

NEW DATA ON THE ECOLOGICAL DISTRIBUTION OF CLADOCERANS AND
FIRST LOCAL OBSERVATIONS ON REPRODUCTION OF
EVADNE NORDMANNI AND *PODON INTERMEDIUS*
(CRUSTACEA, CLADOCERA) IN ARGENTINE SEA WATERS*

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RESUMEN

Nuevos datos sobre la distribución ecológica de los cladóceros y primeras observaciones locales sobre reproducción de *Evadne nordmanni* y *Podon intermedius* (Crustacea, Cladocera) en el mar argentino.

*Fue efectuado el análisis de 200 muestras extraídas entre marzo de 1978 y febrero de 1979, de las cuales 26 presentaron cladóceros, con un total de 3451 ejemplares entre setiembre y enero. Fue observado el contenido del saco embrionario de las especies *Evadne nordmanni* y *Podon intermedius*, y se confrontó su potencial reproductivo con algunas variables como la temperatura del agua, la talla materna y los meses del año. El incremento relativo del número de hembras sexuales, la disminución del contenido embrionario y la reducción de las tallas de las poblaciones partonogénicas al final del ciclo, son relacionadas con la Hipótesis de la Depresión formulada por Berg (1931).*

Knowledge on the abundance and ecological distribution of marine cladocerans is most important for considering their role in the trophic chain, which includes their presence in the food of fish larvae and postlarvae. Their distribution in Argentine waters had been indicated previously (Ramírez and De Vreese, 1974), but without knowledge of their reproductive ecology, which has been partly covered now in the present work. Among the principal works which focus on this aspect in other regions, the following are worthy of mention: Bainbridge (1958), Della Croce (1964), Onbé (1968, 1974), Specchi *et al.* (1975), Corni and Gardenghi (1975), Cheng (1947), Della Croce and Bettanin (1967, 1969), Onbé *et al.*, (1977).

MATERIAL AND METHODS

Plankton samples were obtained by R/V "Walther Herwig" (from the German Federal

Republic) and "Shinkai Maru" (from Japan) between May 1978 and February 1979, in the sector limited by 37°02' - 43°32' S, and 54°48' - 64°65' W (fig. 1), which constituted part of a wide region where environmental and fishery investigations were carried out (Ciechomski *et al.*, 1979; Cousseau *et al.*, 1979). A bongo net, with 60 cm diameter mouth, equipped with a gauze of 330 μ m was obliquely towed never exceeding 100 m even in deep waters, and samples were preserved with 5% formalin. Information on temperature and salinity from surface, 50 and 100 m depth was also obtained. Taking into account that volumes of filtered water were provisional, the numeric results obtained for each species are expressed in percentage values, and not in real figures. 200 samples were analyzed under microscope; of these, 26 collected within the period from September to January were proved positive, summing a total of 3451 specimens. All specimens were set aside for later identification and measurements. Standard length was taken as the distance between anterior margin of head and the tip of the caudal furca. All measurements were carried out with an eye-piece micrometer, in which each division was

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represented 18 μm . Eggs and embryos were counted after dissecting them from each female. Brood pouches contents were classified as "early" and "late" developmental stages; "early" ones corresponded to embryos with developed eye, though as yet unpigmented, and with thoracic feet (which in previous stages were held in a lateral position) facing each other along the sagittal plane (fig. 13 a - e); "late" stages corresponded to embryos with pigmented eye, provided or not with eggs in their brood pouches (fig. 13 f and g).

RESULTS

Monthly and spatial distribution.

Fig. 1 shows positive sampling stations, i.e., stations with presence of cladocerans, and

specific abundances referred to are illustrated in fig. 2. The following results can be extracted from these graphs:

a) the number of positive samples (26) represents 13% of the total observations (200) and their occurrence is restricted to 5 months of the year (from September to January).

b) *Podon intermedius* was the most abundant species, being distributed throughout the latitudes of the region, and extended from coastal to middle shelf waters.

c) *Evadne nordmanni* was a subdominant species, markedly less abundant than *Podon intermedius*.

d) *Podon polyphemoides* was almost absent during the sampling period, except in September, when positive samples were obtained near Mar del Plata.

