A comparative study on the movement patterns of two sympatric tropical chitons (Mollusca: Polyplacophora)

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Abstract

The individual positions of 200 intertidal chitons [*Acanthopleura brevispinosa* (Sowerby) and *A. gemmata* (Blainville)] were recorded throughout 55 low tides on a Somalian shore, using a discrete sampling method. Both species feed during nocturnal low tide and rest during the day and high tide. Due to this activity rhythm, individual positions recorded during diurnal and nocturnal low tides give information on the rest habits of the chitons and on their movements, respectively. The resting and feeding fixes were analyzed with two new complementary methods. Both species show a distinct homing behaviour with periodical shift to new homes more frequent in *A. brevispinosa* than in *A. gemmata*. The latter species shows a stronger constancy to its feeding ground. The two species differ most in the orientation and length of their excursions. Due to their different movement pattern the two species minimize zonal overlapping during the night, which in turn reduces the interspecific competition for food.

Introduction

Many aspects of the behavioural ecology of intertidal chitons have been reported since the first study of Arey and Crozier (1919) on *Chiton tuberculatus*. Several species studied show a "homing behaviour" similar to the movement pattern described in prosobranch and pulmonate limpets and in opisthobranchs (for ample reviews on the movements of intertidal molluscs see Newell, 1979; Underwood, 1979; Chelazzi, 1980).

More or less definite homing behaviour has been described in the chitons *Acanthopleura granulata* (Glynn, 1970), *Acanthozostera gemmata* (Thorne, 1968), *Chiton stokesii* (Schmidt-Effing, 1980), *Chiton tuberculatus* (Arey and Crozier, 1919; Glynn, 1970), *Cyanoplax hartwegii* (Wentworth Lyman, 1975), *Ischnochiton dispar* (Schmidt-Effing, 1980), *Mopalia muscosa* (Stewart Connor, 1975;

Smith, 1975), *Sipharochiton pelliserpentis* (John, in Knox, 1963; Miller and Batt, 1973).

While most of these studies contain interesting information they suffer from the same methodological shortcomings (non-individual recording, small sample size, short study period, inadequate statistical analysis) found in many reports on the movements of other littoral molluscs. We agree with Hamilton (1978) and Underwood (1978) that a more quantitative and statistical approach to the field study of these phenomena is necessary in order to avoid some of the confusion surrounding the previous investigations.

The present study was based mainly on the discrete sampling of positions because the method of frequent monitoring, such as that employed by Hartnoll and Wright (1977) on *Patella vulgata*, Hirano (1979a) on *Cellana toreuma* and Chelazzi (1982) on *Nerita polita*, reveals the tracks of single individuals in detail but is not a useful method for positioning a large number of chitons over a long time.

Both the *Acanthopleura* species chosen are present on shores where the ecology of molluscan assemblages has already been investigated (Chelazzi and Vannini, 1980). Moreover, one of the most interesting – though not exhaustive – studies on chitons' movements was conducted by Thorne (1968) on *Acanthozostera* (=*Acanthopleura*) *gemmata*, constituting a useful background for a quantitative and statistical analysis.

Both species feed on epi- and endolithic microflora without important differences in their diet (Chelazzi and Sartoni, in press), which makes interspecific food competition an important ecological factor in areas where both are present.

Materials and methods

Study area, species and surveys. The study was conducted 20 km south of Mogadishu (Somalia) on the rocky shore

of the Nimù peninsula, where *Acanthopleura brevispinosa* (Sowerby) and *A. gemmata* (Blainville) are the most common algal grazer molluscs. The zonation and density of the two species were reported by Chelazzi and Vannini (1980) for various Somalian shores; in that paper *A. brevispinosa* and *A. gemmata* were referred to as *A.* cf. *borbonica* (Deshayes) and *A. spinigera* (Sowerby), respectively. The new identification of the two species was made by Ferreira (in press). The two species, morphologically very similar, differ in size on the Nimù shore: *A. brevispinosa* never exceeds a length of 5 cm, while *A. gemmata* as long as 8 cm have been found. Their zonation also differs: *A. brevispinosa* reaches a maximum density about 155 cm above the cliff foot, while *A. gemmata* is most abundant about 85 cm above the foot; however, their zones partially overlap.

Nearly all chitons (40 *Acanthopleura brevispinosa* and 160 *A. gemmata*), longer than 25 mm and present in a segment of the coast 7 m long, were individually marked with numbered plastic labels (diameter 2.5 mm) attached to the middle of the second shell plate.

Individual positions were recorded once during each of 55 low tides (August, 1980) when the study area was systematically inspected for about 2 h. Tides are mixed semidiurnal along the Somalian coast (Vannini *et al.*, 1977): at spring tides one low tide is diurnal and the next nocturnal, while at neap tides both are crepuscular.

Plotting of positions. A reference grid for fixing the chitons' position was obtained by screwing 29 numbered steel stakes into the rock. The distance between the stakes provided the rectangular coordinates of each stake relative to arbitrary x_0, y_0. The cliff has a typical intertidal notch near the mean level of high spring tides, but the reference grid was assessed to permit the plotting of coordinates on the plane by taking into account the main features of the shore. The distance of the chitons from three convenient stakes was recorded in the field and then the trio of distances was elaborated to obtain the fix.

Analysis of data. Due to the combined diurnal-tidal rhythm of their activity (see "Results"), the diurnal and nocturnal positions of the chitons could be assumed, respectively, as resting and activity points. Since no sure statements could be made about the activity at twilight, positions recorded during neap tides were omitted from the successive analysis. A total of 3 461 resting and 3 558 feeding positions were obtained.

The spatial activity of chitons was analyzed using two methods (A and B). Method A classified the behaviour of each chiton according to the global compactness of the spatial distribution of its resting points and the number of subunits (foci) present in each individual system. First, the mean value ($\bar{c}$) of the distance between each rest position of the chiton and its nearest fix was computed, giving information on the compactness of the system regardless of the number of foci present. The mean value of this index ($\bar{\bar{c}}$) relative to the whole sample of each species, plus
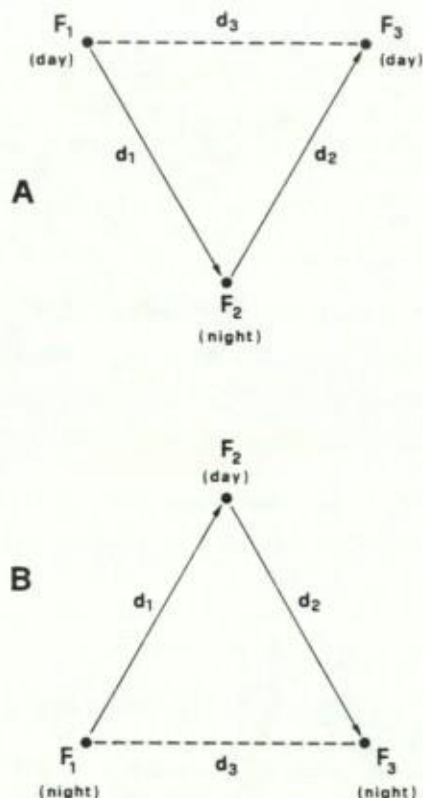

Fig. 1. *Acanthopleura brevispinosa* and *A. gemmata*. Schematic representation of Method B used for the analysis of the homing performance (A) and pattern of nocturnal movement (B) in chitons. F_{1-3} represent three ideal consecutive fixes on which the t rapport is computed

its standard deviation, was then used to obtain the number of subunits of the system (f): two resting fixes were considered as belonging to the same subunit if their distance was less than or equal to $\bar{c} + SD$. Fixes whose distance from the nearest resting point was longer than this threshold were considered free-points. Only individual systems consisting of ten or more resting points were considered for this analysis. The two species were compared by considering separately the frequency distribution of $\bar{c}$ and f, using the Mann-Whitney U-test and the chi-square test, respectively. A comparison was also made relative to the free points.

