

Abstract.—Three cohorts of *Penaeus indicus* were sampled with a beam trawl at 6-week intervals over 2 years in the St. Lucia Lake system. Shrimp recruited to the system over September–November (spring) and March–May (autumn) and overwintered in the estuary. Mean growth rates of cohorts over the size range 7.25–17.66 mm carapace length (CL) ranged from 0.032 to 0.058 mm CL per day with the autumn cohorts exhibiting the slowest growth and longest residency times. Up to 26.5°C, growth rates were positively correlated with water temperature. Growth was negligible at temperatures between 19 and 22°C. Shrimp emigrated from the estuary between the sizes of 18 to 25 mm CL. The onset of emigration appeared to be related to declining water temperatures.

Growth and Emigration of *Penaeus indicus* H. Milne-Edwards (Crustacea:Decapoda:Penaeidae) in the St. Lucia Estuary, Southern Africa

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The commercial importance of penaeid shrimp is well documented with 1987 United States commercial landings valued in excess of \$515 million (U.S. Department of Commerce 1988). Shrimp fisheries in the Indo-Pacific region generate considerable revenue, and India is the region's major shrimp supplier. *Penaeus indicus* H. Milne-Edwards, 1837 is numerically the most important species in the Indian shrimp fishery (Silas et al. 1984) and likely formed the majority of the \$56.9 million of shrimp exported to the United States by India in 1987 (U.S. Department of Commerce 1988).

The distribution of *P. indicus* extends along the east African coast into the inshore waters of Natal, South Africa (Champion 1983). In common with many inshore penaeids, it utilizes estuaries during the juvenile phase of its life cycle and migrates offshore for subsequent maturation and reproduction (Garcia and Le Reste 1981). The proximity of St. Lucia to the southern limit of distribution of this essentially tropical species suggested the desirability

of investigating the relationship between the growth of *P. indicus* and temperature as well as the factors responsible for onset of offshore emigration.

The St. Lucia Lake system is the largest estuary in southern Africa and provides a nursery habitat for *P. indicus* and several other penaeid species (Joubert and Davies 1966, Forbes and Benfield 1986a). The Natal Parks Board has operated a bait fishery for shrimp in the system since 1952 (Joubert and Davies 1966), with annual landings of approximately 16 t. *Penaeus indicus* typically constitutes 80–90% of this catch (Forbes and Benfield 1986a). An offshore South African commercial fishery also depends largely on *P. indicus* (Forbes and Benfield 1985).

Most penaeid shrimp exhibit rapid growth which is frequently correlated with water temperature. Little information is available on the growth of the St. Lucia penaeids. Joubert and Davies (1966) conducted four surveys over a 1-year period and provided estimates of growth for *P. indicus* and two other numerically

important penaeids. However, their sampling frequency was too low to follow the growth of individual cohorts or identify principal periods of emigration from the system.

While the timing of shrimp emigration from estuaries varies with species and geographic area, a number of factors have been suggested as causal stimuli. These include declines in temperature (Lindner and Anderson 1956, Pullen and Trent 1969, Chen 1983, Matylewich and Mundy 1985), declines in salinity (Rothlisberg et al. 1985, Staples and Vance 1986, Jayakody and Costa 1988), increased tidal amplitude and currents (Cöpeland 1965), and an endogenous rhythm coupled with tidal currents (Hughes 1972).

This study was initiated to provide information about the growth and emigration of *P. indicus* in St. Lucia and operated concurrently with a plankton sampling program that provided information about the immigration of *P. indicus* postlarvae (Forbes and Benfield 1986b). The present paper contains estimates of seasonal differences in growth rates and periods of emigration for *P. indicus*.

Methods

Beam trawling

Sampling was conducted in South Lake and the St. Lucia Narrows, a 21-km channel connecting the lakes with the Indian Ocean; twelve sampling stations were selected (Fig. 1). Samples were collected 17 August 1982–6 November 1984 at 4–6 week intervals coincident with spring tides and the plankton sampling program. Sampling during the first half of 1984 was disrupted when a cyclone struck at the end of January and cut off access to the area. A single sample was obtained in April and routine sampling resumed in July 1984.

