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Life Histories and Breeding Patterns of Three Intertidal Sand Beach Isopods

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With 10 figures and 3 tables

Key words: Intertidal isopods, life history, breeding patterns.

Abstract. Three-weekly transects were done over a 14-month period at Sundays River Beach, a high energy beach in Algoa Bay, South Africa, to determine the life histories, breeding patterns, and fecundities of three intertidal cirolanid isopods, *Eurydice longicornis, Pontogeloides latipes,* and *Excirolana natalensis. E. longicornis* exhibits an annual, multivoltine life history with a more extended breeding period than the other two species. *P. latipes* and *E. natalensis* both have biennial, univoltine life histories with lower fecundities than *E. longicornis.*

Problem

The life history and reproductive patterns of *Eurydice pulchra* and *Eurydice affinis* have been well studied, both in warm temperate (Salvat, 1966) and cold temperate climatic regimes (Fish, 1970; Jones, 1970). Differences in life histories and reproductive patterns in the same species in different climates have been ascribed to temperature differences (Salvat, 1966; Fish, 1970) and were also noted by Donn & Croker (1986) in haustoriid amphipods. Klapow described ovoviviparity (1970) and a fortnightly cycle of reproduction (1972) in *Excirolana chiltoni,* and Dexter (1977) studied the reproductive patterns of *Excirolana braziliensis* in Panama.

Despite the widespread occurrence of *E. longicornis, E. natalensis,* and *P. latipes* in southern Africa (McLachlan, 1977 b, c; Bally, 1981; McLachlan *et al.,* 1981; Wendt & McLachlan, 1985; Donn, 1988 a, b; Donn & Cockroft, 1989), no detailed work has been undertaken on their population structure or reproduction. The life histories and breeding patterns of these isopods were studied to better understand their ecology and their observed distribution and activity patterns.

Material and Methods

1. Study Area

Sundays River Beach (33° 43′S, 25° 53′E) in Algoa Bay, South Africa lies east of the Sundays River estuary and stretches without interruption for 40 km. On McLachlan's (1980) 20 point exposure rating system it rates 15.0, which classifies it as exposed to very exposed. Although the beach is occasionally dissipative, its modal morphodynamic state is high energy intermediate (see Short & Wright, 1983 and McLachlan & Bate, 1984 for description of beach morphology). The surf zone is approximately 150–250 m wide. Water temperature in the surf zone has an annual range of 14–23 °C (McLachlan, 1977 a). The sand consists of well sorted medium quartz particles with diameters of 225–335 µm, with a $CaCO_3$ content of 29–47 % (Wendt & McLachlan, 1985).

Two sites, 5 km and 25 km from the Sundays River estuary were chosen. The mean intertidal slope varied between $1/19$ and $1/42$. No significant difference in sand particle size between the two sites has been found (McMurray, 1985; Donn, 1987), but the intertidal slope tends to be slightly steeper and the wave height greater at 25 km (pers. obs.; W. K. Illenberger and M. M. B. Talbot, pers. comm.).

2. Sampling and data analysis

The intertidal isopod populations at Sundays River Beach were sampled at three-weekly intervals from December 1987 to January 1989 at both sites. The transects extended from above the drift line downshore as far as isopods were still obtained. Along each transect, five replicate 0.1 m² quadrats of sand were taken to a depth of 25 cm at 3 m intervals across the beach, in a modified stratified random design (Pielou, 1974). The sand was sieved through 1 mm mesh and all isopods retained were preserved in 10 % formalin in seawater.

The first two collections in December 1987 were sieved through a 1.5 mm mesh. However, small *Eurydice* juveniles were observed to crawl through this and subsequently a 1 mm mesh size was used; this retained most individuals larger than 2 mm length. Due to practical sieving problems, a smaller mesh size could not be used.

In the laboratory the isopods were identified, counted, sexed, and measured to 0.1 mm length with a stereomicroscope fitted with an ocular micrometer. Isopod length was defined as the distance along the median axis from the front of the cephalon to the posterior border of the telson. Four sex classes were distinguished:

1) males: stylets present on the second pair of pleopods.

2) ovigerous females: with mature or immature eggs or embryos present in the brood pouch. The terms 'breeding' or 'reproductive' refer to ovigerous females with only mature ova or embryos.

3) females: no characteristics in non-ovigerous females, apart from absence of stylets, made sexing possible; oöstegites become discernible only at sexual maturity. The smallest *E. longicornis* male was 3.1 mm and 80 % of all males caught over 14 months exceeded 3.4 mm. Thus, all individuals ≥ 3.4 mm and lacking a stylet were classified as females. Similarly, the smallest *P. latipes* and *E. natalensis* males sampled were 4.6 mm and 7.2 mm, respectively, and 80 % of *P. latipes* males exceeded 5.5 mm and 8.0 mm for *E. natalensis*. Thus all *P. latipes* and *E. natalensis* individuals ≥ 5.5 mm and ≥ 8.0 mm, respectively, and lacking stylets were regarded as females.

4) unsexables: all individuals ≤ 3.3 mm for *E. longicornis*, ≤ 5.4 mm for *P. latipes*, and ≤ 7.9 mm for *E. natalensis* and lacking stylets. This group consisted mainly of juvenile females, late maturing males, and newly released individuals. The term 'juveniles' was used to describe all individuals, including males, smaller than or equal to 3.3 mm, 5.4 mm, and 7.9 mm, respectively, for *E. longicornis, P. latipes,* and *E. natalensis* and thus included the unsexables.

