	1.36		
	R-Square		0.49			

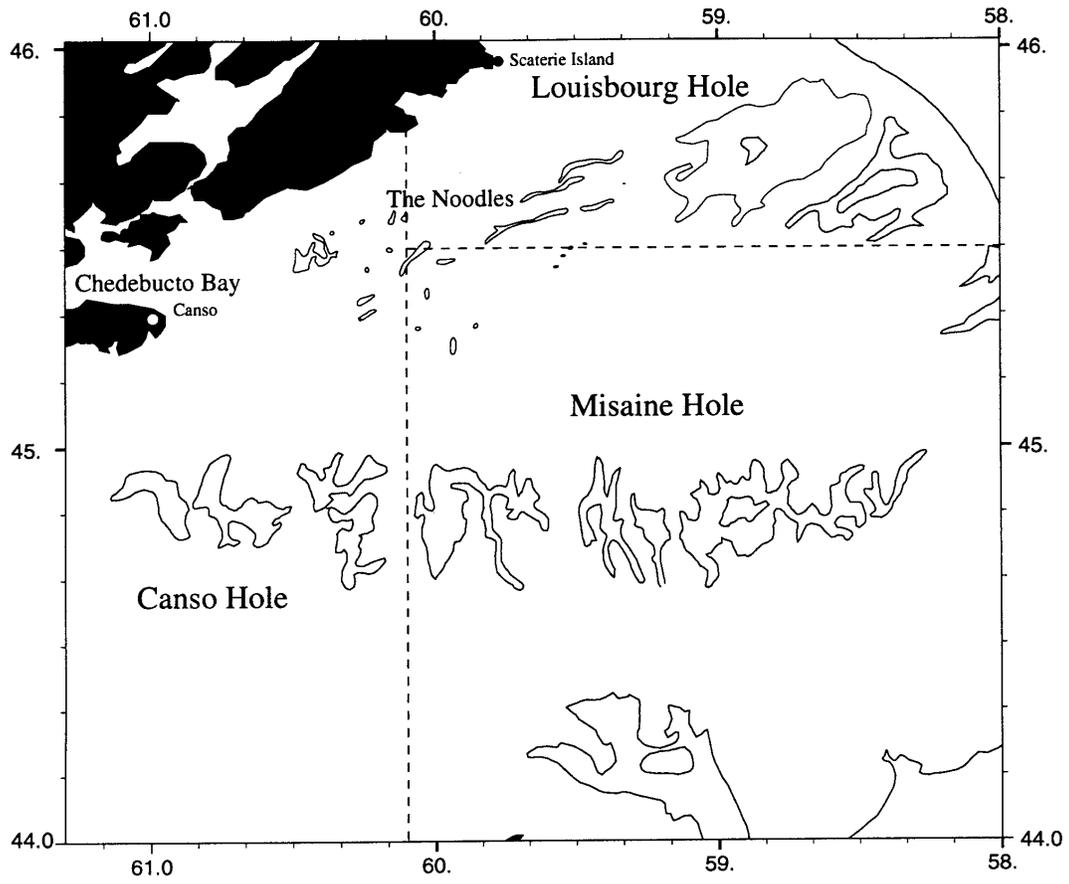


Fig. 1. Study area including the three main shrimp "holes" and the inshore area (The Noodles) surveyed by DFO and industry vessels from 1982-88 and 1995-97.