A 1-m beam trawl with a frontal area of 0.3 m² was attached to a 12-mm stretched mesh nylon bag with 25-mm mesh nylon wings and a nylon 6-mm mesh cod. The bag was fitted with a floating headrope, weighted baserope, and a tickler chain. The trawl was towed 6 m behind an open boat fitted with two outboard engines. At each site, a 10-min trawl was taken against tidal flow (where present) parallel to, and within 10 m, of the shore. Tow distances were not measured but were probably similar because tidal currents were generally weak in the vicinity of the sampling stations. Catches were frozen and returned to the laboratory where species, sex, and carapace length were determined. Water temperatures were recorded mid-trawl at each station.

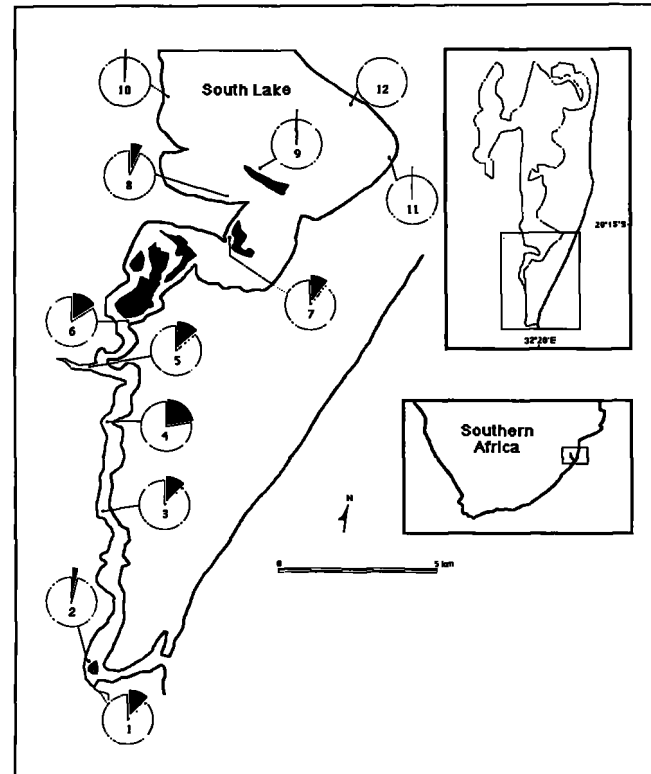


Figure 1

Sampling stations in the St. Lucia Lake system. Pie charts indicate the contribution of each sampling station to the total beam trawl catch of *Penaeus indicus*.

Bait fishery

A bait fishery operates throughout the Narrows (vicinity of stations 1–7) and in lower South Lake (vicinity of stations 8–10) and employs 3.7-m gate trawls with a frontal area of 3.45 m² and a 25.4-mm stretched mesh bag. Frozen samples, provided at irregular intervals of several days to several months between 17 September 1982 and 2 April 1985, were treated in the same manner as the beam trawl samples.

Data analysis

The beam trawl length-frequency data from all sites were pooled because sample size differences among sites were frequently large, and the sample sizes from individual sites were often too small to construct meaningful length-frequency histograms. A computer program (MIX) (MacDonald 1986) was used to fit normal curves to the component cohorts in each distribution. Growth rates were estimated by following the mean size of the youngest cohort over consecutive sampling periods. Older cohorts were excluded from the analysis because of the confounding effect of emigration on the cohort mean. The appearance of a new cohort in the

beam trawl catch was related to prior pulses of postlarvae in the plankton. Over this interval, the growth rate was estimated by relating the mean size of postlarvae to the mean size of the subsequent cohort of juveniles in the beam trawl catch.

Length-frequency histograms were constructed from the sum of all shrimp caught over the entire sampling period for the beam trawl and bait fishery samples. These two histograms were used to estimate the approximate size of shrimp at the onset of emigration. Declines in the frequency of shrimp within the emigrating size classes over successive sampling intervals were used to identify possible periods of emigration.

Results

Distribution and abundance

Shrimp were captured throughout the Narrows and in limited numbers along the western shore of South Lake. Five specimens were taken along the eastern shore (station 11). Catches were highest in the middle Narrows (stations 4–6) and declined in either direction from that section (Fig. 1).