The number of eggs or embryos in the brood pouches of ovigerous females was determined. Embryos were defined as the second to fourth stages of development of the ova in the marsupium, as described by Jones (1970) for *Eurydice pulchra*. The system described by Klapow (1970) for *Excirolana chiltoni* was applied to *Pontogeloides latipes* and *Excirolana natalensis*, since the development stages looked morphologically similar except for size differences.

Abundance was calculated per meter wide strip of beach, from above the drift line down to the low water mark. This makes allowance for uneven distribution of fauna that exhibit vertical zonation across the beach and for the dynamic morphology of sandy beaches with changing profiles (McLachlan, 1983). Log_{10} (x + 1) transformation was done prior to analysis in order to normalize the data (patchy isopod distribution). Due to the low numbers of *E. longicornis* and *P. latipes* collected at the 25 km vs. 5 km site, population structure and cohort analyses were done only on the data from the latter site. The low abundance of *E. natalensis* at both 5 km and 25 km made it necessary to combine data from the two sites to facilitate cohort and life history analyses. This was considered justifiable because there was no significant difference in abundance between the two sites. Length frequency separation by means of the probability paper method (Cassie, 1954) was used to determine the number of cohorts present.

Results

1. *Eurydice longicornis*

The abundance of *E. longicornis* and the percentage of juveniles at 5 km is presented in Fig. 1. Two of the four peaks in abundance coincided with increases in juveniles, *i. e.*, the peaks between March and the end of May (autumn) and between October and December. However, the main peak from July to August was not associated with an increase in juveniles.

The female : male ratio in individuals larger than 3.4 mm fluctuated markedly, ranging from 0.5–15.5 females per male. Females outnumbered males throughout the year except on two occasions. Breeding females were present throughout the year except in early May and June. Only two females in the 7–8 mm size class (1.2 % of the population; 2 % of females) were found breeding in late May. The smallest female bearing immature ova was 3.4 mm and the smallest size at which males could be distinguished was 3.1 mm. The largest individual sampled was a 10.5 mm male.

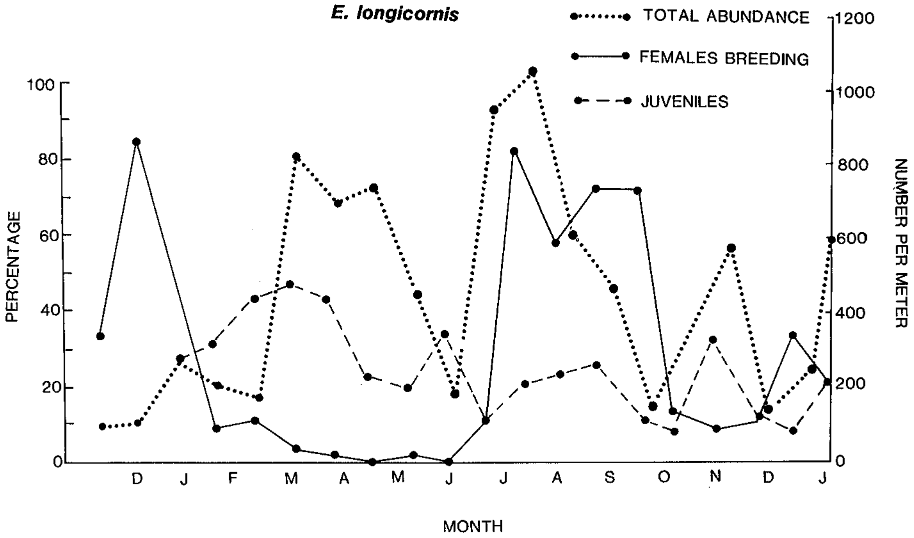


Fig. 1. Total abundance, percentage juveniles, and percentage females breeding of *E. longicornis* at the 5 km site.

The percentage of breeding females as a percentage of all females at 5 km followed a bimodal pattern (Fig. 1). The first peak, between July and October, produced a sharp, relatively low peak of juveniles in November (the spring brood); the second, from December to February, produced an extended, relatively high peak of juveniles from late December to May (the autumn brood).

In early July, 83 % of the ovigerous females had immature ova; most ova had matured by late July, suggesting a maturation period of approximately 3 weeks. In addition, this indicates that egg development continues in winter. The maximum percentage of females that were breeding at any particular time was 87 % (late July, Fig. 1). At the start of peak breeding season (early July to August) most of the ovigerous females occurred in the 4–5 mm size class. Only from September onwards did significant numbers of ovigerous females measure 5–6 mm.

Fecundity was estimated by regressing number of ova and embryos versus female body length (Fig. 2). The two equations were compared using analysis of covariance (KLEINBAUM *et al.*, 1988) and were found to be significantly different ($P < 0.01$). Therefore, data for females carrying ova and embryos could not be pooled to yield a single equation.

The mean length of females bearing ova and embryos was 5.3 mm and 5.1 mm, respectively, with each female producing on average 26 ova and 20 embryos. This discrepancy constituted an average loss of 11–14 % of ova during the incubation period for 3.5 to 9.4 mm long females, as calculated from the regression equations (Fig. 2). Two groups of breeding females are evident, one at 3.5–5 mm and the other at 8–9.5 mm (Fig. 2). This suggests two breeding cohorts or females breeding twice in a life cycle.