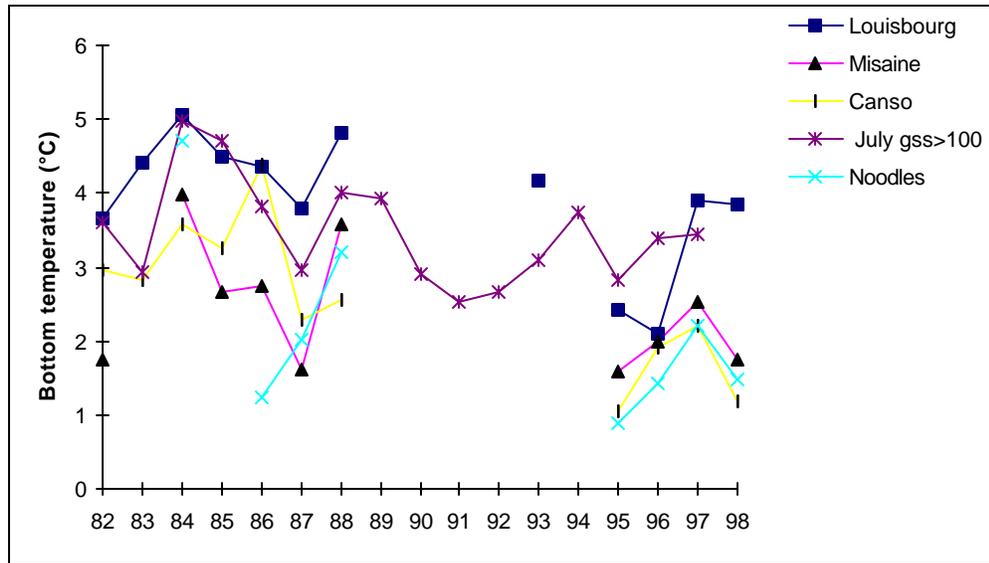


Fig. 2. Mean bottom temperatures in the four study areas from shrimp (1982-88; 1995-97) and groundfish (1982-98) surveys.

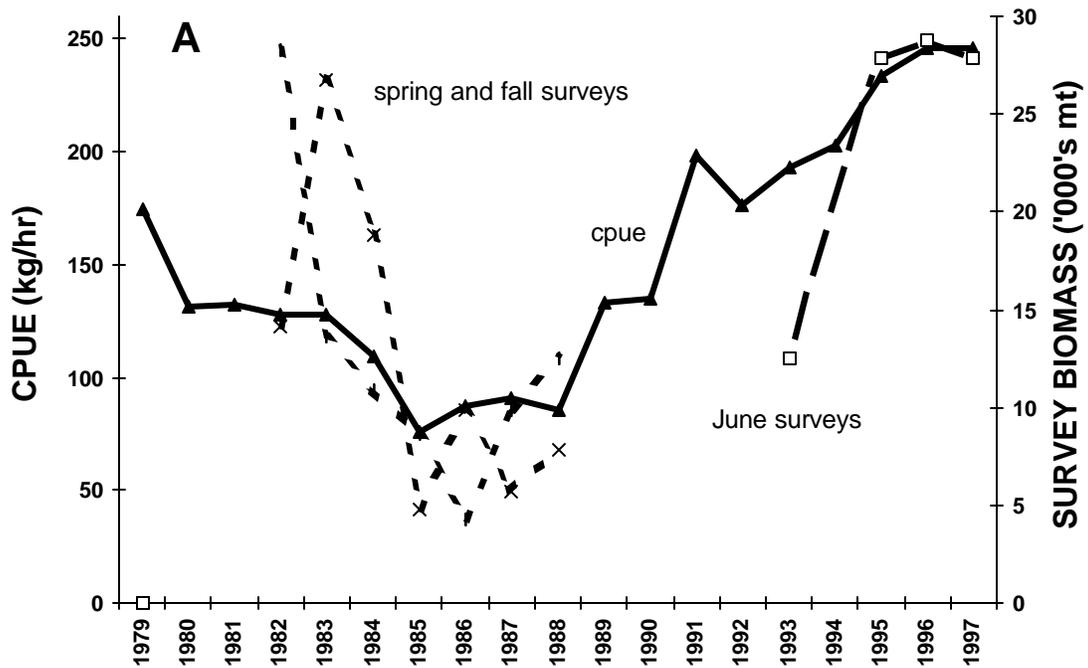


Fig. 3. Shrimp abundance on the eastern Scotian Shelf shrimp grounds from catch per unit effort (commercial vessels) and biomass estimates from DFO/industry surveys.