Shrimp concentrated in the middle Narrows for most of the year with some seaward shift in their distribution evident December–February (summer) (Fig. 2). The apparent shift towards the lower Narrows during June–August (winter) is a consequence of the capture of large numbers of 7–12 mm CL shrimp at station 1 in August 1983 (Fig. 2).

Juvenile shrimp were present throughout the year, declining over January–February (late summer) toward a March–May (autumn) minimum and increasing during June–November (winter and spring) (Fig. 3).

A substantial proportion of the *P. indicus* population was presumed to have been washed out of the system during the January 1984 cyclone. During the months following the cyclone, shrimp numbers increased slowly, and by July 1984 shrimp were sufficiently abundant for the bait fishery to resume operation. Beam trawl sample sizes remained too low to adequately define the population structure, and growth estimates could not be provided for the post-cyclone samples.

Growth

Growth rates were estimated over the size range 1.72–20.12 mm CL for three cohorts that entered the system prior to the cyclone (Fig. 4). These estimates ranges from 0.0005 to 0.1634 mm CL per day. Cohort 1 exhibited approximately linear growth up to 13.92 mm CL (Fig. 4) and had a mean growth rate of 0.058 mm CL per day over the size range 7.25–13.92 mm CL. Cohort 2 displayed a pronounced seasonal fluctuation

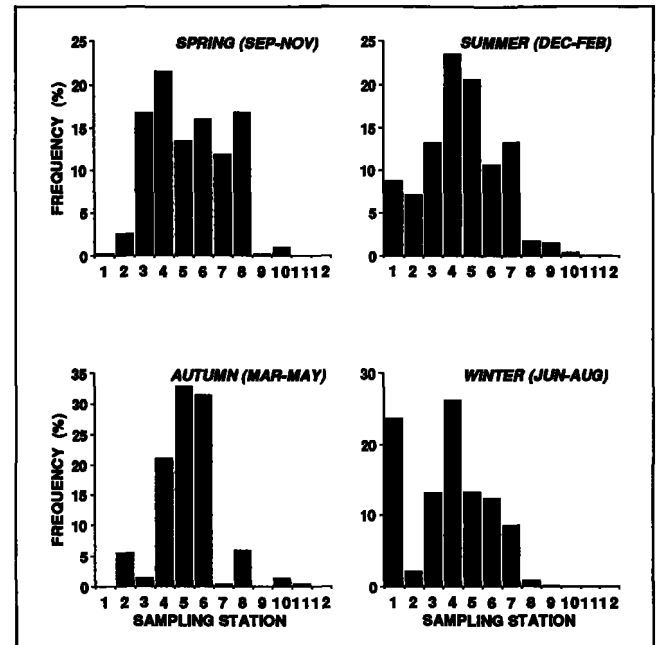


Figure 2

Mean seasonal distribution of *Penaeus indicus* in the St. Lucia system. See Figure 1 for sampling station locations

in its growth pattern (Fig. 4). The mean growth rate of this cohort was 0.035 mm CL per day over the size range 8.99–17.66 mm CL. Cohort 3 also displayed seasonal fluctuation in its growth. The mean growth of this cohort was 0.040 mm CL per day over the size range 8.83–14.81 mm CL.

For the size range 7.25–17.66 mm CL, growth was significantly correlated with the mean water temperature of each sampling interval (Spearman's coefficient of rank correlation $r_s = 0.746$, $t = 3.361$, 9 df, $p < 0.01$) (Fig. 5). This response was particularly evident in cohorts 2 and 3 which showed a pronounced decline in their growth during the cooler winter months (Fig. 4). Cohort 1 also overwintered and probably followed a similar pattern while it was too small to be effectively sampled by our gear.