The mean cohort length, based on length frequency separation, for *E. longicornis* from December 1987 to January 1989 is shown in Fig. 3. Three cohorts were present in the population at any one time. Despite the undersampling of individuals less than 2 mm, juveniles appeared to be recruited at 3.5–4 month intervals, resulting in approximately three cohorts produced per year. The

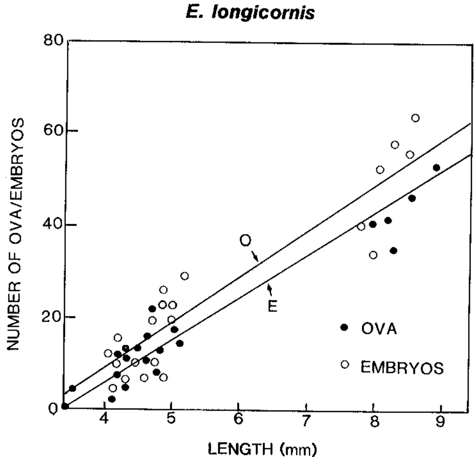


Fig. 2. Regression of numbers of ova (O) and embryos (E) versus *E. longicornis* female body length. The equations are:
$O = 11.5\ (\text{Length}) - 35.6$ ($n = 36$; $r^2 = 90\%$) and
$E = 9.9\ (\text{Length}) - 30.4$ ($n = 53$; $r^2 = 86\%$).

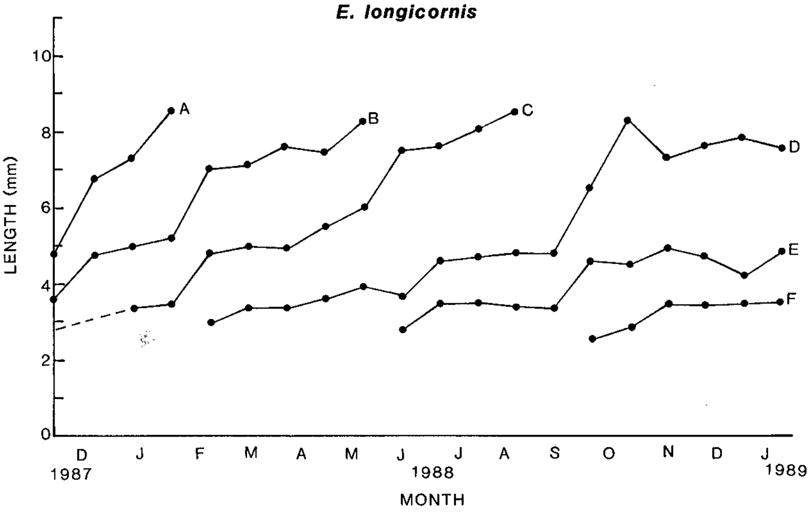


Fig. 3. Mean lengths of *E. longicornis* cohorts from December 1987 to January 1989.

recruitments in late February and June coincided with the peaks in juvenile abundance shown in Fig. 1, but the recruitment in October was out of phase with the November peak in juvenile abundance. The mean length of the early October cohort was 2.6 mm; it may not have been sampled efficiently (small size) and may have been retained in the sieves only in November.

The average growth rate of cohorts D, E, and F in the first three weeks after they appeared in the samples was 0.5 mm per month. If the same growth rate is assumed for juveniles after emerging from the brood pouch at the mean size of 1.7 mm (pers. obs.), they would reach 2.2 mm and thus become available for sampling only 3 to 4 weeks after release from the brood pouch. Hence it can be assumed that cohorts D, E, and F were released 3–4 weeks earlier than is indicated in Fig. 3. Based on this assumption and the recruitment of juveniles at 3.5–4 month intervals, it appears that cohort C was released from the brood pouch in mid October 1987 and would be retained in the sieves only from mid November 1987, approximately four months prior to the appearance of cohort D in late February. Cohort C disappeared from the samples in mid August, approximately 10 months after release from the brood pouch. From this a life span of 10 to 12 months can be deduced for *E. longicornis* at Sundays River Beach, with continuous reproduction and possibly two breeding cycles per female.

2. *Pontogeloides latipes*

The abundance and composition of the *P. latipes* population at 5 km is presented in Fig. 4. The maximum abundance during February–March coincided with recruitment of juveniles into the population. The increase in abundance in

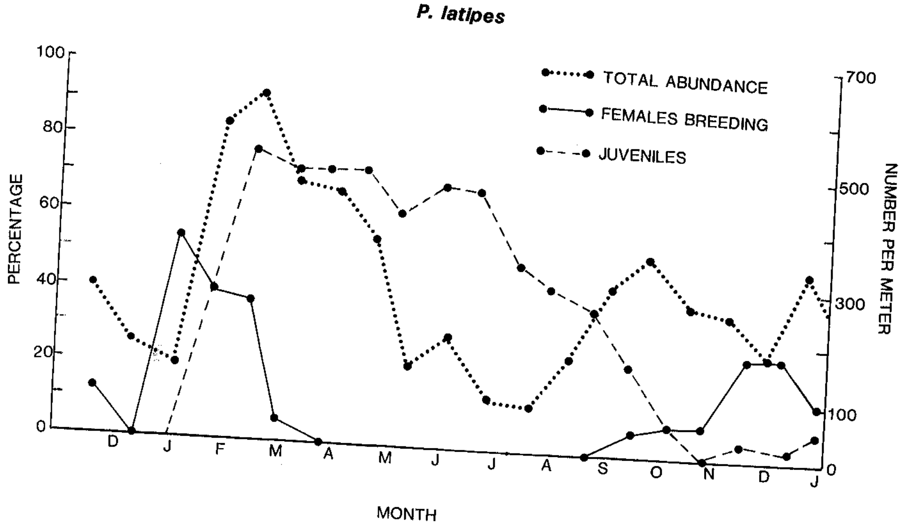


Fig. 4. Total abundance, percentage juveniles, and percentage breeding females for *P. latipes* at the 5 km site.