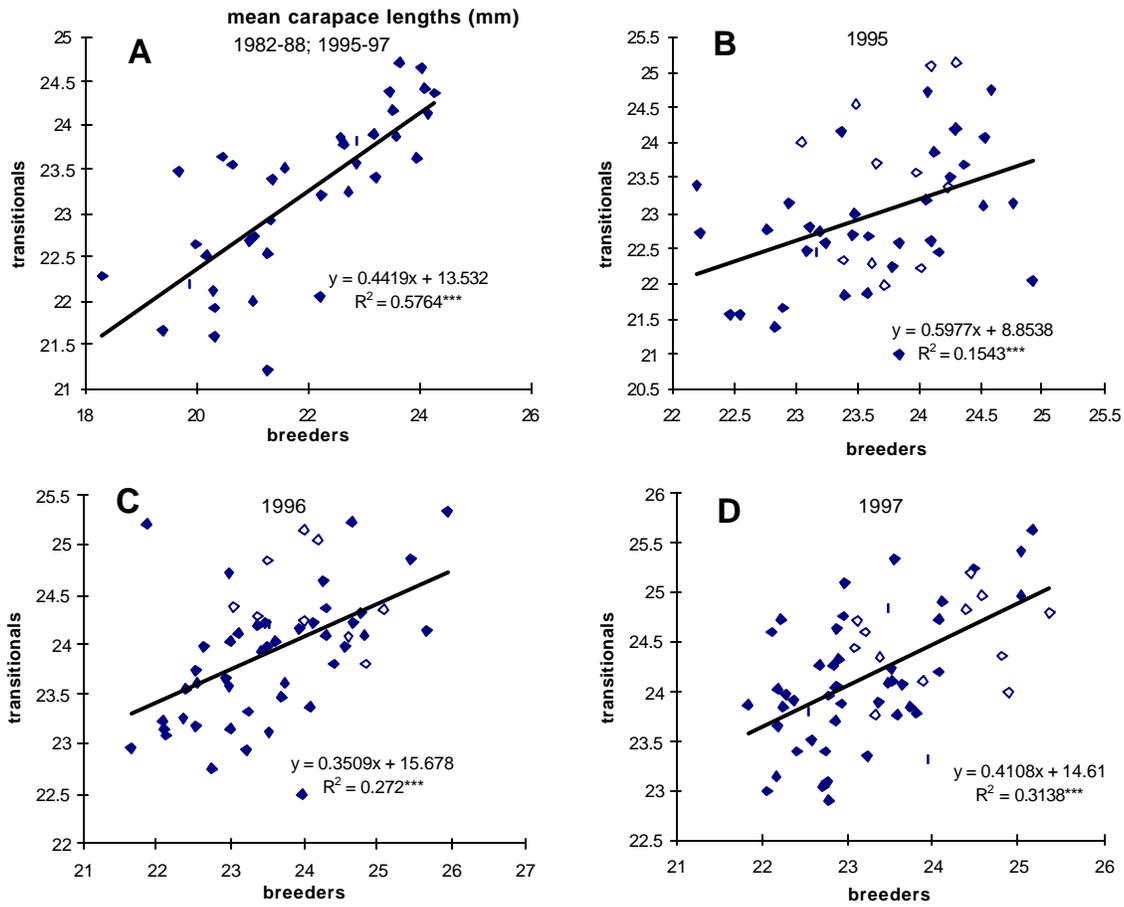


Fig. 4. Mean carapace lengths of transitional shrimp *versus* breeders (males and females) for A. annual means in each area for all surveys, and set means for the A. 1995, C. 1996, and D. 1997 surveys. The open markers in C-D represent sets conducted in Louisbourg Hole.