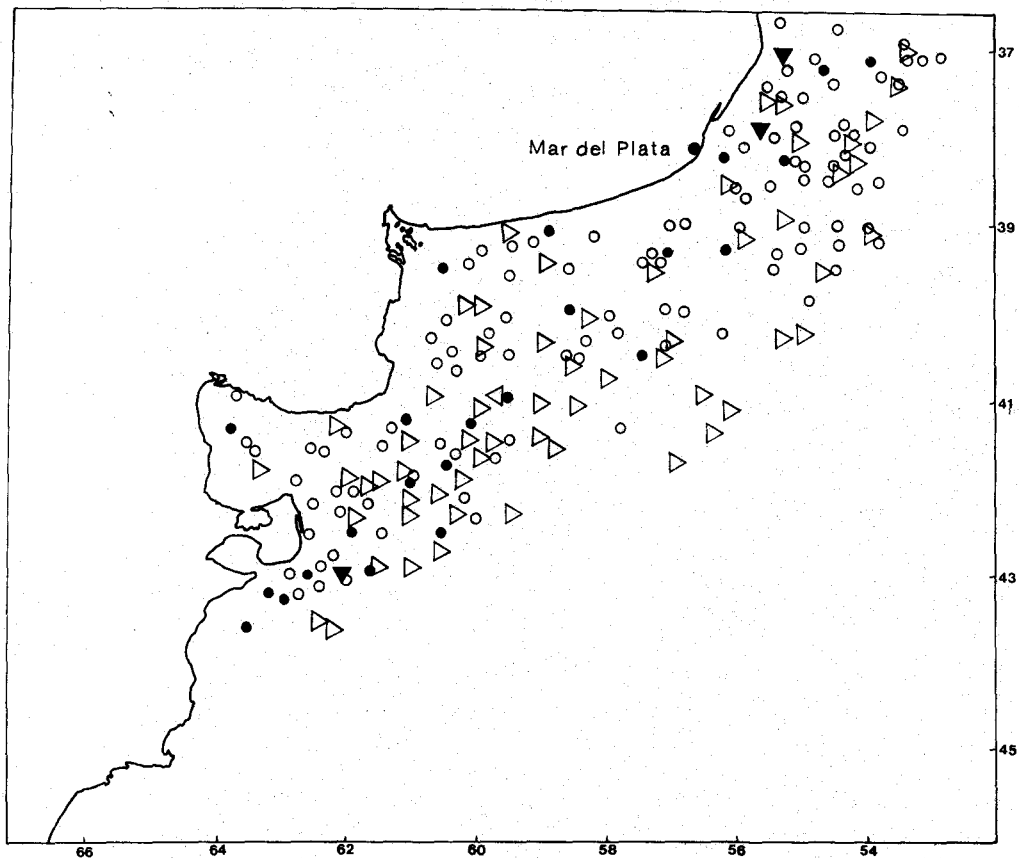


Fig. 1.— Locations of the sampling stations in "Shinkai Maru" (circles) and "Walther Herwig" (triangles) cruises. White: absence; black: presence of specimens.

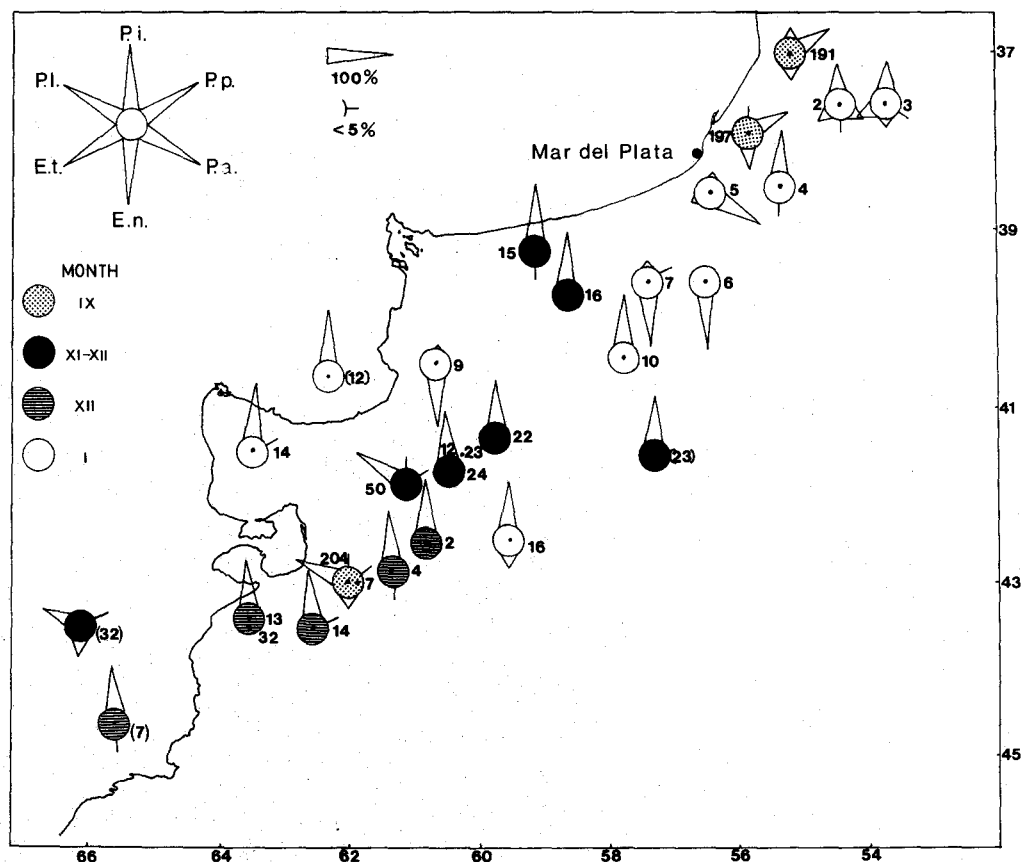


Fig. 2.— Distribution and relative abundance of the cladoceran species. Figures indicate station number.

e) *Penilia avirostris* was found at the northern extreme of the region (38°S) and *Podon leuc-karti* south of 41°S, during the summer and spring cruises, respectively. This last species is recorded for the first time from the region.

T-S graph of positive stations.

Temperature and salinity of the 26 positive stations are shown in fig. 3, based on data obtained at depths between surface and 10 m. The following results can be deduced:

a) Temperatures of Group A, obtained from "W. Herwig V" cruise (September and October) ranged from 9,5° to 11°C, and salinities from 32,26 to 33,49‰.

b) The highest temperatures, which ranged between 18° and 19,8°C, belong to samples of Group D from "Shinkai Maru X" cruise

(January) and salinities ranged from 33,49 to 33,90‰.

c) Samples of Groups B and C, corresponding to "Shinkai Maru VIII" (November and December) and "Shinkai Maru X" (January) had a similar thermic range (14° to 18°C), though differing from each other in salinities, which in the last mentioned cruise reached a maximum of 33,95‰.

Species distribution in relation to temperature and salinity.