September, after a minimum in winter, did not correspond with an increase in juveniles. The percentage of juveniles followed a unimodal pattern, with a peak in late summer and a steady decline during the following months as growth continued. During winter they represented 50–73 % of the population.

The female : male ratio ranged from 0.4–2.3 females per male during the study period but did not differ significantly from unity, except on one occasion. Females bearing mature ova and embryos were present from October to March. The minimum size at which females became sexually mature (immature ova observed in the internal marsupium) was 8.3 mm and the minimum length for females with mature ova was 9.1 mm. The smallest size at which males could be distinguished was 4.6 mm and the largest individual sampled was a 14 mm male. The majority of breeding females were in the 10–11 mm size class.

The percentage of breeding females (Fig. 4) followed a unimodal pattern, with a peak in December–January, followed by a peak in juvenile abundance approximately two months later, in February-March. This suggests an incubation period of approximately 2 months for *P. latipes*. The unimodal pattern in both breeding females and juveniles indicates the production of one generation per year.

The maximum percentage of females breeding at any one time was 56 % (January 1988, Fig. 4). As in *Eurydice longicornis*, a small percentage with immature ova were found throughout the year; only during winter did they constitute a significant part of the ovigerous females.

Analysis of covariance showed a difference ($P < 0.01$) between the equations of numbers of ova and numbers of embryos versus female body length (Fig. 5). The difference constituted a loss of 15–22 % of ova per female in the 9.5–13 mm size range during the incubation period. The mean length of females bearing ova and embryos was 11.3 mm and 11.6 mm, respectively, with each female produc-

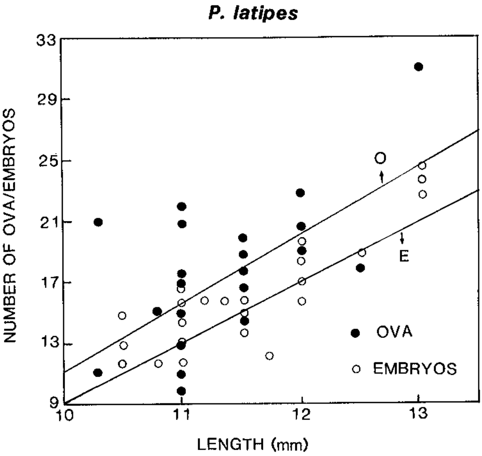


Fig. 5. Regression of numbers of ova (O) and embryos (E) versus *P. latipes* female body length. The equations are:
$O = 4.5 \text{ (length)} - 33.7$ ($n = 35$; $r^2 = 57.1\%$) and
$E = 4.0 \text{ (length)} - 31.08$ ($n = 34$; $r^2 = 50\%$).

ing on average 17 ova and 15 embryos. The breeding females belonged to one size group, indicating a single breeding cycle per female.

Two *P. latipes* cohorts were present for most of the year except in February (Fig. 6), when three cohorts were present (recruitment of juveniles). The recruitment of cohort C coincided with the peak of juvenile abundance shown in Fig. 4. Cohort A died off in February, the same time that cohort C appeared, suggesting that most females reproduce once and die shortly thereafter.

Since cohorts B and C required approximately 12 months to grow from 8 mm to 12 mm and from 4 mm to 8 mm, respectively, *P. latipes* may reach the average breeding size of 11.3 mm within 16–22 months after release from the brood pouch. It thus follows that *P. latipes* has a life span of 1.5–2 years, incorporating a single breeding cycle per female. The population breeds once a year.

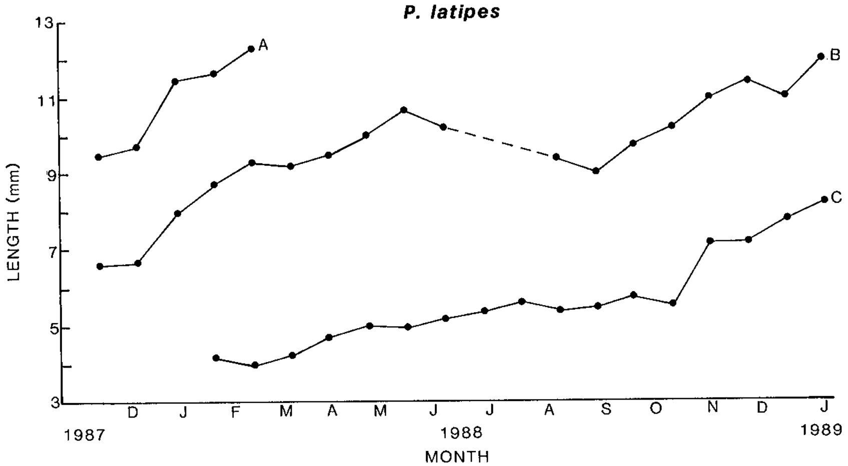


Fig. 6. Mean lengths of *P. latipes* cohorts from December 1987 to January 1989.

3. *Excirolana natalensis*

The abundance of *E. natalensis* and the percentage of juveniles at 5 km is shown in Fig. 7. Similar to *Eurydice longicornis*, the *E. natalensis* population showed marked fluctuations unrelated to season or peaks in juvenile abundance. Maximum abundance was reached during June with secondary peaks in April, September–October, and January. A high percentage of juveniles was present throughout the year and 60–85 % of the population overwintered as juveniles.