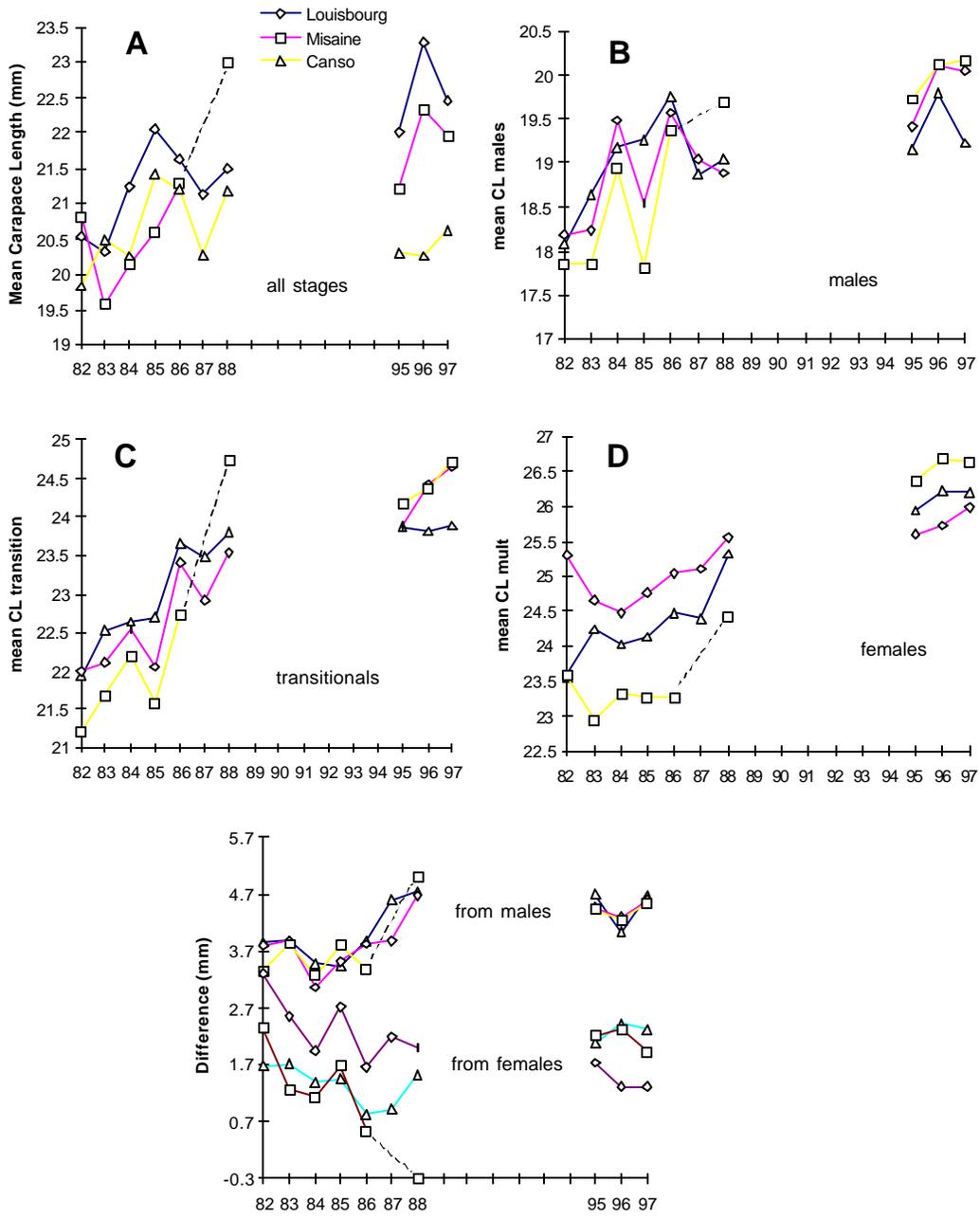


Fig. 5. Annual mean carapace lengths in the three shrimp holes for A. all shrimp, B. males, C. transitionals and D. females. E - difference between means of transitionals and males/females in the three holes.