The percent abundance of each species for each group above mentioned is shown in fig. 4. Several facts can be pointed out:

a) *Podon polyphemoides* is almost exclusively included in Group A (99,3%).

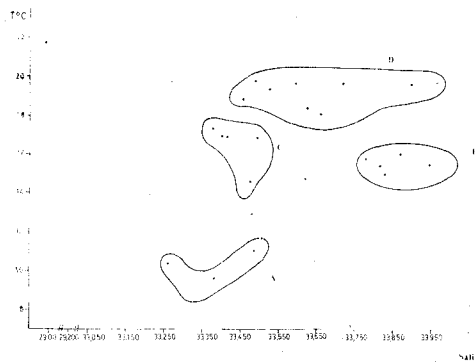


Fig. 3.— T-S diagram of the positive stations. For signs A to D, see fig. 4.

b) *Penilia avirostris* is a species found exclusively in Group D. *Evadne tergestina* distribution is similar to *P. avirostris*, though being also present to a small degree in Group B (0,24%).

c) *Podon intermedius*, *Podon leuckarti* and *Evadne nordmanni* were found each in two of the Groups considered, their presence being shared with the remaining species.

Remarks on *Evadne nordmanni* and *Podon intermedius*.

Monthly size variation. Monthly variation in the average size of both species can be seen in fig. 5. A reduction in length can be observed in both species prior to their disappearance from the plankton.

Reproductivity potential and size. Fig. 6 shows the number of embryos related to maternal length. Adults were grouped by classes of 90 μm . Early and late-stage embryos are separately considered, and their abundance is expressed by different hatching in their corresponding squares. It can be pointed out that:

- a) The maximal number of late-stage embryos in *P. intermedius* is 2,5 times overpassed by that of early ones.
- b) The total number of late-stage embryos per female is greater in *Evadne nordmanni* (range from 1 to 14) than in *Podon intermedius* (1 to 7).
- c) The predominating number of early and late-stage embryos per female of *Podon intermedius* were 3-8 and 2-5, respectively.

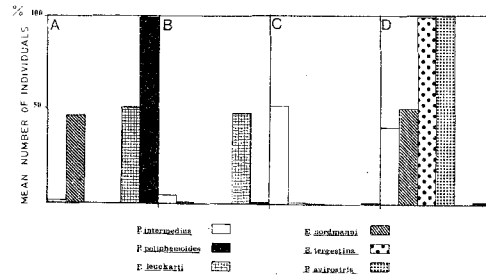


Fig. 4.— Percent distribution of marine cladocerans with respect to temperature and salinity.

d) Embryo number of *Evadne nordmanni* exhibits a more homogeneous distribution, the prevailing number of late and early-stage embryos per female being 1-6 and 2-5 respectively; late-stage embryos are absent at the 828 μm length females.

Fig. 7 shows regression lines corresponding to mean values of late-stage embryos of both species; the slope in *E. nordmanni* is steeper than that corresponding to *Podon intermedius*, and the correlation coefficients for both species are respectively 0,79 and 0,75. Graphs on early-stage embryos are not included, as the coefficients obtained between both variables were too low.

Numerical relationships between early and late-stage embryos per female. Fig. 8 shows comparative histograms, where females are grouped by classes of each 150 μm . An increase in embryo production according to their sizes is remarkable in both species. This is more sudden in *Evadne nordmanni*, specially at 350 and 600 μm lengths.

Quotients between the number of early-stage and late-stage embryos seem to indicate a higher precocious mortality at *Podon intermedius*, where values reached up to 1,82 (900-1050 μm body length). The lowest quotient (1,07) of *Evadne nordmanni* was found at the 450-600 μm body length class. This tendency of the organisms was considered as related to their specific biology, since the observed environmental variables of the samples did not give another answer.

Monthly changes in embryo number as related to adult size. As shown in fig. 9, a net change in the average number of embryos per female was observed through the period considered;

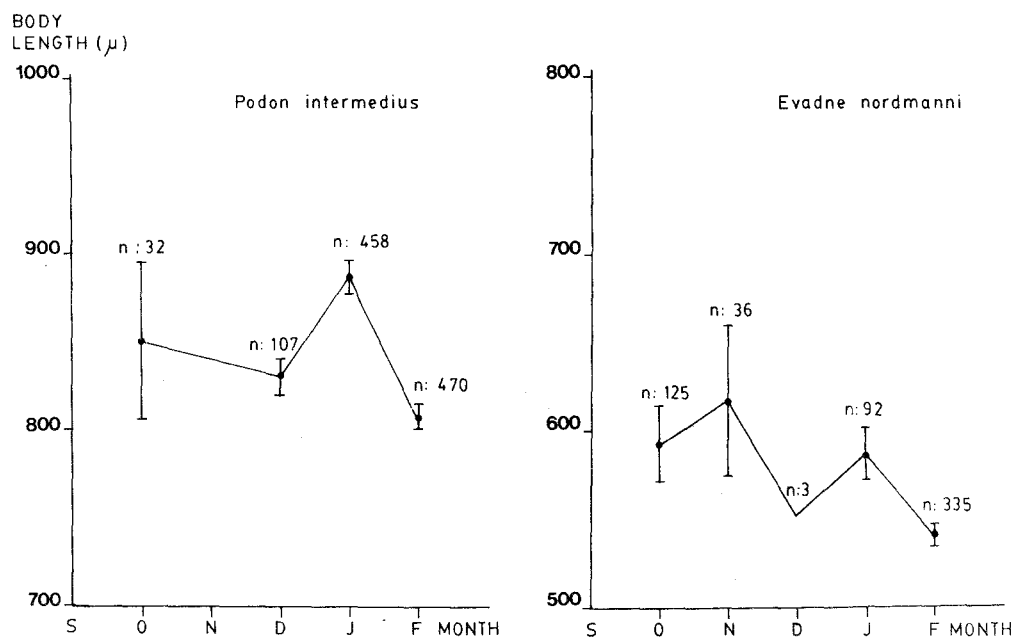


Fig. 5.— Monthly variation in body size of *Evadne nordmanni* and *Podon intermedius*; the vertical lines represent confidence intervals.

the maximum average corresponds to December for *Evadne nordmanni* and September for *Podon intermedius*, and the minimum corresponds to January for both species. These data refer to both stage groups. A remarkable resemblance is observed in the average number of late-stage embryos of *Podon intermedius* in November, December and January samples, especially at adult sizes from 950 μm onwards.