Method B analyzed the homing behaviour of each chiton relative to the length of its feeding excursions. Trios of consecutive fixes were considered (Fig. 1 A): the distance (d_3) between two resting points recorded during successive diurnal low tides was divided by the mean distance $(d_1 + d_2)/2$ between the two fixes and the feeding point recorded during the interposed nocturnal low tide. This ratio (t) tends toward zero when the d_3 distance is very small compared to the excursion length (signifying a good homing performance), while it nears a value of two when the d_3 distance is very large compared to the feeding excursion (signifying dispersive movement). With random movements t assumes values between zero and two, depending on the actual random pattern. When d_1 and d_2

are nearly equal and the chitons have the same probability to move in the different directions of the plane, its value lies around 1.4. The t ratio was not computed when d_1 was shorter than 5 cm (in order to avoid considering the lack of nocturnal movement as a good homing performance), except when the d_2 distance was longer than 5 cm. The mean value of this ratio $(\bar{t})$ for each chiton with three or more trios was taken as the index of individual homing performance. The two species were compared by testing their $\bar{t}$ distribution using the Mann-Whitney U-test. Moreover, the overall t distributions of each species were compared. Finally, the temporal evolution of the homing performance was assessed by considering the individual cumulative curves of t in time.

Method B was also used to analyze the feeding pattern of both species, by merely reversing the trios (Fig. 1 B): the t ratio was computed from the distance separating two feeding points recorded during successive nocturnal low tides and the mean segment connecting both points to the interposed diurnal fix. In this case, the t ratio tends toward zero when the chiton makes reiterative use of the same feeding point, toward two when successive feeding points lie in opposite directions relative to the resting point, and assumes intermediate values when they move randomly during successive feeding trips. The t ratio for the feeding activity was not computed when either d_1 or d_2 was shorter than 5 cm, in order to avoid classifying the lack of nocturnal movement as a reiterative use of the same feeding area.

Further analysis was conducted on the feeding activity of chitons. Each vector connecting a diurnal point to the following nocturnal fix was considered as a feeding excursion. The azimuth of these vectors with respect to the vertical (Φ_i) were pooled to obtain the individual (m_a) and session (m_s) mean vectors, with mean direction $\bar{\Phi}$ and length r. The second-order resultant vectors for individual and session samples were calculated from the $\bar{\Phi}_a$ and $\bar{\Phi}_s$ distributions, respectively. Circular distributions were analyzed with the methods proposed by Batschelet (1981): Rayleigh's test was used for randomness and the Watson's U^2 test for comparing two circular distributions. The lengths of feeding excursions (l_i) were also considered, obtaining the individual $(\bar{l}_a)$ and sessions $(\bar{l}_s)$ mean excursions. The m_a and $\bar{l}_a$ parameters were computed only for chitons recorded in ten or more diads of successive diurnal-nocturnal sessions.

Results

Checking the position of a few chitons at 30-min intervals during low tide, and inspecting the study area at high tide, revealed that both species follow a diurnal-tidal rhythm of activity (Fig. 2A–B). During high tides and diurnal low tides they rest in natural depressions and small crevices of the cliff (*Acanthopleura brevispinosa*) or mostly in hollows actively dug in the rock (*A. gemmata*). When the receding nocturnal tide (20:00–04:00 hrs) reaches their rest posi-

tions, the chitons move out quickly, then slow down and start to feed. The noise made by their scraping of the algal film from the rocks is clearly audible throughout the low tide. Before the return of the tide to their feeding level, the chitons quickly return to a resting point.

Qualitative analysis of all the diurnal and nocturnal positions mapped for both species (Fig. 3A–C) shows that most of the rest positions are clumped in a few restricted areas, while the spatial distribution of the feeding points is comparatively scattered.

Homing behaviour. According to Method A the spatial pattern of the rest points is the same for individuals of both species (Fig. 4A–B). Though some individuals had up to five foci, about 50 percent showed a single-focus pattern and strong compact resting points $(\bar{c} \leq 10$ mm). The second-order mean value of the distance between nearest fixes is nearly identical for *Acanthopleura brevispinosa* $(\bar{c} = 14.0$ mm) and *A. gemmata* $(\bar{c} = 13.5$ mm), and no statistical difference between the two species emerged from the comparison of individual compactness (Mann-Whitney U-test: $U = 1\,592$; $z = 0.710$; $P = 0.239$) and number of subunits (chi-square $= 0.558$; $P > 0.70$). Also the number of resting points not belonging to a focus – which can be taken as an index of imprecision in the relocation of the resting point – is almost equal in the two species; the individual systems with more than 5 percent of free points are 32 of 112 in *A. gemmata* and 12 of 31 in *A. brevispinosa* (chi-square $= 1.172$; $P > 0.20$).

Method B confirmed that in both species, the most frequent movement pattern is homing behaviour. The frequency distributions of all the computed t's (Fig. 5A–B) show that site-conservative patterns $(0 \leq t \leq 0.5)$ are predominant, that random movements $(0.5 < t < 1.5)$ are nearly absent and that dispersive movements $(1.5 \leq t \leq 2.0)$ are a minor fraction of the total both in *Acanthopleura brevispinosa* (14.4 percent) and *A. gemmata* (7.6 percent). Analysis of the distribution of individual $\bar{t}$ (reported in the same diagrams) reveals a slightly stronger homing performance in *A. gemmata* $(\bar{t} = 0.243)$ than in *A. brevispinosa* $(\bar{t} = 0.415)$. However, the difference is minimal and not statistically significant with the present sample size $(U = 1\,144$; $z = 1.90$; $P = 0.138)$.

The $\bar{t}$ distributions suggest that there is no sharp distinction between homer and disperser individuals in both species, but most chitons are more or less affected by dispersive movements. The cumulative curves of t in time obtained for each chiton (Fig. 6A–D) reveals that the most frequent pattern consists of sequences of constant homing behaviour, interrupted by a few dispersive events.