Emigration

The first cohort entered the system during early May 1982 and emigrated over January–March 1983. A second cohort which may have recruited during early summer 1982 emigrated over December 1983 and January 1984. Emigration of the third cohort, which entered in April 1983, may have been prematurely initiated by the cyclone at the end of January 1984. Two cohorts thus entered the system during April–May (autumn) with possible recruitment during November–December (early summer) by the remaining cohort. All

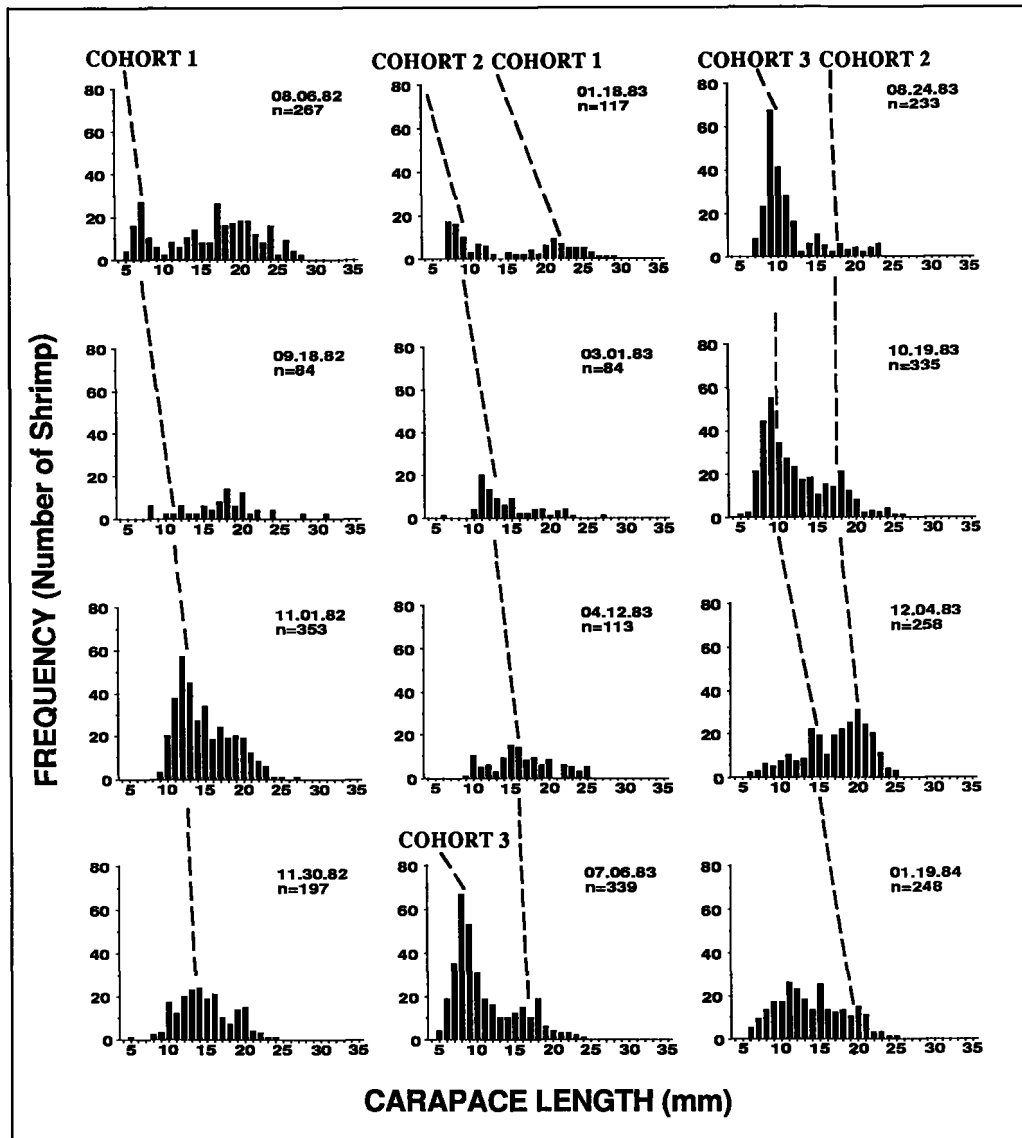


Figure 3

Length-frequency histograms for three cohorts of *Penaeus indicus* in the St. Lucia system between 6 August 1982 and 19 January 1984. Dashed lines indicate positions of fitted cohort means.

three cohorts overwintered in the estuary and emigrated during December–March (summer–autumn).