Variation in embryo number in relation to temperature. Regression lines of fig. 10 show negative correlations between temperature and average embryo number per female in both species. In *Evadne nordmanni*, the slope of the line seems to indicate a closer relation to thermic changes, though correlation coefficient of data (r) is low. Conversely for *Podon intermedius*, the slope of the line is lower, being r values more important.

Seasonal variation in abundance of males and gamogenetic females. Females with resting eggs were sorted from the samples between September and January. Their abundance, related with those of the parthenogenetic population, are expressed as percent values in

fig. 11. It can be observed that, while low values are present in the spring samples, both species showed a sudden increase in January, especially in *Evadne nordmanni*, which reached up to 95% in the summer samples. A temporal increase in the percentage of *Podon intermedius* males is also observed, with a maximum of 5% in the January samples. No males of *Evadne nordmanni* were found; no explanation was found for their absence in the samples.

DISCUSSION

Temporal and spatial distribution.

Cladocerans may be considered as circannual organisms, owing to their absence during the winter, when survival is ensured by the presence of their resting eggs at the sea bed. Their appearance and numerical increase are determined by the warming and stability of upper water levels, both causing the eclosion of parthenogenetic females. As it was mentioned by Gieskes (1971), the greater the geographical separation of two areas (or group of areas), the less is the similarity in the annual fluctua-

		Embryo number																				
Body length (Late stage)		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
648			1	5	1																	
738		3	28	26	31	4	3								Podon intermedius							
828		14	56	55	65	27	1	2														
918		3	30	41	62	25	4	1														
1008			5	2	21	16	3															
1098			1	3	8	4																
Early stage																						
648		1	4	5	4	2	4	5	3													
738		1	15	18	34		27	25	18	12	3	3	2									
828		8	21	33	52	46	52	48	48	25	11	4	5	1					2			
918		6	17	30	35	24	31	36	25	14	20	7	2		2		1					
1008			4	10	12	6	8	9	15	9	12	3	2		2							
1098				2	5	2	2	1	2	4	1	1										

		Embryo number																				
Body length (Late stage)		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	
450		5	7	2		1		1	1		1											
540		16	34	15	18	25	16	15	9	7	2	2	2		Evadne nordmanni							
630		1	8	8	1	8	7	7	6	4		2	3	1	2							
720		1	1	1				4	1	2	1		2									
828																						
Early stage																						
450		11	26	12	13	4	1	1	1	2												
540		7	18	12	21	16	15	10	2		5	1		3	1		1	1				
630		2	3	4	2	4	3	1	3	5	3		6	4	5		4	1			1	
720			1			1			1	2	1		1	1	2		1		1		2	
810				3										1			1					

Fig. 6.— Variation in embryo number (early and late stages, separately grouped) per female of *Evadne nordmanni* and *Podon intermedius*; adult sizes are grouped by classes.

tion pattern between the areas (or group of areas) compared. This would limit the comparison of local results from our collection, which was made along a latitudinal front of almost 7 degrees. Nevertheless, equal thermic and saline values of upper waters were found to be obliquely orientated from South to North and East to West.

Likewise, the appearance and abundance of cladocerans in the area under consideration vary from year to year, due to local differences in the oceanographic conditions. A comparison of the results from two annual studies performed between Mar del Plata and the slope in the years 1972 and 1981 (fig. 12) seems to indicate that reproductivity peaks reached

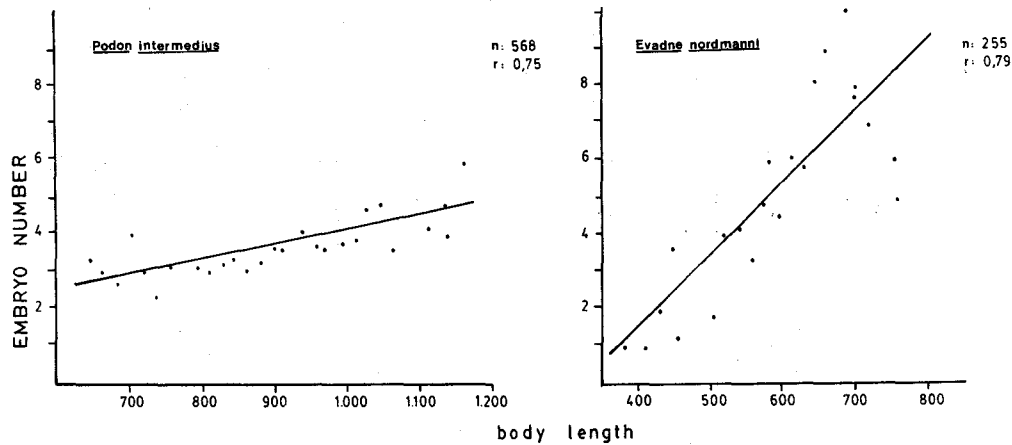


Fig. 7.— Regression lines of late embryo number versus body length of *Evadne nordmanni* and *Podon intermedius*.