Feeding excursions. Method B was applied to the night-day-night trios of fixes. The frequency distribution of all the t computed (Fig. 7A–B) show a first peak for $0.4 \leq t \leq 0.6$ in *Acanthopleura brevispinosa* and for $0.2 \leq t \leq 0.4$ in *A. gemmata*, while dispersive movements $(t \geq 1.5)$ are respectively, 30.9 and 21.0 percent of the total. The individual $\bar{t}$ distributions show *A. gemmata* to be relatively
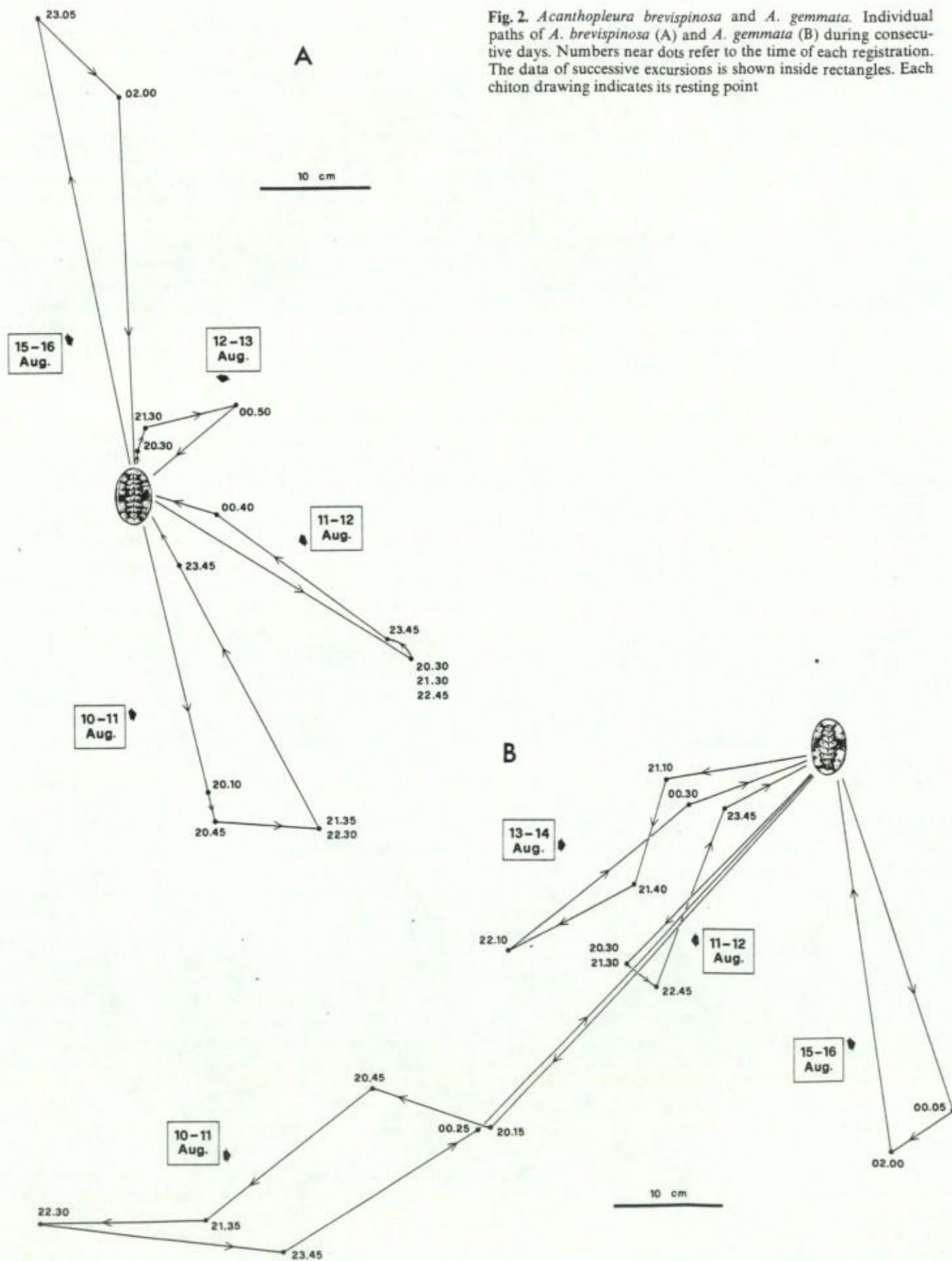
Fig. 2. *Acanthopleura brevispinosa* and *A. gemmata.* Individual paths of *A. brevispinosa* (A) and *A. gemmata* (B) during consecutive days. Numbers near dots refer to the time of each registration. The data of successive excursions is shown inside rectangles. Each chiton drawing indicates its resting point
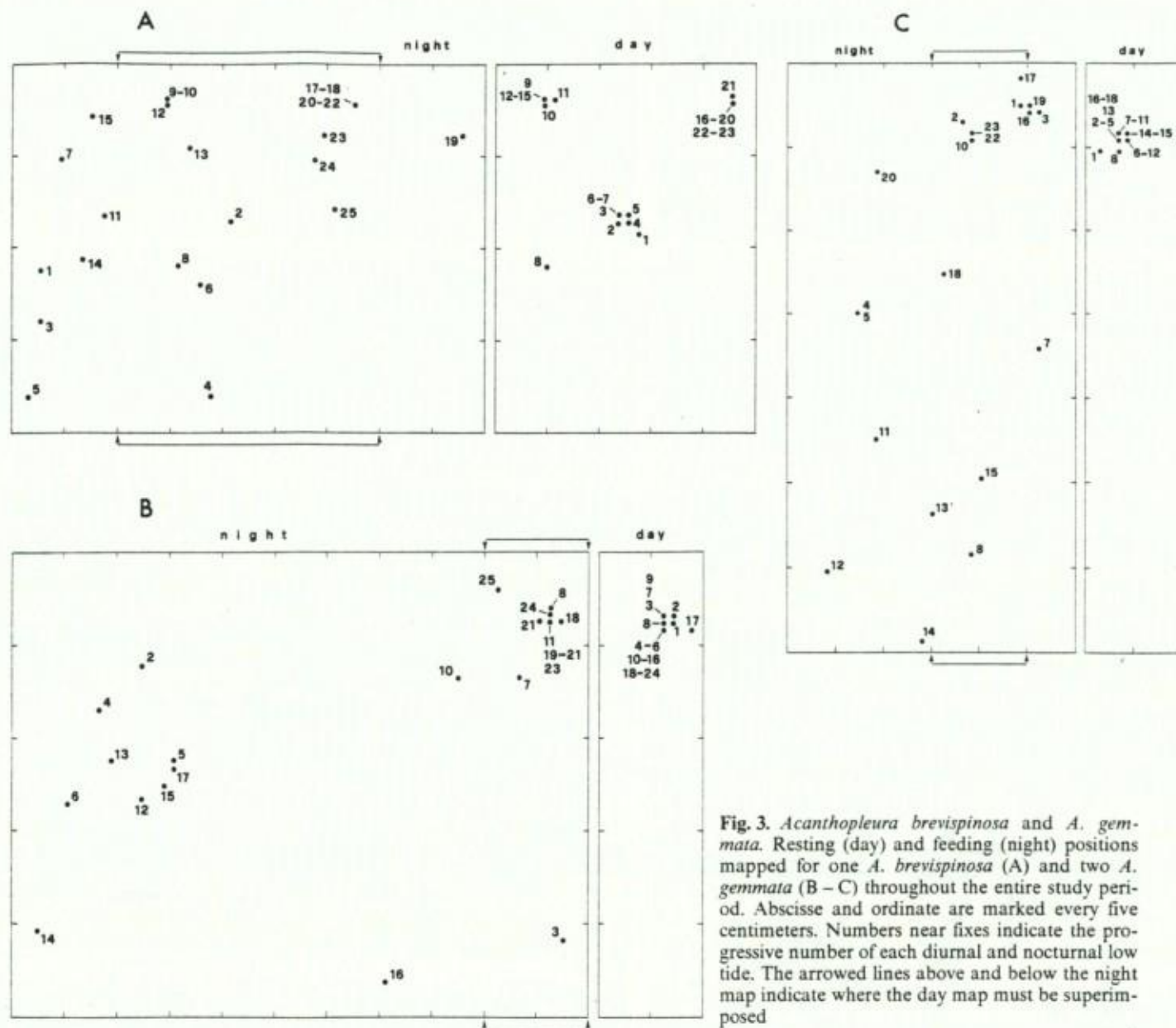
Fig. 3. *Acanthopleura brevispinosa* and *A. gemmata*. Resting (day) and feeding (night) positions mapped for one *A. brevispinosa* (A) and two *A. gemmata* (B – C) throughout the entire study period. Abscisse and ordinate are marked every five centimeters. Numbers near fixes indicate the progressive number of each diurnal and nocturnal low tide. The arrowed lines above and below the night map indicate where the day map must be superimposed

more site-conservative even while feeding; the second-order mean value of its t is smaller ($\bar{t} = 0.851$) than that of *A. brevispinosa* ($\bar{t} = 1.048$), and this difference is statistically significant (U = 982; z = 2.28; P = 0.01).