Penaeus indicus began to leave the system upon attaining approximately 18 mm CL with most emigration occurring between 20 and 25 mm CL (Fig. 6). Declines in the proportions of 20–25 mm CL shrimp in both the beam trawl (Fig. 3) and bait fishery samples (Fig. 7) supported the December–May (summer–autumn) emigration hypothesis. Emigrating size classes declined sharply in the baitfishery samples over April–May 1983 and January–April 1985 (Fig. 7).

Emigration did not appear to be related to salinity fluctuations. The wet and dry seasons are not well

defined in St. Lucia, which receives 62% of its annual precipitation (1971–81 data for the estuary mouth, Natal Parks Board, unpubl.) during summer and autumn when most emigration appears to occur. During our study period, salinities in the lower Narrows showed little fluctuation during the emigration of the first cohort, but did decline prior to and during the emigration of the second (Fig. 4).

A more convincing relationship exists between emigration and declining water temperatures. Water temperatures decreased during the emigration of cohort 1 (Figs. 4 and 7) and may have begun to cool by the onset of emigration in the second cohort. The

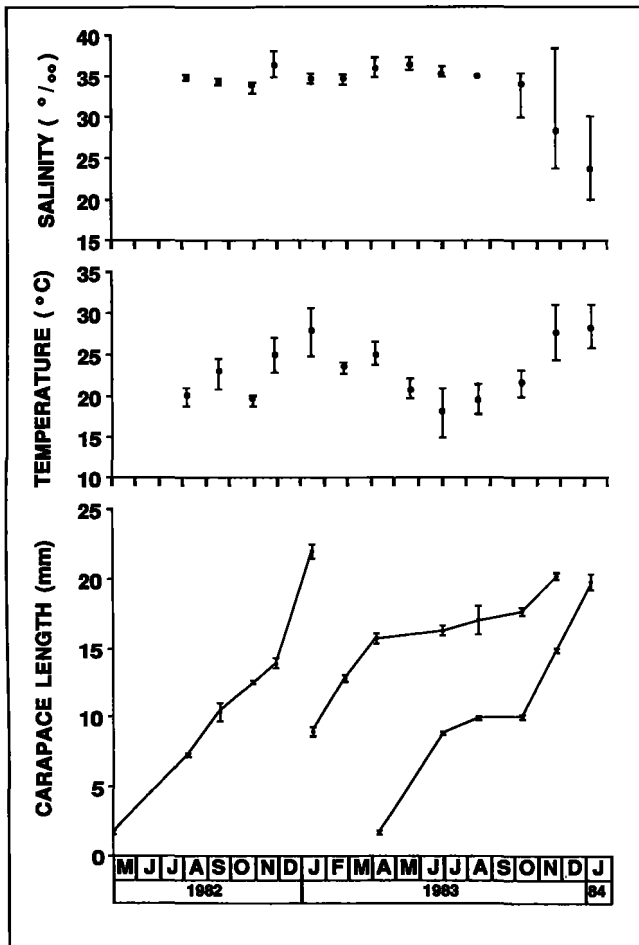


Figure 4

Mean carapace length of *Penaeus indicus* cohorts in the St. Lucia system over time; vertical bars indicate 1 standard deviation. Upper scales indicate corresponding mean temperatures and salinities averaged across sampling stations 1-7; vertical bars indicate maxima and minima.

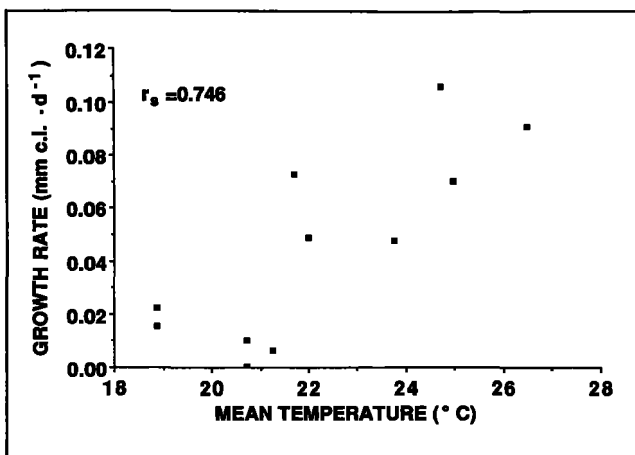


Figure 5

Relationship between growth rates of *Penaeus indicus* (7.25-17.66 mm CL) and corresponding mean water temperatures in the St. Lucia system determined for consecutive sampling intervals.