The female : male ratio ranged from 0.3–8 females per male during the study period. It did not differ significantly from unity during the breeding season (October to early May) but changed during winter (late May to September) to approximately 2 females per male.

Marked fluctuations occurred in the percentage of breeding females (Fig. 7), even within the breeding season (October to April). The maximum percentage breeding at any particular time was 67 % (January 1988). The sharp increase in juveniles approximately 9–12 weeks later suggests an incubation period of approximately 2.5–3 months.

Females bearing mature ova and embryos were present from October to April. Ovigerous females with immature ova were present in small numbers throughout the year but constituted a significant proportion of females only during winter. The smallest female with immature ova measured 11.5 mm, the smallest male 7.2 mm, and the largest individual sampled was a 17.5 mm male.

The regression equations of ova and embryos against female body length were not significantly different (ANACOVA, P >0.05), indicating no loss of ova; thus the data were pooled (Fig. 8). The mean length of females with ova or embryos was 13.8 mm, with each female producing an average of 19.5 offspring.

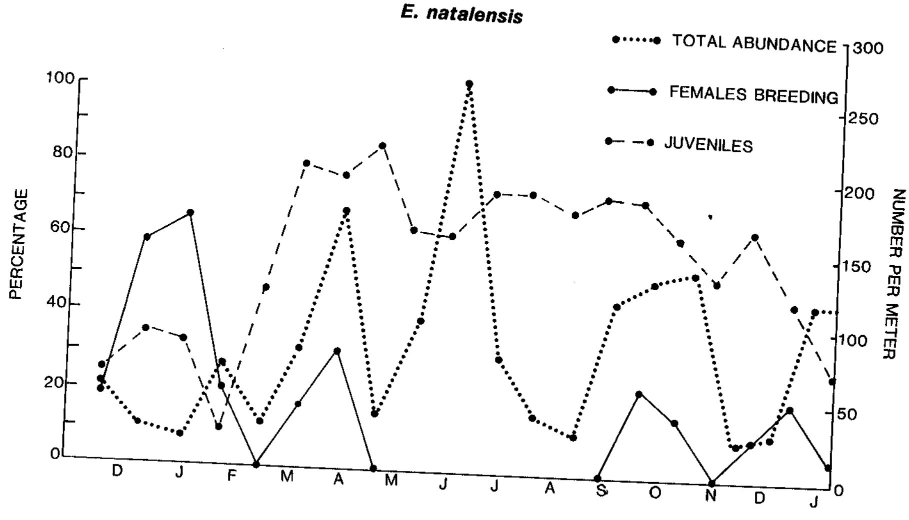
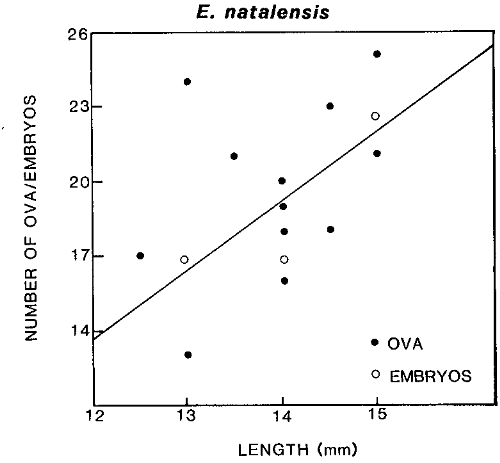


Fig. 7. Total abundance, percentage juveniles, and percentage breeding females for *E. natalensis* at the 5 km site.

Fig. 8. Regression of numbers of ova or embryos combined (OE) versus *E. natalensis* female length. The equation is: OE = 2.8 (length) − 19.3 (n = 22; r^2 = 52.5%).



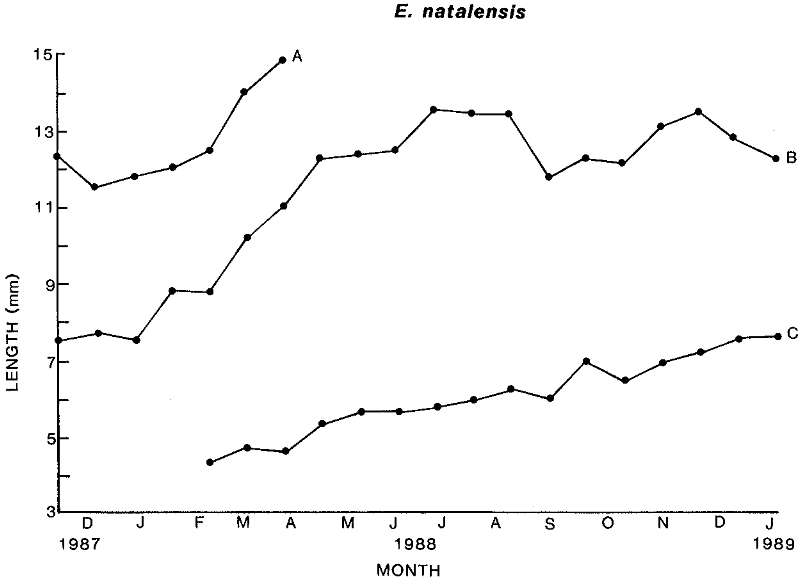


Fig. 9. Mean lengths of *E. natalensis* cohorts from December 1987 to January 1989.

The observation that breeding females belong to one size group supports the hypothesis of one breeding cycle per female.