Supplementary information on the feeding movements of the two species emerged from the analysis of the orientation and length of their nocturnal excursions. The frequency polygon of all the recorded trips (Φ_i), and the individual and session mean directions ($\bar{\Phi}_a$ and $\bar{\Phi}_s$, respectively) show a small vertical component in the pattern followed by *Acanthopleura brevispinosa* (zone conservative), while *A. gemmata* shows vertical movements with a dominant downward component (Fig. 8 A–B).

The Rayleigh test gives a statistical difference from the uniformity when applied to the distribution of $\bar{\Phi}_a$ in *Acanthopleura gemmata* (P < 0.01), but not in *A. brevispinosa* (P > 0.1). Analogies exist between the two distributions: a slight up-down bimodality and weak leftward component (probably due to the local micromorphology of the shore), but with a difference in orientation of 63°. The lack of statistical difference ($U^2_{29,99} = 0.109$; P > 0.1) is probably due to the large size difference between the two samples. Moreover, the lengths of individual resultant vectors reveal that *A. gemmata* performs excursions in a narrower range of directions ($\bar{r}_a = 0.471$) than *A. brevispinosa* ($\bar{r}_a = 0.395$).

The distribution of $\bar{\Phi}_s$ is not uniform in both *Acanthopleura brevispinosa* (P < 0.01) and *A. gemmata* (P < 0.001), but the mean length of the resultant vectors of the sessions is longer for the latter ($\bar{r}_s = 0.626$) than for the former ($\bar{r}_s =$
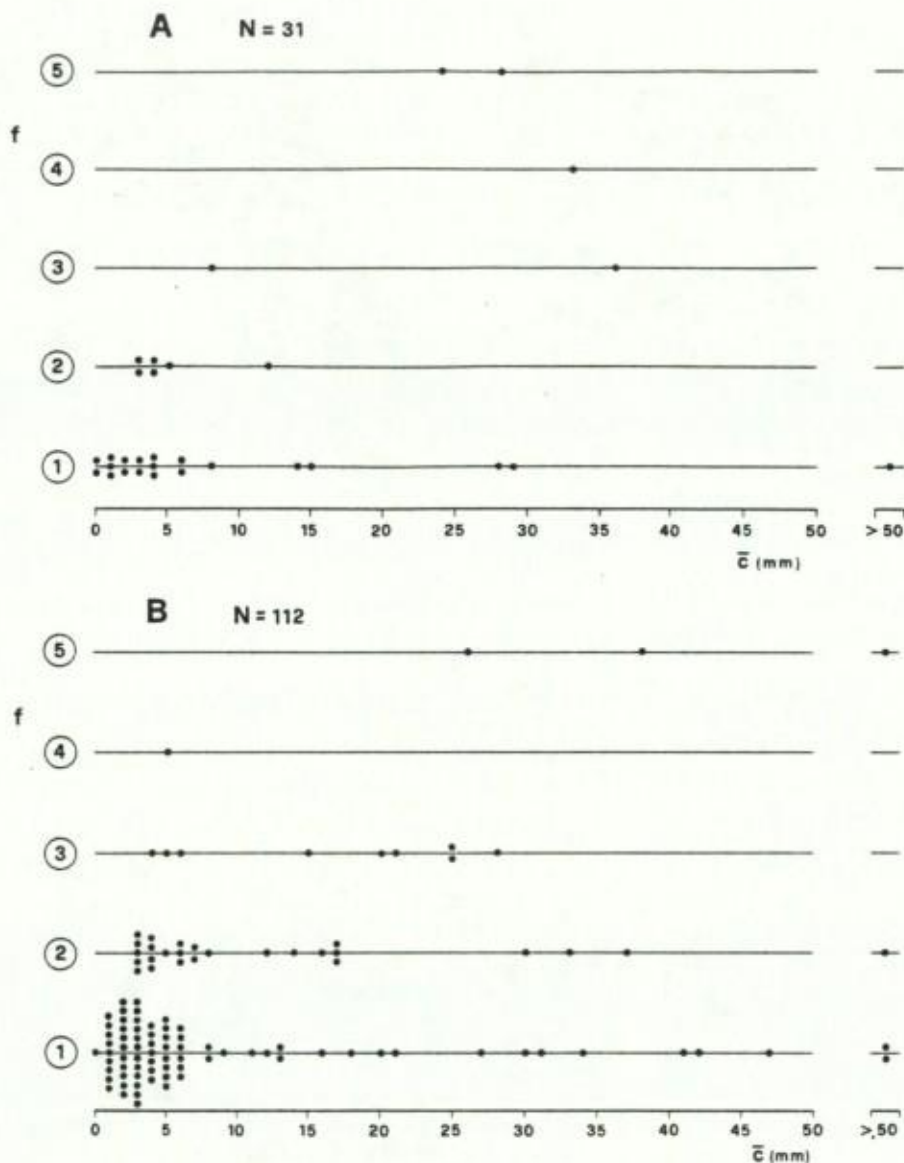
Fig. 4. *Acanthopleura brevispinosa* and *A. gemmata.* Individual systems of resting points of *A. brevispinosa* (A) and *A. gemmata* (B) analyzed according to method A. Abscisse: mean distance between resting fixes of each chiton ($\bar{c}$). Ordinate: number of subunits of each individual system (f)

0.509). The two second-order resultant directions differ by 86°; direct comparison revealed a significant difference ($U^2_{22,22} = 0.414$; $P < 0.01$).

Both species show a regular variation in the length of their feeding excursions throughout the spring-neap cycle: the mean length ($\bar{l}_s$) reaches a minimum around neap tides and a maximum between neap and spring (Fig. 9A–B). Nevertheless, the two species differ in the second-order mean length of their excursions, larger in *Acanthopleura gemmata* ($\bar{l}_a = 22.8$ cm) than in *A. brevispinosa* ($\bar{l}_a = 10.7$ cm); the difference between the two distributions of individual $\bar{l}_a$ (Fig. 10A–B) is statistically significant (U = 477; z = 5.46; $P < 0.00003$).

Discussion

Use of the discrete sampling method in studying animal movement patterns requires a knowledge of their activity rhythms in order to sample all the relevant parts of their behavioural cycle and avoid the uncontrolled mixing of positions relative to the different phases of their activity rhythm. This is particularly true in the study of intertidal animals, whose activity is shaped in time by complex interactions of diurnal and tidal rhythms.