their maxima at the beginning and at the end of spring, respectively(*). The secondary peaks in autumn also differ from each other. These facts are influenced by the particular ecology of each species, which differ numerically owing to the effect produced by the gradient of inshore-offshore ecological conditions, from late autumn to the summer period:

a) *Podon polyphemoides* is an estuarine species, living between 5 to 30‰ salinity, and its presence in open waters "may be regarded as an indicator of originally estuarine waters (Gieskes, 1971; see also Jeffries, 1967). It was also found in abundance in Argentine coastal waters of the "Transeccion" cruises (Ramírez and De Vreese, 1974), gradually diminishing towards open waters. In the present work the species mainly occurs in waters of salinities below 33.55‰ (fig. 4). A remarkable fact was the finding of 23,000 and 11,000 ind/m² during the May cruises in inshore waters influenced by the River Plate estuary, with the coexistence

of subtropical indicators, like the Copepods *Centropages furcatus*, *Labidocera fluviatilis* and *Corycaeus amazonicus* (Axelman *et al.*, in prep.).

b) *Penilia avirostris* was found in the northern sector relating to water temperatures higher than 18°C, this confirms its thermophilic nature. *Evadne tergestina* was closely related to this distribution, ratifying results of the "Transeccion" cruises (*op. cit.*) where its presence coincided with the highest surface temperatures (19.9°C).

Thiriot (1972) refers that at the Gulf of Lyon the maximal number of both species was reached at higher temperatures than the remaining species of the genus *Evadne*.

c) *Podon intermedius* has not been ecologically defined. According to Gieskes (1971), in the North Atlantic it lives between coastal and oceanic sectors, although it seems to prefer warmer waters (13°-16°C) than in *Podon leuckarti* (10°-13°C). This thermic preference seems to be confirmed in our collection, as thermic ranges of surface waters were higher for *Podon intermedius* (15°-20°C) than for *Podon leuckarti* (9°-16°C).

Reproductive capacity

The estimation of the reproductive capacity of females was made by counting the actual num-

* These studies were carried out after the "Transeccion" and "Proyecto" cruises performed from VI/72 to II/73 and III/81 to IX/81, respectively; each one included six oceanographic stations between Mar del Plata and the shelf border; their planktonic samples were taken by means of vertical hauls, never exceeding 50 meters depth (for detail, see Ramírez and De Vreese, 1974).

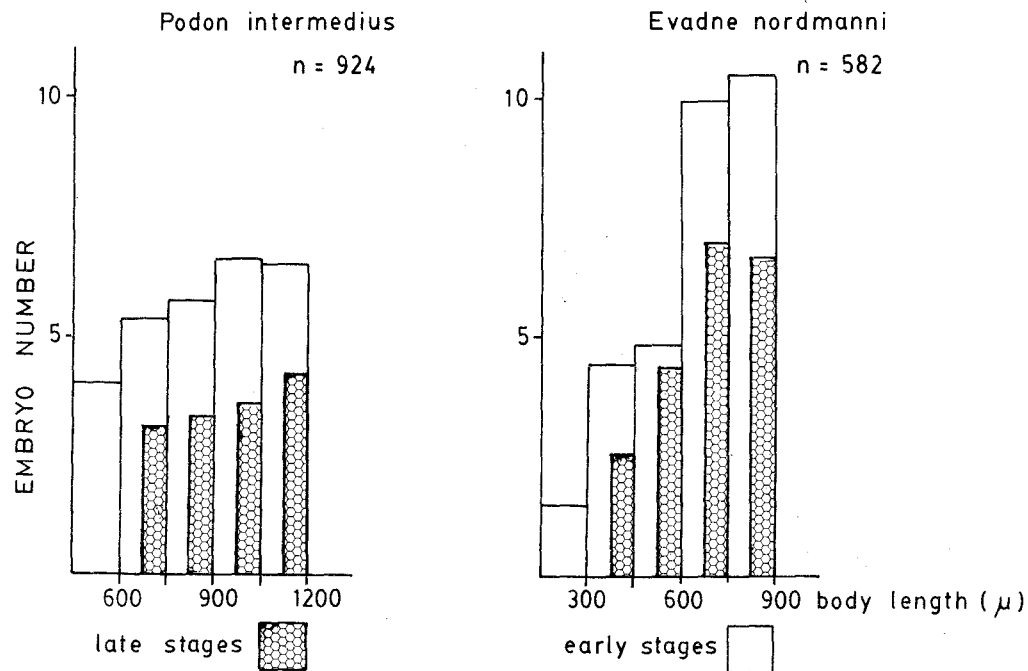


Fig. 8.— Histograms of maternal body length versus embryo number (early and late stages separately grouped) of *Evadne nordmanni* and *Podon intermedius*.

ber of embryos in their brood pouches; early and late-stage embryos were separately considered in this work, as partial reabsorption of early stage embryos was previously mentioned by other authors. Bainbridge (1958) found in *Evadne nordmanni* "disintegrating embryos and undifferentiated patches of tissue in the brood pouch of some females". As shown in fig. 8, early-stage embryos always outnumbered late-stage ones, which suggests a considerable loss by reabsorption during embryonal development. A recommendation by Bainbridge (*op. cit.*) was followed in the sense that "the best measure... can be obtained when only those individuals with late-stage embryos are considered". This author considered "late" embryos as being those showing at least the first traces of eye pigmentation.