The population consisted of two cohorts for most of the year (Fig. 9) except from late February to April, when a third cohort (C) was discernible. The recruitment of cohort C coincided with a late February peak in juvenile abundance (Fig. 7). Cohort A disappeared approximately six weeks after the appearance of cohort C, suggesting that females reproduce once and die shortly thereafter. This is also reflected in the sudden absence of ovigerous females after April (Fig. 7).

Cohort C took 12 months to grow from 4.2 mm (at release from brood pouch) to 8 mm. Cohort B grew from 8 mm in early February to the average breeding size of 13.8 mm in 6 months. *E. natalensis* at Sundays River Beach thus apparently reaches sexual maturity at about 18 months, has a life span of 1.5–2 years, and breeds once in a life time. As in *P. latipes,* the population breeds once a year.

Discussion

1. Abundance

Eurydice longicornis was the most abundant cirolanid isopod on Sundays River Beach during the study period, *Excirolana natalensis* the least abundant (Figs. 1, 4, and 7). The abundance of *E. longicornis* at 5 km showed marked non-seasonal fluctuations (Fig. 1) which can partly be explained by the production of multiple broods during the year. The low number of *E. longicornis* in June is unexpected, since cohort C appeared in the population at that time (Fig. 3) and the population three weeks later showed a marked increase. Three possible reasons can be forwarded. The weather conditions during June sampling were most unfavourable (strong south-westerly winds, wave height 3–4 m). The isopods may have been washed from the sand by the waves or have actively migrated offshore. Offshore migrations of *Eurydice pulchra* during stormy winter conditions have been described by Jones & Naylor (1970) and Hastings & Naylor (1980). Leber (1982) reported that the bivalve *Donax parvula* in North Carolina migrated offshore during winter to a subtidal habitat, while Ansell *et al.* (1972) found that *Donax incarnatus* disappeared from beaches in south-west India during the monsoon and reappeared afterwards. Secondly, with the recruitment of cohort C at this time, much of the population would be expected to consist of individuals smaller than 2 mm (already 37% of the population during June measured 2–3.4 mm; Fig. 1); since the sieves retained only isopods larger than 2 mm, a significant proportion of the population may not have been sampled. These newly released juveniles could grow large enough within three weeks to be retained by the 1 mm mesh, hence the increase in numbers by early July. A third reason for the low June abundance could be mortality in cohort B (Fig. 3).

Pontogeloides latipes showed the clearest seasonal fluctuation in abundance, with a gradual change from a late-summer maximum to a winter minimum (Fig. 4). After the February peak, numbers decreased (disappearance of cohort A) and reached a minimum in July. However, the September increase, unrelated to recruitment, does not reflect undersampling of juveniles (as in *E. longicornis*), since juveniles were retained by 1 mm mesh from the time of release from the brood pouch.

E. natalensis abundance showed marked non-seasonal fluctuations (Fig. 9), although to a lesser extent than in the *E. longicornis* population. A sharp decrease in numbers occurred in early May due to the mortality of cohort A (Fig. 9), but other peaks and troughs cannot be accounted for.

E. longicornis showed greater fluctuations in abundance than *P. latipes* and *E. natalensis*. This variability can be partially explained by the production of multiple broods (Fig. 3), whereas *P. latipes* and *E. natalensis* produced one brood per year (Figs. 6 and 9) and showed more stable populations. The fluctuations, unrelated to recruitment of juveniles or mortality of cohorts, could also be due to longshore patchiness in isopod distribution, which introduces variability into the abundance estimates. Patchiness in the distribution of *E. longicornis, P. latipes,* and *E. natalensis* on sandy beaches on the west coast of South Africa was also described by BALLY (1981). Alternatively, the fluctuating numbers and the absence of males in *E. longicornis* and *E. natalensis* during certain periods of the year could be explained by offshore movement of parts of the population, *i. e.*, males, similar to intraspecific zonation in the mysid shrimp, *Gastrosaccus psammodytes,* where males and juveniles are found furthest offshore and females move progressively inshore as the broods develop (WOOLDRIDGE, 1981).

2. Breeding season

The peak breeding season for *E. longicornis* stretched from July to March (Fig. 1), although low numbers of breeding females were present in April and May, suggesting some breeding throughout the year. The breeding period for *Eurydice pulchra* was 7 months in France (SALVAT, 1966), 5 months in South Wales (JONES, 1970), and 3 months in the Dovey Estuary, Britain (FISH, 1970). Similarly, the breeding period for *Eurydice affinis* was 7 months in France (SALVAT, 1966) and 3 months in South Wales (JONES, 1970). This demonstrates that the breeding season for the same species is prolonged in locations with higher temperatures (SALVAT, 1966; JONES, 1970). The temperature of the sea water in Algoa Bay seldom drops below 15 °C (CHRISTENSEN, 1980), and then only for a few days when occasional summer upwelling occurs due to easterly winds (BECKLEY, 1988; SCHUMANN *et al.*, 1988). Hence the seasonal temperature variation (14–23 °C; McLACHLAN, 1977 a) in Algoa Bay is minimal.

The breeding season for the other two species was more limited: October–March for *P. latipes* (Fig. 4) and October–April for *E. natalensis* (Fig. 7). DEXTER (1977) reported that *Excirolana braziliensis* at Naos Island, Panama, reproduced throughout the year but that the percentage of reproductive females was lowest during the dry season. During the peak breeding season, reproductive *E. natalensis* females constituted up to 40 % of the population, a high proportion compared to 1.5 % throughout the year for *E. chiltoni* (KLAPOW, 1972) and 2.4–4.5 % and 0.13–0.94 % during the wet and dry season, respectively, for *E. braziliensis* (DEXTER, 1977).