No general rules can be obtained for the time modulation of activity in littoral molluscs where the intraspecific differences are sometimes very large. Prosobranch limpets seem to move mainly once a day, during high tide or by night (Hartnoll and Wright, 1977; Newell, 1979), while pulmonate limpets move mostly when splashed by the ebbing or flooding tide (Thomas, 1973). Such chiton species as *Mopalia lignosa* (Fulton, 1975) move and rest according to the time of the day, while *Nuttalina californica* (Nishi, 1975) moves according to the tidal regime. *Chiton stokesi* (Schmidt-Effing, 1980) and, probably, *Cyanoplax hartwegii* (Wentworth-Lymann, 1975) show a
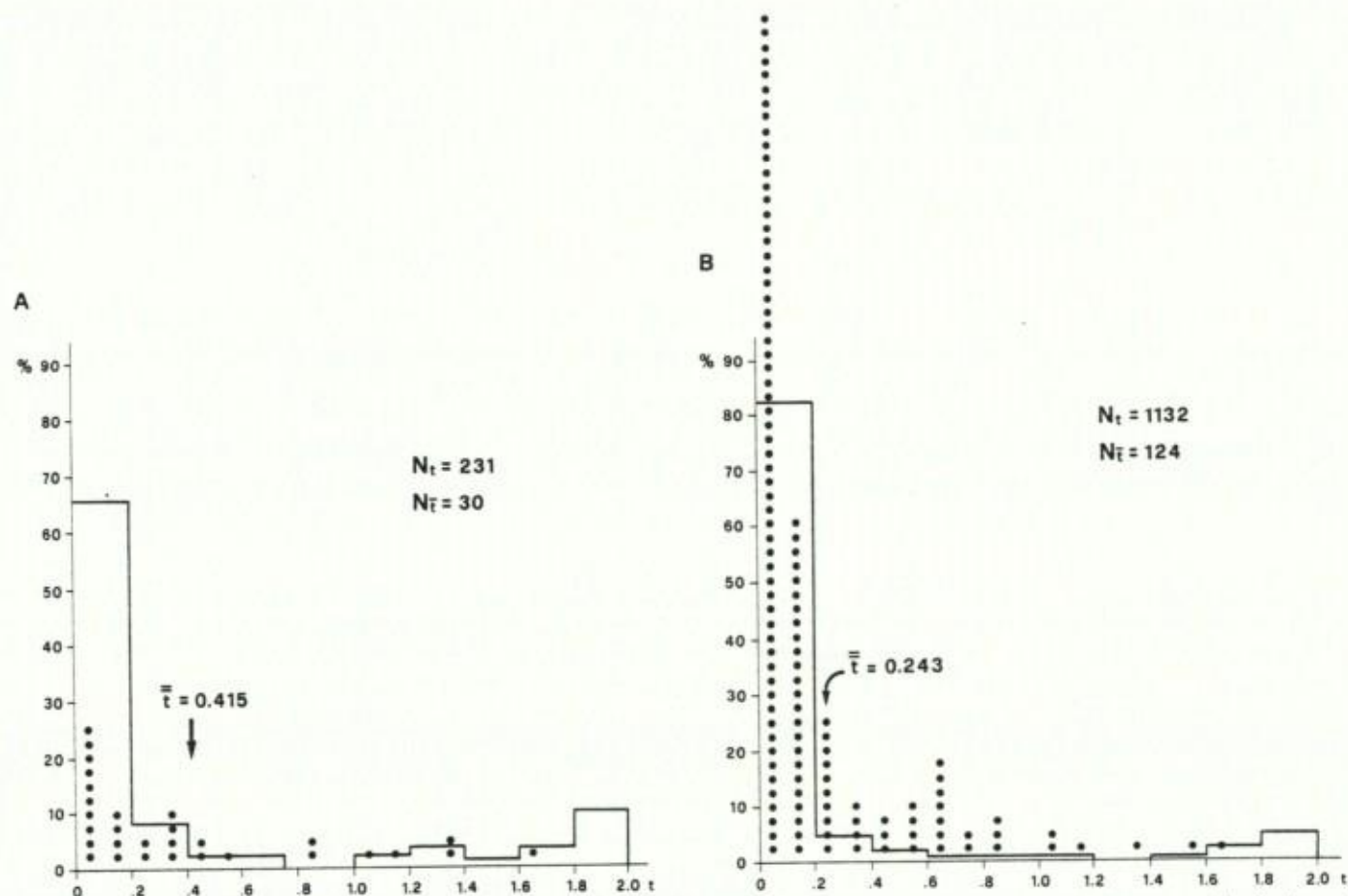
Fig. 5. *Acanthopleura brevispinosa* and *A. gemmata*. Analysis of the day-night-day trios of positions (method B). Frequency distribution of all t computed (histogram) and t̄ of each chiton (dots) for *A. brevispinosa* (A) and *A. gemmata* (B)
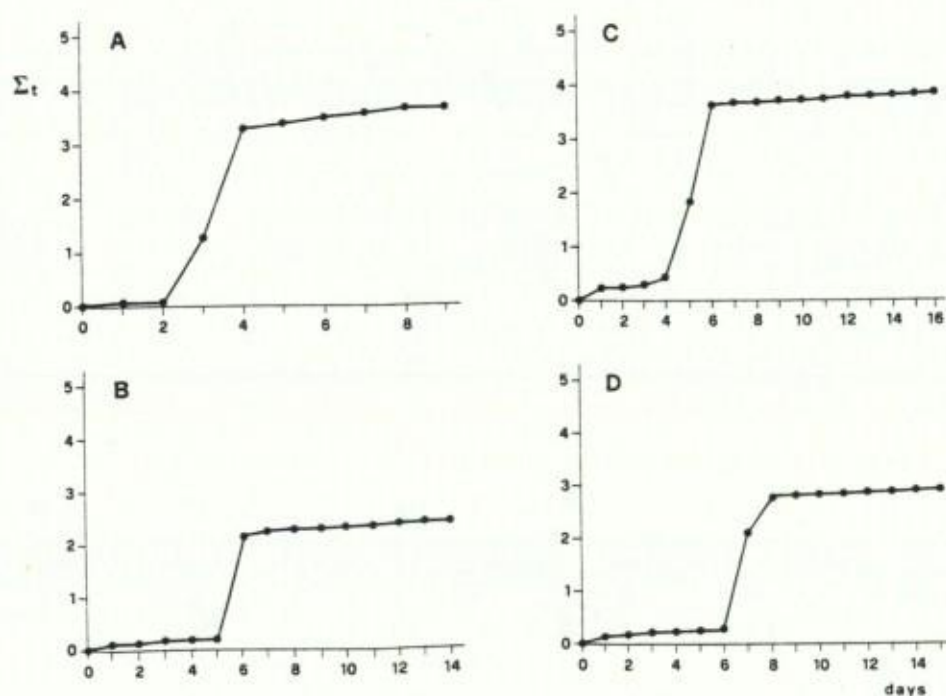

Fig. 6. *Acanthopleura brevispinosa* and *A. gemmata*. Cumulative curves of t in time, relative to the day-night-day trios of positions. Two examples for *A. brevispinosa* (A – B) and *A. gemmata* (C – D) are shown
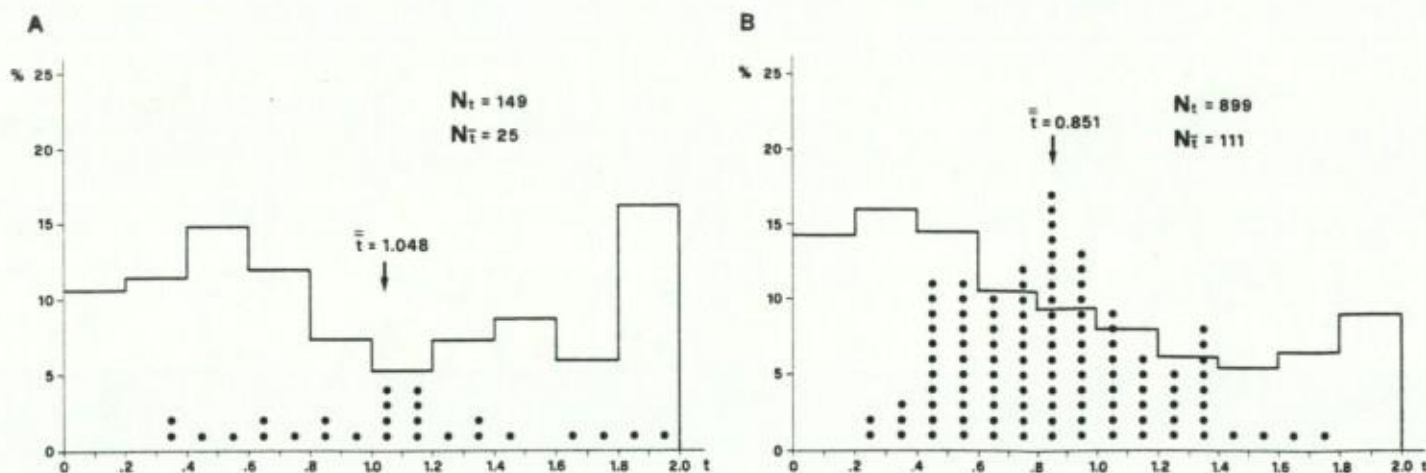
A