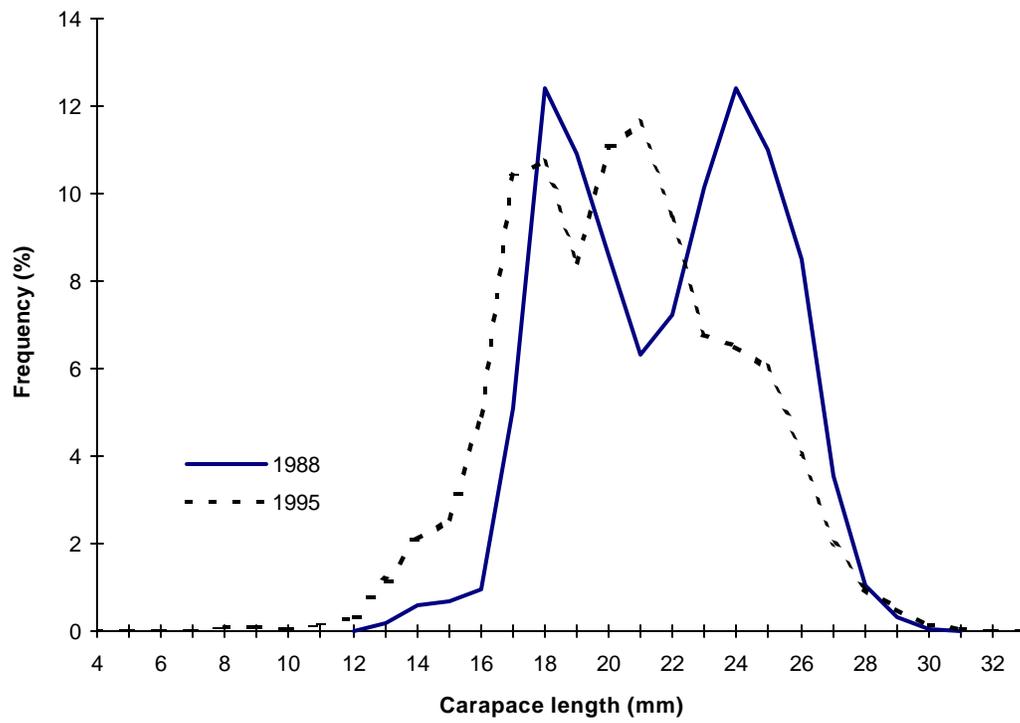


Fig. 6. Length frequencies from the last year of the first survey series and the first year of the second series, and results of modal analysis from the same data (inset).

