A CONTRIBUTION TO THE REPRODUCTIVE BIOLOGY AND GEOGRAPHICAL DISTRIBUTION OF ANTARCTIC OCTOPODIDAE (CEPHALOPODA).

Silke Kuehl

Institut für Polaroekologie, Universitaet Kiel, Olshausenstrasse 40–60, 2300 Kiel, W. Germany[1]

ABSTRACT

Benthic octopods were collected during a bottom trawl survey on the western shelf of Elephant Island (South Shetland Islands, Antarctica) in mid-March 1981. Twelve hauls between 68 and 470 m yielded five species; most abundant was *Pareledone charcoti* (n = 114 or 50.2% of individuals) followed by *P. polymorpha* (n = 55 or 24.2%) and *P. turqueti* (n = 47 or 20.7%). Another species of the genus *Pareledone* not yet identified and one species of the genus *Benthoctopus* were present with 7 (3.1%) and 4 (1.8%) individuals, respectively. In *Pareledone charcoti*, wet weight ranged from 1.8 to 136.1 g in specimens of 2.1 to 8.2 cm mantle length. Wet weight ranged from 9.8 to 164.6 g in *Pareledone polymorpha* of 3.1 to 9.7 cm ML. *Pareledone turqueti* weighed 5.3 to 275.4 g wet weight and were 2.9 to 14.1 cm in ML. The largest specimen recorded was a female *P. turqueti* of 6907 g wet weight and 22.5 cm ML. In general, fecundity was low and egg size large when compared to other octopodid species from temperate and warmer seas. Fecundity of females was highest in one of the smaller species, *P. polymorpha*. From the large variation of the gonad index and the size/frequency distribution of ova as well as from the morphology of gonads, there was evidence that spawning in mid March had already commenced.

Keywords: Octopoda; Antarctica; zoogeography; distribution; reproductive biology.

INTRODUCTION

Cephalopods are believed to form major elements of the Antarctic benthic and pelagic ecosystems (Everson, 1977; Roper, 1981). Closer reviews of the existing literature indicate that the significance of squids, e.g. as krill predators, has been overestimated (Kock, 1985), and knowledge of the role of benthic cephalopods is still rather poor. Most studies have focussed on the taxonomy and geographical distribution of octopods (e.g. Robson, 1932; Taki, 1961; Voss, 1976). Of the about 10 species described from S of the Antarctic Convergence, only two have a circumantarctic distribution (Dell, 1972), but this figure is likely to increase once the taxonomy of antarctic octopods undergoes detailed revision (Voss, in preparation). Moreover, only one attempt has been made to describe the octopod fauna of a certain area, namely the Kerguelen Province of the Indian Ocean (Lu & Mangold, 1979).

What little information is available on biology and ecology is limited to occasional reports on food or gonad development (e.g. Massy, 1916; Taki, 1961; Voss, 1968). Investigations on the stomach contents of Weddell Seals and Elephant Seals in the zone of seasonal ice cover indicate that benthic octopods may form significant portions in the diets of these warm-blooded top predators (Clarke & Macleod, 1982a, b). Benthic octopods themselves are likely to represent important top predators of the benthic food webs, along with fish.

The antarctic environment is characterized by high seasonality of the annual light cycle and ice cover, to a large extent governing biological processes. Thus, cyclic phenomena like reproduction might be expected to be related to these seasonal events. The present paper contributes to the geographical distribution and reproductive biology of octopodids based on material collected in the Antarctic in mid-March 1981.

MATERIALS AND METHODS

Between March 17 and 20, 1981, 227 specimens of benthic octopodids were sorted from the by-catch of a bottom trawl survey off

[1]Present address: Alfred-Wegener-Institut für Polarforschung, Columbus-Center, D-2850 Bremerhaven, Federal Republic of Germany.