Fig. 7 shows positive correlations found between embryo number and body length, and in fig. 10 we may observe negative correlations of embryo number vs. water temperature. Comparing with Thiriot results (1972), obtained for *Evadne nordmanni*, our correlation values ($r = 0.76$) are almost equal to those obtained

at the Gulf of Lyon ($r = 0.66$). The maximum embryo number, *viz.* 9 per female, reached at similar temperatures, is also coincident.

Though the number of embryos per batch is a specific feature, some factors such as geographical distribution, body size, nourishment, etc. may produce intraspecific variations. In this sense, though some of the analyzed variables in this work seems to show a correlation with maternal production, results must be observed carefully mainly in relation to *reproductive strategy* and *depressive hypothesis*, which will be commented upon:

a) **Reproductive strategy:** brood pouch of *Podon polyphemoides*, *Evadne nordmanni*, *Evadne tergestina* and *Penilia avirostris* had their embryos at similar developing stages, which leads to the idea of their simultaneous emergence. On the contrary, in *Podon leuckarti* and *Podon intermedius* there were dissimilarities, there being found up to 3 developing stages per brood, inferring therefore a liberation by stages. Differences in the slope of regression lines between *Evadne nordmanni* and *Podon intermedius* could be explained on

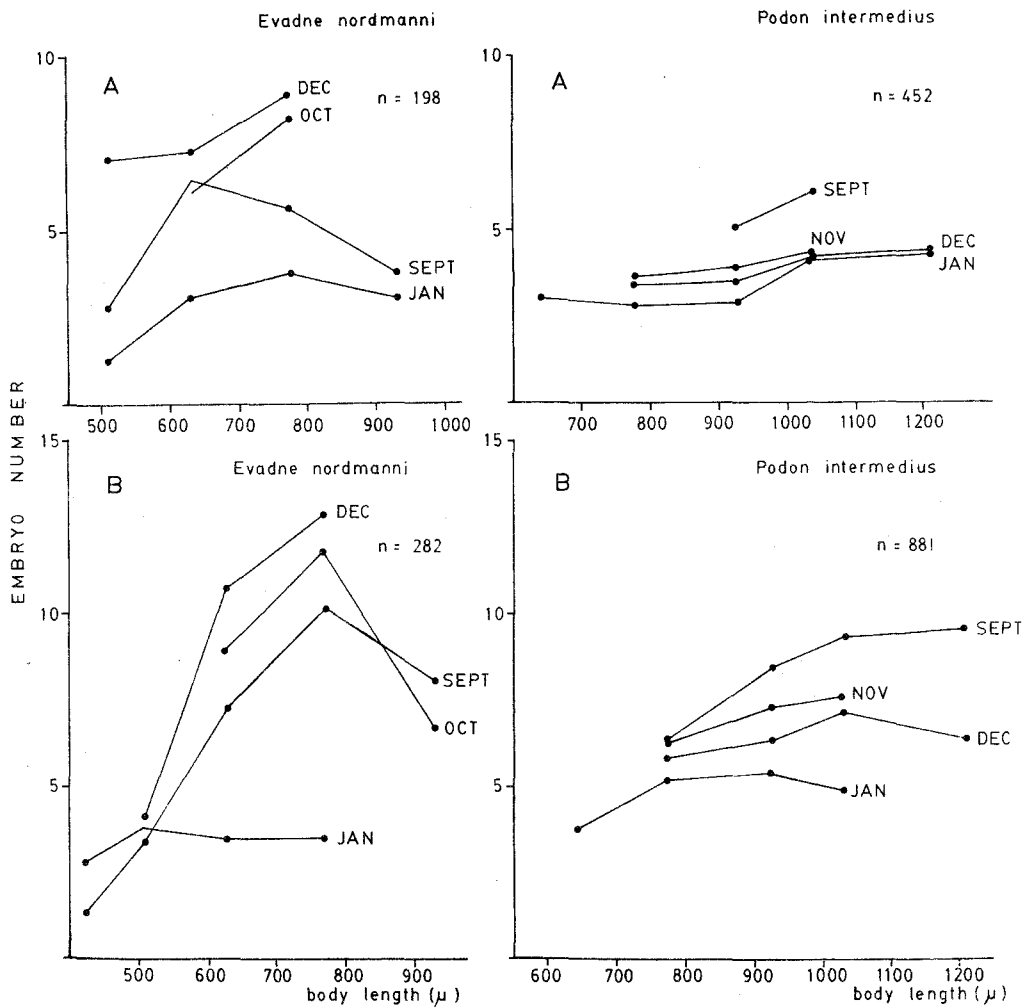


Fig. 9.— Monthly variation in embryo number per female in *Evadne nordmanni* and *Podon intermedius* (A: late stages; B: early stages).

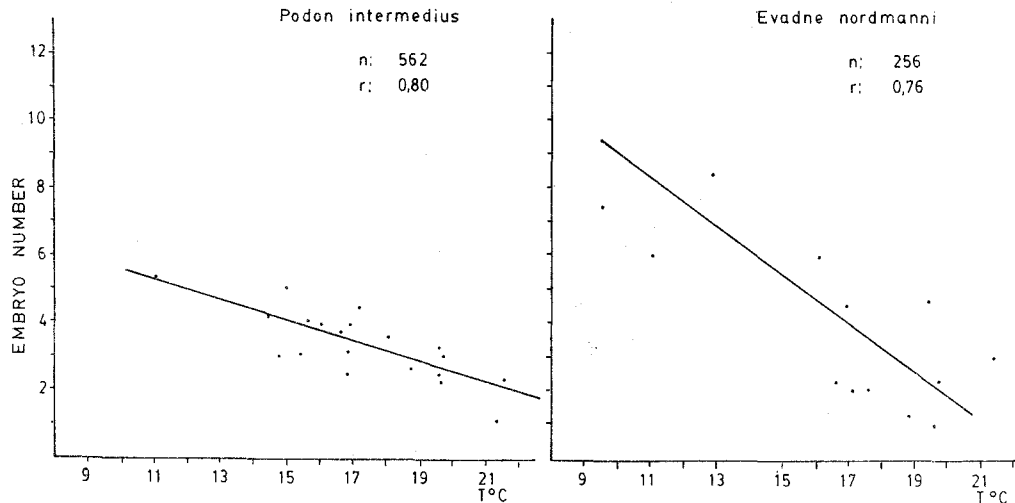


Fig. 10.— Relation between embryo number per female of *Evadne nordmanni* and *Podon intermedius* and water temperature.