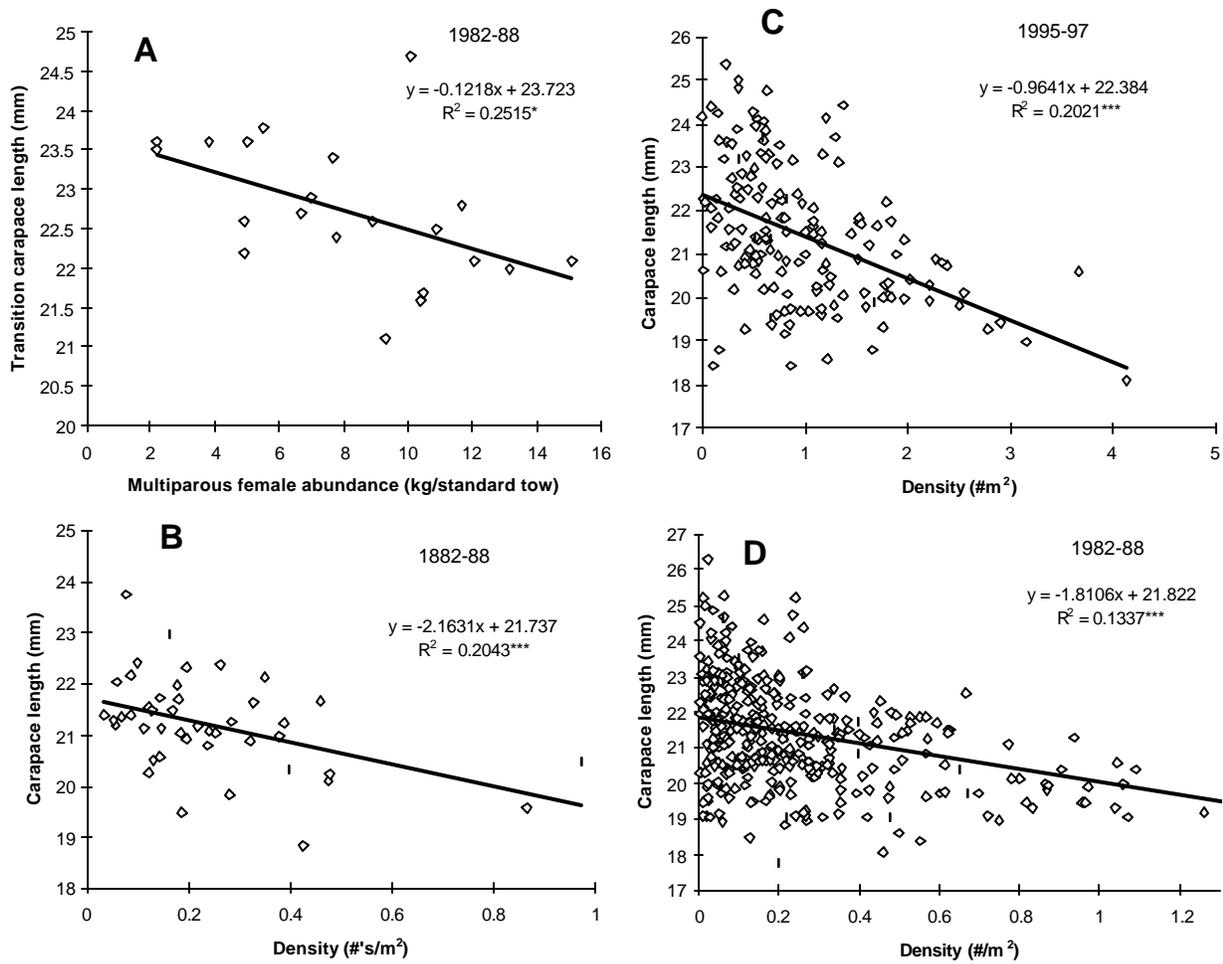


Fig. 7. A. Annual mean carapace length of transitionals *versus* multiparous female abundance in each shrimp fishing hole for the 1982-88 series. B. Overall mean carapace length *versus* density in each fishing hole for the 1982-88 series. Also shown are overall mean carapace length *versus* density at each set for the C. 1995-97 and D. the 1982-88 survey series.