B

Fig. 7. *Acanthopleura brevispinosa* and *A. gemmata*. Analysis of the night-day-night trios of positions (method B). Frequency distribution of all t computed (histogram) and t̄ of each chiton (dots) for *A. brevispinosa* (A) and *A. gemmata* (B)
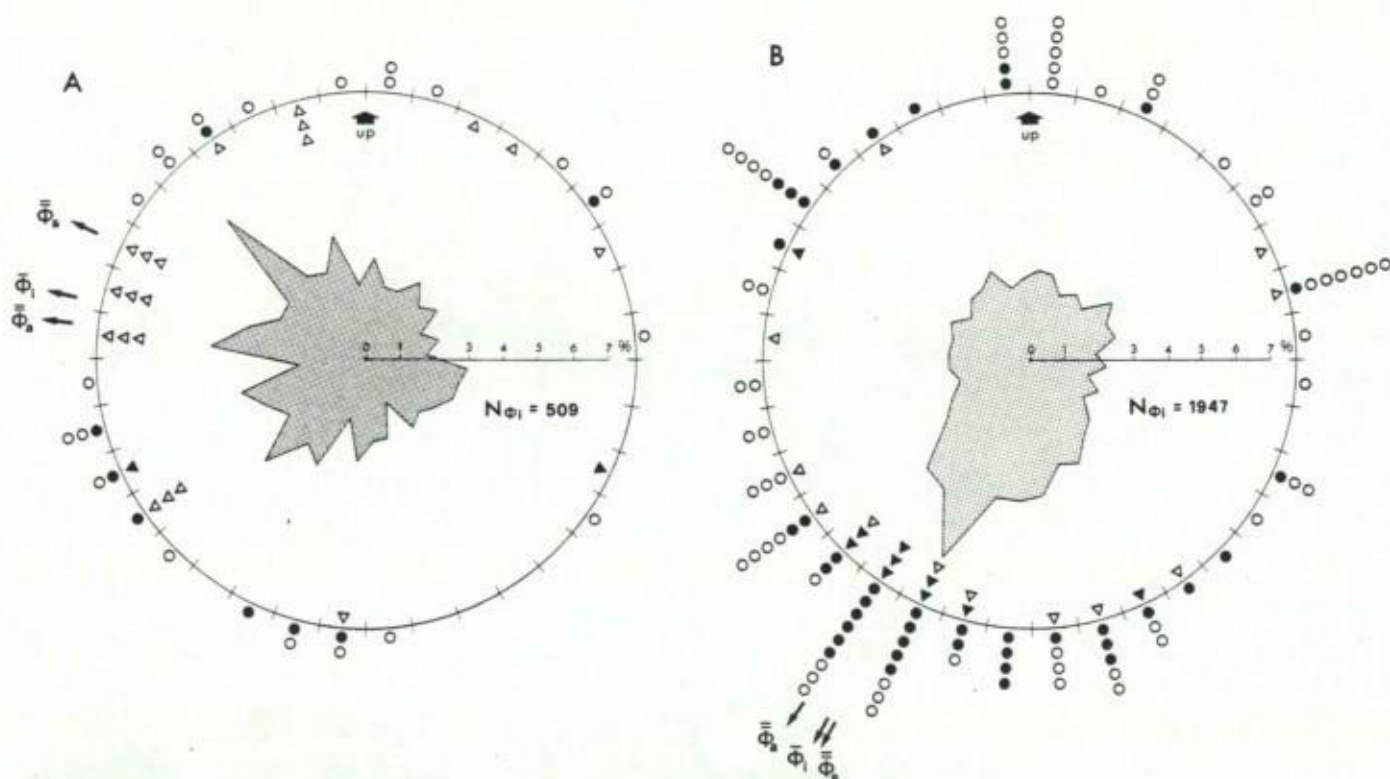
A

B

Fig. 8. *Acanthopleura brevispinosa* and *A. gemmata*. Orientation of the nocturnal excursions of *A. brevispinosa* (A) and *A. gemmata* (B). Frequency distribution (in percentage) of all Φ_i recorded (inner polygon); distribution of $\bar{\Phi}_s$ (triangles) and of $\bar{\Phi}_a$ (circles). Filled symbols refer to resultant directions of non-uniform distributions (Rayleigh test: $P < 0.05$). Outer arrows show the second-order resultant directions of the Φ_i ($\bar{\bar{\Phi}}_i$), of the $\bar{\Phi}_s$ ($\bar{\bar{\Phi}}_s$), and of the $\bar{\Phi}_a$ ($\bar{\bar{\Phi}}_a$) distributions

more complex diurnal-tidal rhythm. Also the *Acanthopleura* spp. of this study share an integrated diurnal-tidal rhythm in common with other littoral molluscs (such as *Nerita* spp.) living on tropical shores with semidiurnal tides (Vannini and Chelazzi, 1978; Chelazzi, 1982). Since their activity (feeding excursions) occurs only during nocturnal low tides, sampling their position at each low tide (twice a day) gives all the information necessary for

the understanding of their spatial behaviour, i.e. resting habits and foraging strategy.