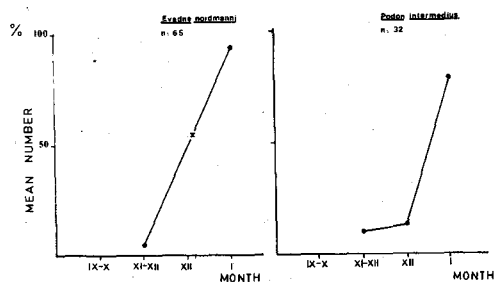


Fig. 11.— Monthly variation in the percent of females of *Evadne nordmanni* and *Podon intermedius* with resting eggs, in their respective total populations (X: no data).

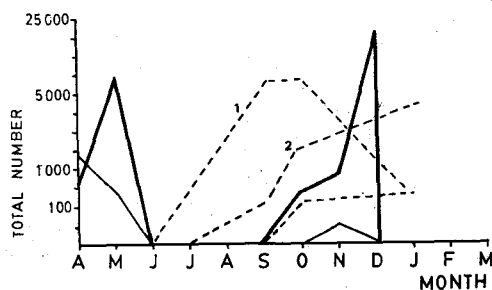


Fig. 12.— Monthly variation in total cladocerans number per square meter between Mar del Plata and the continental shelf slope. *Full line*: "Proyecto" cruises, coastal waters; *narrow line*: idem, middle shelf waters; *broken line*: "Transeccion" cruises, 1: coastal waters; 2: middle shelf waters; 3: waters near the slope.

these circumstances, as each brood pouch in the former species had its maximum and definitive embryo number, while in *Podon intermedius* only last-stage embryos were considered. As a result of this, the total number of embryos of the latter species was underestimated, giving a false idea of the reproductive capacity of the species.

b) **Depressive hypothesis.** Berg's (1931) results on the transition from parthenogenesis to gamogenesis support the hypothesis that this is caused by the influence of unfavourable external conditions, the main environmental factors being temperature, food supply, population density, chemical agents and products of excretion. These create a state of "depression" in the females, which prior to the reproductive change is characterized by a reduction of average size and number of embryos. The dif-

ferences between young populations of parthenogenic females and those at the end of their reproductive cycle have been pointed out by several authors. Onbé (1974) mentioned a remarkable decrease of standard length and number of embryos in *Evadne nordmanni*, *Penilia avirostris* and *Podon polyphemoides* at the end of their reproductive period. This author had previously found (1968) significant changes in *Penilia avirostris*. In 1958 Bainbridge had similar results with *Evadne nordmanni*.

This tendency could explain the correlation observed in fig. 10 between water temperature and average number of embryo per female. The highest thermic values correspond to the last dates of summer, i.e. at the conclusion of the population cycle of both species; this seems to be ratified by the high percentage of gamogenetic females (i.e. with resting eggs) in the total population in January (fig. 11). As previously cited, a reduction of the average sizes from December to January was observed in both species. Variations in their reproductive capacity is shown in fig. 9, which indicates the lowest mean values in January, especially in *Evadne nordmanni* where a marked difference is observed.

Seasonal reproductive cycle. The six degrees of latitude of the considered region would imply thermic differences among their extremes. Nevertheless, as it was previously indicated, isotherms are obliquely orientated from South to North and from East to West. As it has been pointed out in a previous work (Carreto *et al.*, 1981) the vernal increase in temperature of the continental shelf waters of the Buenos Aires province begin in inshore waters, shifting gradually towards oceanic waters with the progress of the seasons. Due to this fact, the correlations of the biological parameters with latitude were neglected in this work.

Population cycles of *Evadne nordmanni* and *Podon intermedius* cannot be inferred from the numeric difference between early and late-stage embryos. Nevertheless, variations of the reproductive capacity of females, expressed as late embryo number per brood, could be related with future population occurrence. The species *Evadne nordmanni* and *Podon intermedius* showed an increase in their embryo number in December and September, respectively (fig. 9), but their progress, if any, could not be expressed in this work since numeric results were