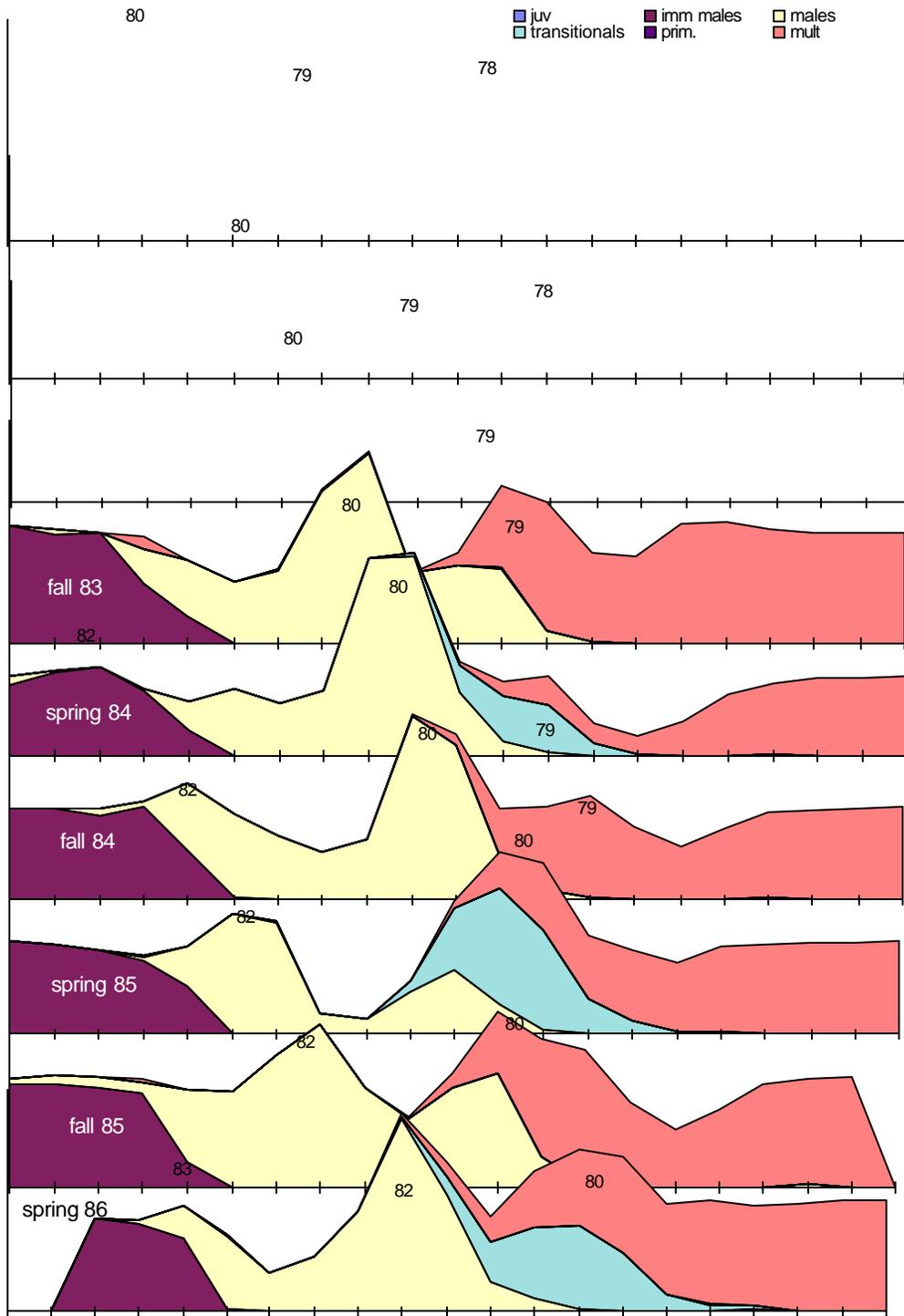


Fig. 8. Deviation analysis for the spring and fall survey series 1982-88.