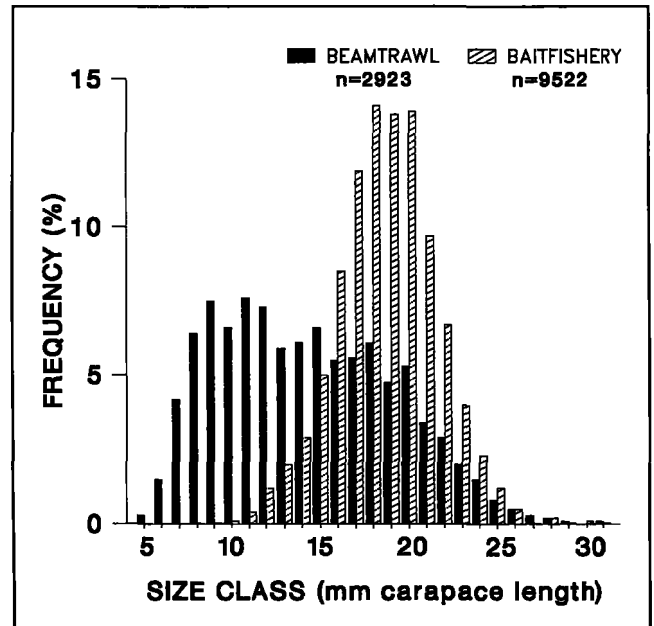


Figure 6

Cumulative length-frequency histogram of *Penaeus indicus* for beam trawl (August 1982–November 1984) and bait fishery (September 1982–August 1985) in the St. Lucia system. Plot truncated at 30 mm CL because larger size classes contributed <0.25% of total catch.

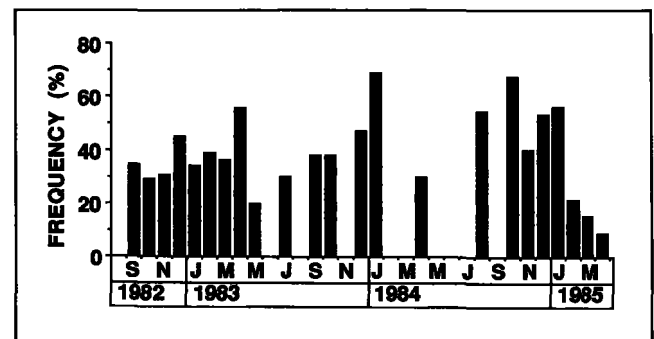


Figure 7

Monthly frequency of *Penaeus indicus* ≥ 20 mm CL in the baitfishery catch in the St. Lucia system. Blank intervals indicate no data available for that month.

emigration of the third cohort would likely have coincided with declining water temperatures if it had not been forced by the cyclone.

Discussion

Estimation of growth rates and emigration size depend on a representative sample of the population at each sampling interval. Trawl samplers typically have a low catch efficiency (Zimmerman et al. 1984) and a selective bias towards certain size classes (Staples 1980). Our beam trawl captured *P. indicus* over the range

4–33 mm CL. The percentage contribution by size class to the total beam trawl catch showed relatively little change between 8 and 18 mm CL (Fig. 6) suggesting that selection bias was not a problem within this range. On this basis, we are confident in using a restricted range of the catch (7–17.66 mm CL) for the growth estimates. However, our growth-rate estimates for sizes above this range may be influenced by emigration and avoidance, and should be used with caution. Similarly, the growth rates determined for small shrimp between the time of recruitment into the estuary and vulnerability to our trawl should be regarded as rough approximations because of the reduced efficiency of our gear and absence of a precise immigration time.