Widely quoted discrete sampling studies of littoral molluscs suffered from inadequate temporal schedules. Frank (1964) recorded the position of a large number of marked *Acmaea digitalis* over a long time, but apparently paid no attention to their activity cycle. Underwood (1977) developed a quantitative method for studying the move-
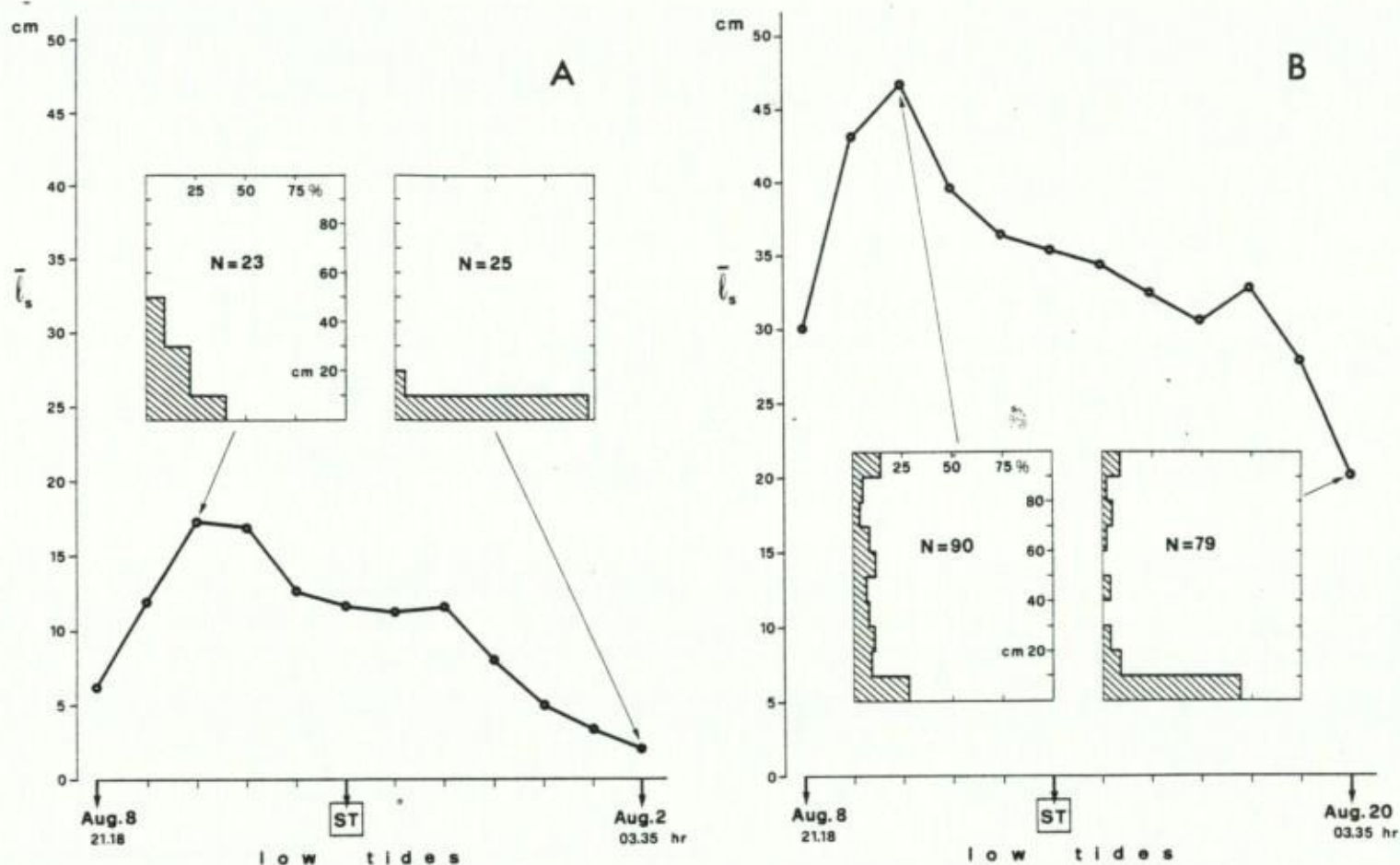
Fig. 9. *Acanthopleura brevispinosa* and *A. gemmata.* Variation of the mean excursion length ($\bar{l}_s$) during the central part of the study period in *A. brevispinosa* (A) and *A. gemmata* (B). The insets show the frequency distributions of individual excursion lengths relative to the nights with the longer and shorter mean value
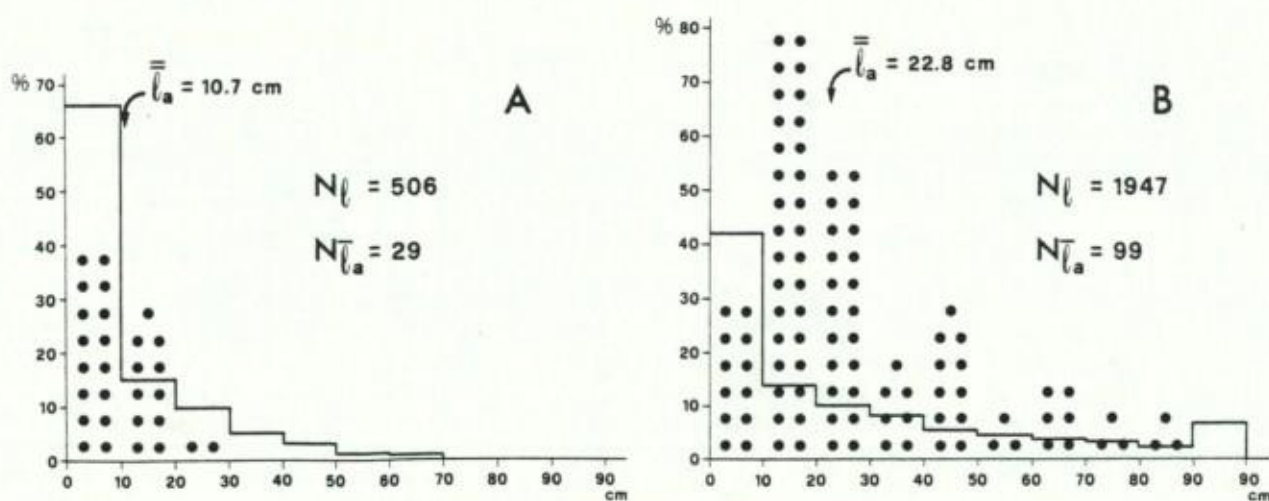

Fig. 10. *Acanthopleura brevispinosa* and *A. gemmata.* Length of the feeding excursions in *A. brevispinosa* (A) and *A. gemmata* (B). Frequency distribution of all distances recorded (histogram) and individual mean values (dots)

ments of some Australian intertidal gastropods, later applied to different ecological investigations (Mackay and Underwood, 1977; Creese and Underwood, 1982), but his diurnal sampling overlooked the feeding phase of the species investigated. Underwood's method allows an analysis of constancy to the resting site, but not a true definition of the movement pattern. The author's correct statistical analysis and his model of random movement
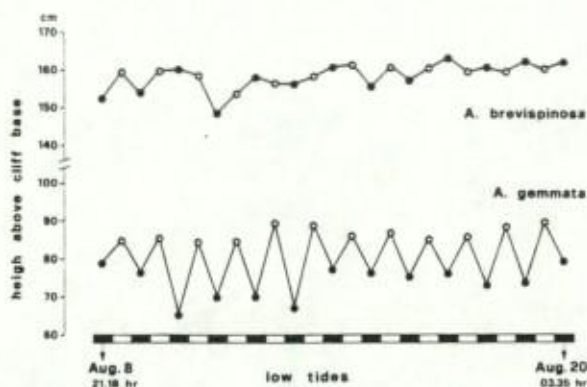
Fig. 11. *Acanthopleura brevispinosa* and *A. gemmata*. Diurnal (open circles) and nocturnal (filled circles) mean levels above the cliff base occupied by the two species in the study area, during the central part of the study period

hardly compensate for the lack of complete information, which obviously includes the feeding strategy of the individuals.

Our Method A, based only on the analysis of the resting points, failed to reveal any significant difference in the behaviour of the two *Acanthopleura* spp. Only Method B, based on both diurnal and nocturnal points, and the direct analysis of the feeding excursions, revealed behavioural differences, which reduce interspecific food competition and allow the two species to colonize the same stretches of coast.

Both species show a strong constancy to their resting site over short periods, but periodically move to a new site. *Acanthopleura brevispinosa* changes its resting position more frequently, probably in relation to the use of less differentiated sites with respect to *A. gemmata* (Chelazzi et al., in preparation). Periodical shifts to a new home are commonly recorded in other littoral molluscs, such as *Cellana nigrolineata* (Hirano, 1979 b) and *Patella vulgata* (Jones, 1948; Lewis, 1954). The frequent shift to a new home seems typical of juveniles among homer limpets, and this behaviour is not surprising in chitons, which lack a protruding shell precisely fitted to the irregularities of the rock at the resting point.