3. Incubation period

The incubation period is approximately 2 months for *E. longicornis* (Fig. 1) and *P. latipes* (Fig. 4), and approximately 3 months for *E. natalensis* (Fig. 7) as estimated from the time between peaks in abundance of gravid females and juveniles. JONES (1970) and FISH (1970) recorded an incubation period of 8 weeks for *Eurydice pulchra,* and JONES (1970) found a 37 day period for

Eurydice affinis, a smaller species. *Excirolana chiltoni* had a 2–3 month incubation period at La Jolla (Klapow, 1971), and *Cirolana harfordi*, a cirolanid isopod slightly larger than *Excirolana natalensis*, a 3–4 month period at Monterey Bay, California (Johnson, 1976). The 1 month shorter breeding season observed here in *P. latipes* vs. *E. natalensis* could possibly be attributed to the shorter incubation period of *P. latipes*.

4. Fecundity

We found a linear relationship between the number of ova or embryos and length of ovigerous females for all three species. This is in agreement with findings of many workers on *Peracarida* (Salvat, 1966; Jones, 1970; Jones & Naylor, 1970; Klapow, 1970; Johnson, 1976; Donn & Croker, 1986; Wooldridge, 1986) with the exception of Fish (1970). The slope of the regression line is steepest for *E. longicornis* (Fig. 2), which has a higher fecundity than the other two species (20–26 offspring per female versus 15–17 and 19.5 for *P. latipes* and *E. natalensis*, respectively). In addition, of the three species, only *E. longicornis* produces multiple broods per year.

Breeding *E. longicornis* females belong to 2 different cohorts (Fig. 2), those in the 3.5–4.5 mm size class presumably producing their first brood and those in the 8–9 mm size class their second. Rapid growth (Fig. 3) could enable the spring brood to grow through summer and reach sexual maturity in time to produce the autumn brood at an age of about 6 months; Salvat (1966) recorded a similar phenomenon in *Eurydice pulchra*. If *E. longicornis* females survived the first brood, they might produce a second brood after a period of growth, at about 8 mm. Johnson (1976) found that females of *Cirolana harfordi*, an isopod with a prolonged breeding period like *E. longicornis*, produced a second brood as early as 60 days after release of the first.

Fish (1970) also found differences between numbers of ova and embryos in *Eurydice pulchra* (Table 1), although she gave no explanation for this phenomenon. The difference constitutes a loss of about 55–65 %, which is considerably more than that for *E. longicornis* (11–14 %). In accordance with observations by Salvat (1966), Fish (1970), and Jones (1970) on *E. pulchra*, all ova and embryos in *E. longicornis* were in the same stage of development and none were ever seen to degenerate. The difference between ova and embryo numbers could be due to loss of ova from the brood pouch during high energy conditions in the surf zone, as also described by Wooldridge (1981) for the sand burrowing mysid, *Gastrosaccus psammodytes*. Ova loss due to handling in the laboratory is unlikely.

E. natalensis females carried an average of 19.5 ova versus 30.7 ova in *Excirolana chiltoni* (Klapow, 1970) and 4–17 in *Excirolana braziliensis* (Dexter, 1977), two smaller species. There was no significant difference between the number of ova and embryos in ovigerous *E. natalensis* females. This suggests no loss from the protected internal brood pouch of *Excirolana* spp. (Klapow, 1970) as compared to the external brood pouch in *Eurydice*, *Pontogeloides* and other cirolanids. However, Klapow (1971) recorded an embryo mortality rate of 19 % over the incubation period in *E. chiltoni*.

5. Life histories

Eurydice longicornis starts reproducing at approximately 6 months of age and breeds a second time, after an interval of 3–4 months. *Pontogeloides latipes* breeds at 16–22 months and *Excirolana natalensis* at approximately 18 months (Fig. 10).

E. longicornis at Sundays River Beach exhibits an annual life history and produces multiple generations per year (Fig. 3, Table 2). Its life history and reproductive strategies compare best with those of *Eurydice pulchra* as described by SALVAT (1966) in France. He found that *E. pulchra* could reach maturity in 8 months, thus enabling juveniles hatched early in the breeding season to reproduce by the end of that same breeding season, thereby making two generations per year possible. However, JONES (1970) and FISH (1970) in Britain found reproduction of the early brood in the same breeding season to be impossible, possibly due to different temperature regimes. JONES (1970) suggested that the autumn brood was produced by the autumn brood of the previous year, which, after overwintering as juveniles, needed most of the following spring and summer to reach sexual maturity. A review of life histories of other cirolanid isopods is given in Table 3 for comparison. Temperature has an effect not only on breeding season length, but also on the life history and life span of the same species in different locations (DONN & CROKER, 1986). JONES

Table 1. Fecundity data for various cirolanid isopod species. * Data for ova and embryos of *E. natalensis* combined.