Growth

The mean growth-rate estimates obtained in our study are lower than those reported for *P. indicus* in other areas. This may be a consequence of the lower temperatures which prevail at the edge of this species' distribution. Parrack (1979) suggested that differences in the growth rates of *P. aztecus* populations from different latitudes could be explained by temperature differences in the bottom waters of each region. Juvenile *P. indicus* grew at 0.102 mm CL per day in Singapore ponds (Hall 1962) while Le Reste and Marcille (1976) recorded more rapid growth of 0.125 mm CL per day in Madagascar. A review of the growth rates recorded for this species (Champion 1983) suggested an average growth of 30 mm total length per month which equates to 0.176 mm CL per day when the conversion factor of Prabhakara Rao (1967) is applied and a 30-day month assumed.

Application of the von Bertalanffy growth function may be justified for some penaeid shrimp (Garcia and Le Reste 1981); however, its use is questionable in areas where growth is reduced at times by low temperatures. The reduced growth of overwintering cohorts accounts for the relatively long residency period of the shrimp in St. Lucia. Between August and October 1983, the water temperatures in the Narrows were 18–23°C. The lowest growth rates from our study occurred over 18–22°C, which may provide an estimate of the low-temperature growth threshold for *P. indicus* in St. Lucia. Comparable data for *P. indicus* were unavailable; however, our estimate of the low-temperature growth threshold is similar to estimates reported for other penaeid species. Latapie et al. (1972) found negligible growth in *P. setiferus* below 20°C, and Phares (1980) used 17°C as the zero growth temperature in a model for the same species. Below 22°C, the growth of juvenile *P. vannamei* was reduced in Mexico (Edwards 1977). In contrast, Zein-Eldin and

Aldrich (1965) reported slow growth of postlarval *P. aztecus* at 18°C and a lower growth threshold of 11°C.

In several instances, the interval growth rates were inversely related to temperature. This may be a consequence of size-specific changes in growth rates overriding the effects of temperature. Hall (1962) reported linear growth up to 25 mm CL for *P. indicus*; however, there is no evidence that more complex growth models were fitted. In juvenile *P. vannamei* (Menz and Blake 1980) and juvenile *P. setiferus* (Phares 1980) growth was negatively correlated with size. While growth rates probably decline with increasing size in *P. indicus*, the observed fluctuations may also be due to changes in the thermal history of each cohort not manifested in the mean interval water temperature.

Emigration

The life cycle of *P. indicus* in St. Lucia appears to follow the generalized pattern outlined for penaeids by Garcia (1985). There appear to be two cohorts each year, the first entering during early summer and emigrating from the system over autumn and early winter; the second recruits during autumn, also overwinters in the estuary, and emigrates during the following spring and summer. A similar pattern of recruitment and emigration was observed for *P. indicus* in Singapore by Hall (1962) and in Madagascar by Le Reste (1978). This pattern has also been noted for *P. merguensis* in Australia (Dredge 1985, Rothlisberg et al. 1985). In an earlier study of the St. Lucia penaeids, Joubert and Davies (1966) reported emigration through summer and autumn but did not indicate that this protracted emigration actually represented the overlapping departures of two cohorts.

Penaeus indicus appears to emigrate from St. Lucia and other systems over similar size ranges. In Singapore, Hall (1962) attributed a decline in the frequency of 20–25 mm CL shrimp to emigration, and in Madagascar *P. indicus* began to emigrate at approximately 20 mm CL. Prabhakara Rao (1967) suggested that *P. indicus* left Chilka Lake, India, between 18.3 and 22.9 mm CL.

Jayakody and Costa (1988) reported that *P. indicus* may emigrate from Sri Lankan estuaries in response to osmotic stress imposed by monsoon rains. The onset of emigration by *P. merguensis* has been linked to elevated rainfall and declines in salinity (Rothlisberg et al. 1985, Staples and Vance 1986). Joubert and Davies (1966) suggested a link between migration and salinity in St. Lucia but had no experimental data to support this connection. Emigration appeared to be related to late-summer and autumn water cooling; however, the apparent correlation does not imply

causality. Other factors associated with declining water temperatures such as food availability or predation (Matylewich and Mundy 1985) may also be contributing agents.

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