A second and more evident difference between the two species concerns the use of the feeding area. Again *Acanthopleura brevispinosa* changes its feeding ground more frequently, probably due to the more uniform distribution of the algal film at the level occupied by this species. On the contrary, *A. gemmata* – which usually frequents a lower level in the eulittoral, where algal diversity is higher and species are distributed in patches – is more site-conservative.

The most striking and ecologically significant difference between the two species emerged from the study of the orientation and extension of their feeding excursions. The prevailing downward orientation and longer excursions to reach the feeding ground allow *Acanthopleura gemmata* to exploit the algal canopy of the lower eulittoral,

where *A. brevispinosa* has never been recorded. The critical mechanism in reducing interspecific competition for food seems to be this different movement pattern (Fig. 11), which amplifies the zonal separation between the two species while feeding. The reason why *A. gemmata* does not rest at the level where it feeds is probably to reduce predation during high tide (Chelazzi et al., in preparation).

A similar mechanism for reducing food competition is probably widespread among intertidal molluscs and seems present also between *Nerita plicata* (zone-conservative) and *N. textilis* (migrator) when both are present on the same shore (Chelazzi, 1980).

These findings indicate that a more deeply ethological and quantitative approach to the field study of these animals may reveal critical adaptations in the colonization of the intertidal environment.

Literature cited

Arey, L. B. and W. J. Crozier: The sensory responses of *Chiton*. J. exp. Zool. *29*, 157–260 (1919)

Batschelet, E. B.: Circular statistics in biology, 371 pp. London: Academic Press 1981

Chelazzi, G.: Zonazione dinamica e meccanismi di orientamento nei molluschi litorali. Atti Accad. Fisiocr. *52*, 275–293 (1980)

Chelazzi, G.: Behavioural adaptation of the gastropod *Nerita polita* L. on different shores at Aldabra Atoll. Proc. R. Soc. Lond. B *215*, 451–467 (1982)

Chelazzi, G., S. Focardi, J. L. Deneubourg and R. Innocenti: Competition for the home and aggressive behaviour in the chiton *Acanthopleura gemmata* (Blainville) (Mollusca: Polyplacophora) (In preparation)

Chelazzi, G. and G. Sartoni: Analysis of food preferences in two sympatric *Acanthopleura* spp. (Mollusca: Polyplacophora). Monitore zool. ital. (N.S.) Suppl. (In press)

Chelazzi, G. and M. Vannini: Zonation of intertidal molluscs on rocky shores of southern Somalia. Est. coast. mar. Sci. *10*, 569–583 (1980)

Creese, R. G. and A. J. Underwood: Analysis of inter- und intraspecific competition amongst intertidal limpets with different methods of feeding. Oecologia (Berl.) *53*, 337–346 (1982)

Ferreira, A. J.: The chiton fauna of southern Somalia. Monitore zool. ital. (N.S.) Suppl. (In press)

Frank, P. W.: On home range of limpets. Am. Nat. *98*, 99–104 (1964)

Fulton, F. T.: The diet of the chiton *Mopalia lignosa* (Gould, 1846) (Mollusca: Polyplacophora). Veliger *18* (Suppl.), 38–41 (1975)

Glynn, P. W.: On the ecology of the Caribbean chitons *Acanthopleura granulata* Gmelin and *Chiton* Linné: density, mortality, feeding, reproduction and growth. Smitson. Contrib. Zool. *66*, 1–21 (1970)

Hamilton, P. V.: Intertidal distribution and long-term movements of *Littorina irrorata* (Mollusca: Gastropoda). Mar. Biol. *46*, 49–58 (1978)

Hartnoll, R. G. and J. R. Wright: Foraging movements and homing in the limpet *Patella vulgata* L. Anim. Behav. *25*, 806–810 (1977)

Hirano, Y.: Studies on activity pattern of the patellid limpet *Cellana toreuma* (Reeve). J. exp. mar. Biol. Ecol. *40*, 137–148 (1979a)

Hirano, Y.: Activity pattern of the limpet *Cellana nigrolineata*. Venus *38*, 35–47 (1979b)

Jones, N. S.: Observations and experiments on the biology of *Patella vulgata* at Port St. Mary, Isle of Man. Proc. Trans. Liverpool biol. Soc. *56*, 60–77 (1948)

Knox, G. A.: The biogeography and intertidal ecology of the Australasian coasts. Oceanogr. mar. Biol. Ann. Rev. *1*, 341–404 (1963)

Lewis, J. R.: Observations on a high-level population of limpets. J. anim. Ecol. *23*, 85–100 (1954)

Mackay, D. A. and A. J. Underwood: Experimental studies on homing in the intertidal patellid limpet *Cellana tramoserica* (Sowerby). Oecologia (Berl.) *30*, 215–238 (1977)

Miller, M. and G. Batt: Reef and beach life of New Zealand, 141 pp. Hong Kong: Collins 1973

Newell, R. C.: Biology of intertidal animals. Marine ecological surveys, 781 pp. Kent: Faversham 1979

Nishi, R.: The diet and feeding habits of *Nuttalina californica* (Reeve, (1847) from two contrasting habitats in Central California. Veliger *18* (Suppl.), 30–33 (1975)

Schmidt-Effing, U.: Beobachtungen zum Heimfinde-verhalten und zum Aktivitäts-rhythmus von *Chiton stokesii* Broderip, 1832 mit Anmerkungen auch zu *Ischnochiton dispar* (Sowerby, 1832) (Polyplacophora). Zool. Anz. *5/6*, 309–317 (1980)

Smith, S. Y.: Temporal and spatial activity patterns of the intertidal chiton *Mopalia muscosa*. Veliger *18* (Suppl.), 57–62 (1975)

Stewart Connor, M.: Niche apportionment among the chitons *Cyanoplax hartwegii* and *Mopalia muscosa* and the limpets *Collisella limatula* and *Collisella pelta* under the brown alga *Pelvetia fastigiata*. Veliger *18* (Suppl.), 9–17 (1975)

Thomas, R. F.: Homing behaviour and movement rhythms in the pulmonate limpet, *Siphonaria pectinata* Linnaeus. Proc. malac. Soc. Lond. *40*, 303–311 (1973)

Thorne, M. J.: Studies on homing in the chiton *Acanthozostera gemmata*. Aust. J. mar. freshwat. Res. *19*, 151–160 (1968)

Underwood, A. J.: Movements of intertidal gastropods. J. exp. mar. Biol. Ecol. *26*, 191–201 (1977)

Underwood, A. J.: The ecology of intertidal gastropods. Adv. mar. Biol. *16*, 111–210 (1979)

Vannini, M., G. Chelazzi, L. Chelazzi, A. Ercolini, F. Ferrara, G. Messana, P. Messeri and L. Pardi: Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 13. Physical environment: geomorphological notes, climate and tides. Monitore zool. ital. (N.S.) Suppl. *11*, 249–271 (1977)

Vannini, M. and G. Chelazzi: Field observations on the rhythmic behaviour of *Nerita textilis* (Gastropoda: Prosobranchia). Mar. Biol. *45*, 113–121 (1978)

Wentworth Lyman, B.: Activity pattern of the chiton *Cyanoplax hartwegii* (Mollusca: Polyplacophora). Veliger *18* (Suppl.), 63–69 (1975)