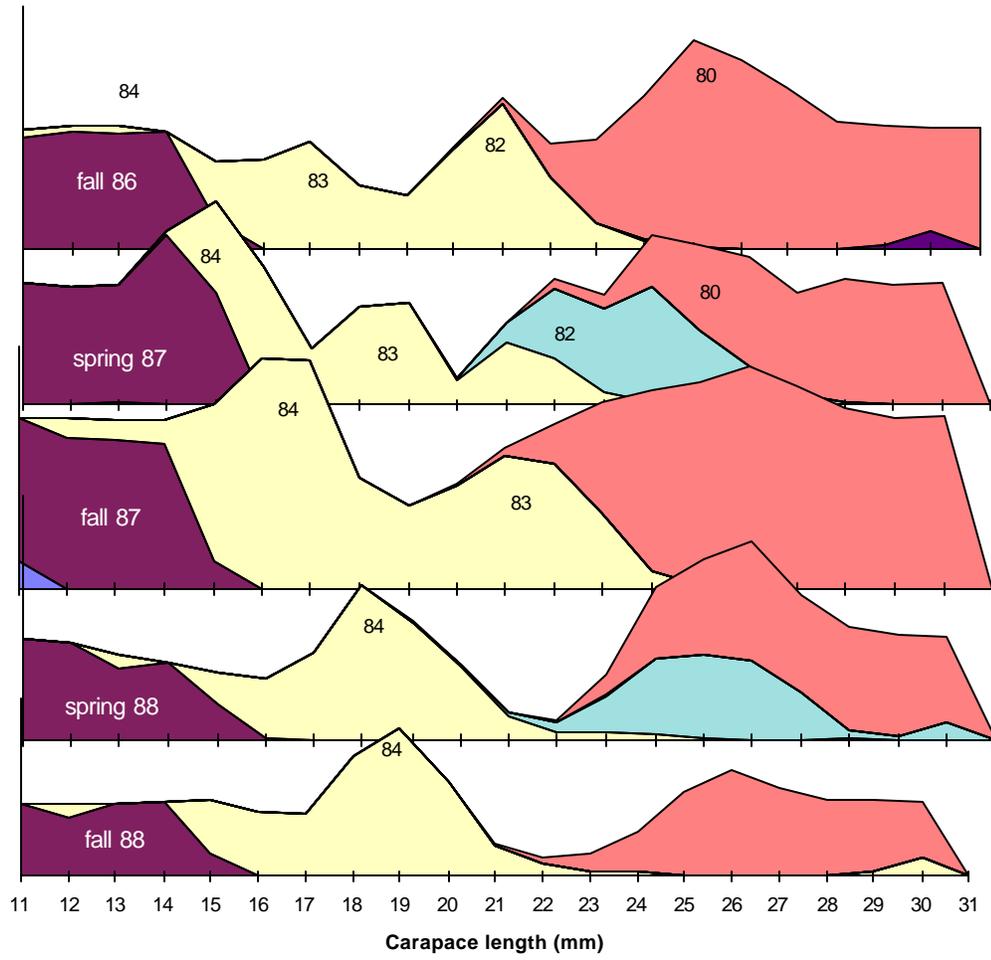


Fig. 8. Continued.

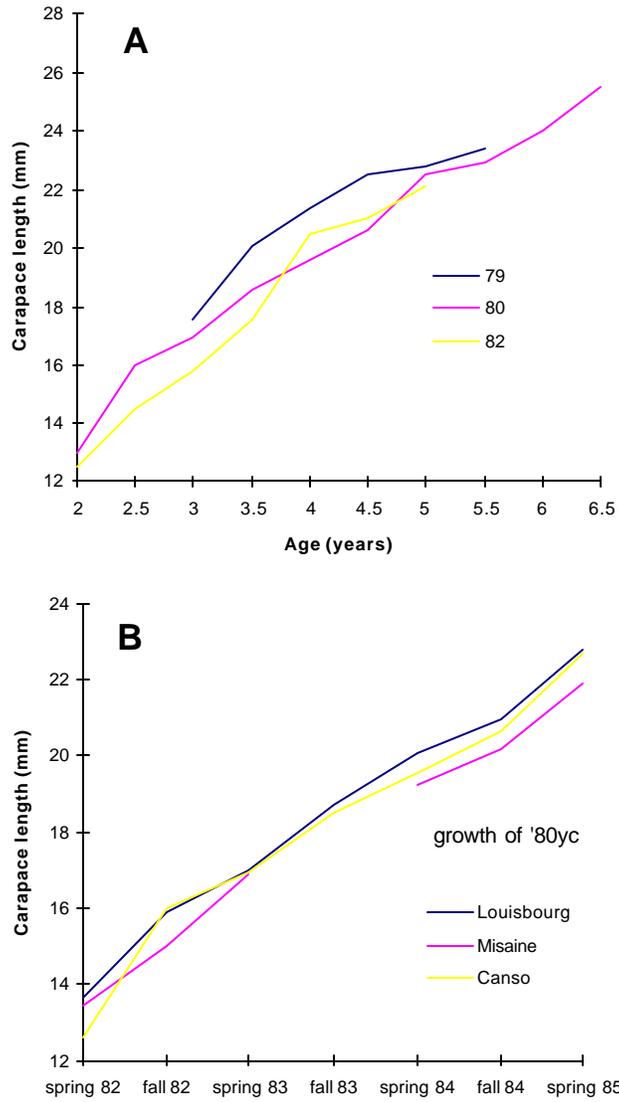


Fig. 9. Growth of the A. 1979, 80 and 82 year-classes and B. the 1980 year-class in the three shrimp holes.