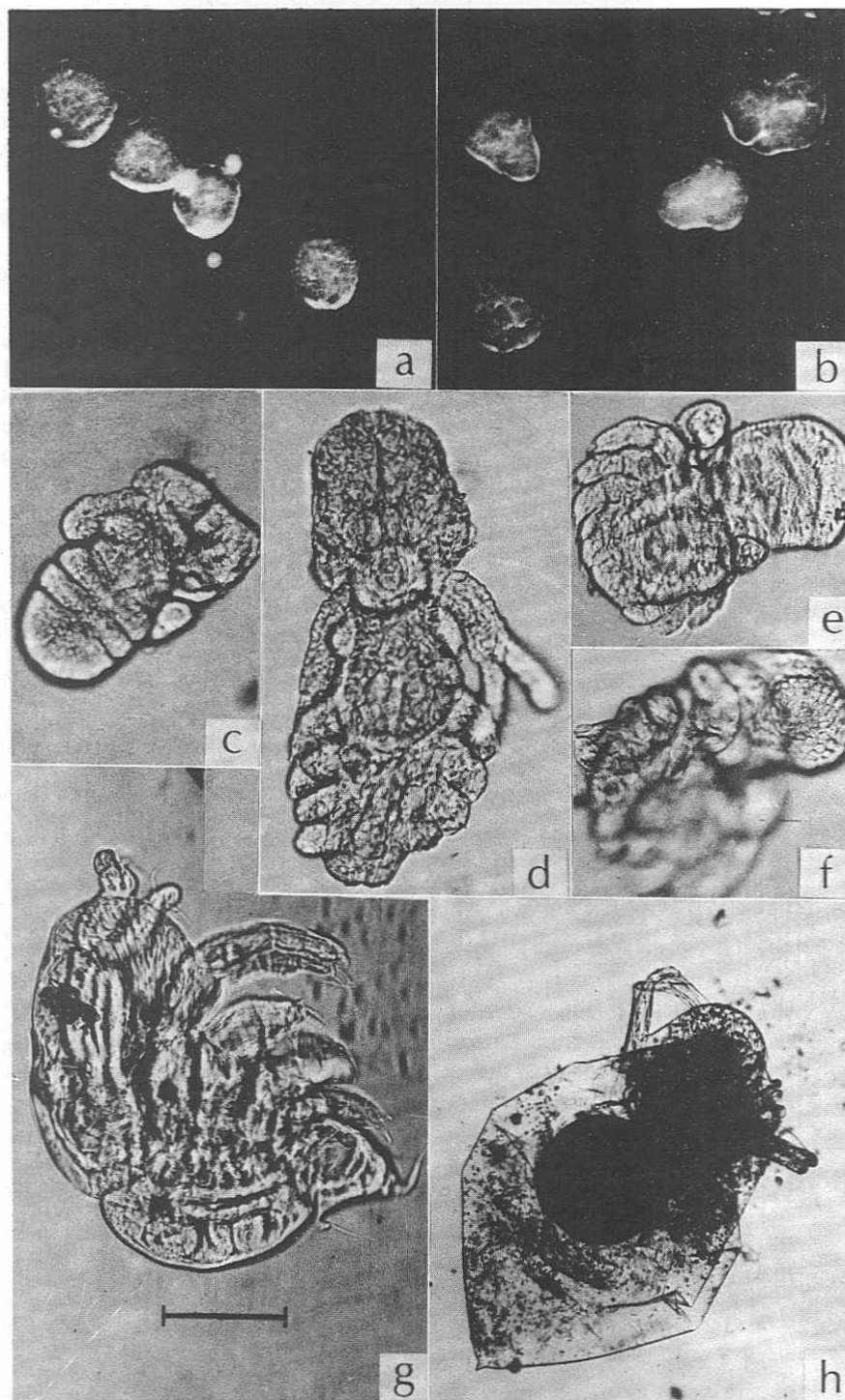


Fig. 13.— Embryo stages of *Evadne nordmanni*. From a to f: "early" developmental stages; g: "late" developmental stage; h: adult female with resting egg. Reference of figs. corresponds to 200 μ m at figs. a, b, d, e, f and g; 100 μ m at fig. c; 150 μ m at fig. h.

considered as percentuals. Nevertheless, a proportional predominance of each species was observed in January and November samples, respectively (fig. 2). The seasonal displacement of both numerical differences was also observed in a previous work (Ramírez and De Vreese, 1974) where the authors suggested that the late predominance of *Podon intermedius* could be related with the higher temperature of upper waters.

Changes in the brood pouch composition of cladocerans were observed by Mordukhai-Boltovskoi and Rivier (1971) and Onbé (1974).

SUMMARY AND CONCLUSIONS

1) Cladocerans from a sector of the Argentine sea, between 37°02' to 43°32' S and 54°48' to 64°65' W were studied during a period from May 1978 to February 1979.

2) 26 positive samples resulted from the analysis of 200, which corresponded to the period between September and January; six species were found, namely *Podon intermedius*, *Podon polyphemoides*, *Podon leuckarti*, *Evadne nordmanni*, *Evadne tergestina* and *Penilia avirostris*.

3) Abundance values are expressed as percentages. The species showed an ecological feature in their distribution, with the exception of *Podon intermedius* and *Evadne nordmanni* which were present in almost the entire sampled sector.

4) Contours of isotherms were obliquely orientated from South to North and from East to West, implying a low thermic gradient in the six latitude degrees of the sector.

5) *Evadne nordmanni* and *Podon intermedius* showed a reduction of body length at the end of the period.

6) Reproductive capacity of *Evadne nordmanni* and *Podon intermedius* was estimated on the basis of their embryo number per brood pouch; the probability of a partial reabsorption of their early stage embryos was considered.

7) The species can be grouped according to their brood pouch composition, namely: with embryos at similar developing stages (*Podon polyphemoides*, *Evadne nordmanni*, *Evadne tergestina* and *Penilia avirostris*) or with embryos differing from each other (*Podon leuckarti* and

Podon intermedius), thus implying a difference in their spawning behaviour.

8) An inverse relationship between temperatures at the upper levels and embryo number per female was observed for *Evadne nordmanni* and *Podon intermedius*.

9) A comparative increase in the number of gamogenetic females was observed at the end of summer for *Evadne nordmanni* and *Podon intermedius*.

10) Relationships between both species reduction of body size—conclusions 5—and embryo number per brood pouch—conclusions 8—prior to the appearance of gamogenetic females—conclusions 9—could be explained by Berg's Depression Hypothesis (1931).

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