Species	Ova[1] or embryos[2]/female		Source
	Range	$\bar{x}$	
Eurydice longicornis	5–90[1] 3–63[2]	26.0[1] 20.4[2]	present study
Eurydice pulchra	30–45[1]		JONES, 1970
Eurydice pulchra	22–54[1] 12–35[2]		FISH, 1970
Eurydice pulchra	21–63[2]		SALVAT, 1966
Eurydice affinis	18–29[1]		JONES, 1970
Eurydice affinis	23–35[2]		SALVAT, 1966
Pontogeloides latipes	9–31[1] 4–25[2]	17.0[1] 15.4[2]	present study
Excirolana natalensis	13–25*	19.5*	present study
Excirolana braziliensis	4–17[1]		DEXTER, 1977
Excirolana chiltoni	–	30.7[1]	KLAPOW, 1970
Cirolana harfordi	18–68[1]		JOHNSON, 1976

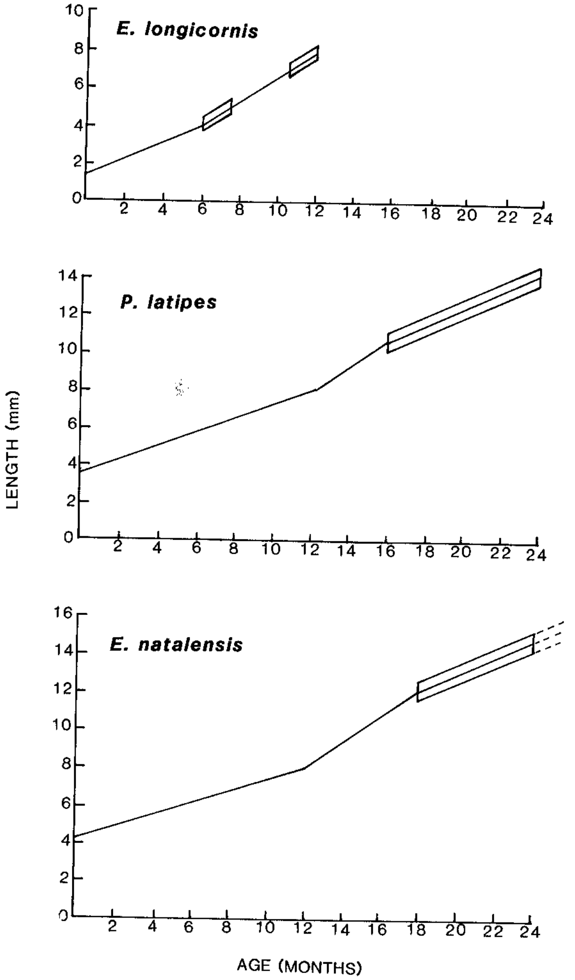


Fig. 10. Summary of the life histories of *E. longicornis, P. latipes,* and *E. natalensis* at Sundays River Beach. Lines indicate growth curves and boxes breeding periods.

(1970) for example recorded a univoltine life history and a life span of 15–20 months and Fish (1970) a life span of 24 months for *E. pulchra* in South Wales and the Dovey Estuary, respectively, whereas Salvat (1966) found a bivoltine life history and a 1-year life span in the same species in the warmer waters of the Mediterranean. Higher temperatures result in a prolonged breeding season and more than one generation per year due to faster growth rates and earlier attainment of sexual maturity (Salvat, 1966; Jones, 1970). Growth and egg maturation in *E. longicornis* at Sundays River Beach apparently continued through winter. The small seasonal water temperature fluctuation provides a favourable environment for a prolonged breeding season and a multivoltine life history. Jones (1970) also recorded growth in *Eurydice pulchra* during winter in South Wales, where temperatures are generally lower than at Sundays River Beach.

Both *P. latipes* and *E. natalensis* exhibit a biennial life history at Sundays River Beach, with a life span of 1.5–2 years, and produce one brood (Table 2;

Table 2. Comparison of various reproductive characteristics of *E. longicornis, P. latipes,* and *E. natalensis* at Sundays River Beach.

Parameter	*E. longicornis*	*P. latipes*	*E. natalensis*
Breeding season	Jul.–Mar. ± 9 months	Oct.–Mar. ± 6 months	Oct.–Apr. ± 7 months
Incubation period	2 months	2 months	3 months
Life cycle	Multivoltine	Univoltine	Univoltine
Life span	1 year	1.5 to 2 years	1.5 to 2 years

Table 3. Life histories of some cirolanid isopods from different locations around the world.

Species	Location	Life cycle	Source
Eurydice pulchra	France	Bivoltine	SALVAT, 1966
	South Wales	Univoltine	JONES, 1970
	Dovey Estuary	Univoltine	FISH, 1970
Eurydice inermis	Marseille	Bivoltine	
	Ireland	Bivoltine	TULLY & O'CEIDIGH, 1986
Excirolana chiltoni	California	Bivoltine	KLAPOW, 1971
Cirolana harfordi	California	Multivoltine	JOHNSON, 1976

Figs. 6 and 9). This compares well with the 2 year life span described for *Cirolana harfordi,* a slightly larger, multivoltine cirolanid isopod in California (JOHNSON, 1976), and for *Ligia dilatata* on the Cape Peninsula of South Africa (KOOP & FIELD, 1980). HARVEY (1968), in her work on *Sphaeroma serratum* and *Sphaeroma rugicauda* in Britain, recorded a life span of 2–2.5 and 1–1.5 years for these species, respectively, the former at the northern limit of its distribution.

The bimodal pattern in breeding *E. longicornis* females is similar to the findings of JONES (1970) and SALVAT (1966) in *Eurydice pulchra.* KLAPOW (1971) similarly describes a spring and autumn brood and two generations per year for *Excirolana chiltoni* in California.

Summary

Eurydice longicornis has a life history of about 1 year, an extended and possibly year-round breeding period, and produces multiple broods, while *Excirolana natalensis* and *Pontogeloides latipes* have life spans of 1.5–2 years, shorter

breeding periods, and only one brood per year. This may explain the numerical dominance of the former on this warm temperate, high energy beach.

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