Elephant Island (South Shetland Islands) by the FRV *Walther Herwig* in the Atlantic Sector of the Southern Ocean. The original intention of the survey was to do a stratified random sampling program for fish stock assessment on the shelf of the island (Hempel *et al.*, 1982), i.e. to sample the depth strata adequately to define their extent and area. Unfortunately, the survey had to be abandoned due to problems with the ship's engine. Therefore, only 13 bottom-trawl stations were carried out on the north-western shelf between 68 and 480 m (Fig. 1). The gear was a 67 m bottom trawl with a narrow mesh cod end. Specimens were deep-frozen at $-30°C$ immediately after removal from the catch. In the laboratory, various morphometric measurements were taken from specimens after thawing, and radula as well as statoliths and beaks were removed, examined and measured. Species were identified following part of an unpublished manuscript by G.L. Voss (Rosenstiel School of Marine and Atmospheric Science, Miami, Florida) and information given by Joubin (1905), Massy (1916), Berry (1917), Robson (1932), Taki (1961), Voss (1976) and Palacio (1978).

Before dissection, total wet weight was determined to the nearest g. Total length (TL) and dorsal mantle length (ML) (see Roper & Voss, 1983) were measured to the nearest mm, statolith length to the nearest 0.1 mm. Specimens were sexed and gonads inspected to determine the state of sexual maturity. In females, ovaries with oviducts and oviducal glands were weighed and the colour of the oviducal glands as well as the appearance of eggs through the wall of the ovary (see Mangold-Wirz, 1963; Boyle & Knobloch, 1982) were recorded; in males, the genital bag (penis, Needham's sac, spermatophoral glands and testis) was weighed. Ovaries and Needham's sac were opened to count and measure (nearest 0.1 mm) the ova and spermatophores, respectively.

RESULTS

Vertical distribution

Benthic octopodids occurred in 12 of 13 hauls; one tow was heavily biased by huge numbers of pelagic organisms and therefore the by-catch was only inspected briefly. Four species of the genus *Pareledone* and one species of the genus *Benthoctopus* were

identified; four specimens of *Pareledone* and the *Benthoctopus* specimens could not be determined to species and possibly represent new species that are being investigated. The hauls were grouped into two strata: 50 to 200 m and 200 to 500 m, represented by six tows each and the results are set out in Table 1. The water temperatures at fishing depths were around 0°C and salinities were in the 34.5 to 34.8% range. The *Pareledone* species were present over the whole depth range fished, whereas *Benthoctopus* sp. was restricted to the deeper shelf below 200 m. *P. charcoti* was most abundant, with more than 50% of individuals, followed by *P. polymorpha* and *P. turqueti*. The *Pareledone* species were equally abundant in both depth strata, although *P. charcoti* appeared to be more numerous at the shallower part of the shelf.

Size and sex composition

The mantle length frequencies of the three most abundant species are given in Fig. 2. In *P. charcoti* and *P. polymorpha* the distribution shows only one maximum at 4 and 5 cm ML, respectively, whereas at least two peaks can be recognized in *P. turqueti*, with distinct modes at 4 or 5 to 10 cm ML, the latter exclusively represented by males. The largest specimens were females in all three species. The absence of small octopods less than 1 or 2 cm ML may either be due to the mesh size of the net bag or to the cursory inspection of the by-catch, i.e. due to inadequate sampling or sorting. The total wet weight of specimens ranged between 1.8 and 136.1 g in *P. charcoti*, between 9.8 and 164.6 g in *P. polymorpha* and the bulk of *P. turqueti* weighed 5.3 to 275.4 g, with one large specimen attaining 6907 g (22.5 cm ML). The latter values represent the largest benthic octopodid so far recorded S of the Antarctic Convergence (Nesis & Propp, 1968 cited in Dell, 1972). The sex ratio was close to unity in *P. charcoti* and *P. polymorpha* but far more males than females were present in *P. turqueti*, particularly in specimens larger than 9 cm ML. Differences in sex ratios with regard to depth were not observed.

Maturity and fecundity

The morphology and size of ova as well as the morphology and the relative size of gonads provide possible estimates of maturity (Voss, 1983). Mangold-Wirz (1963) and Boyle
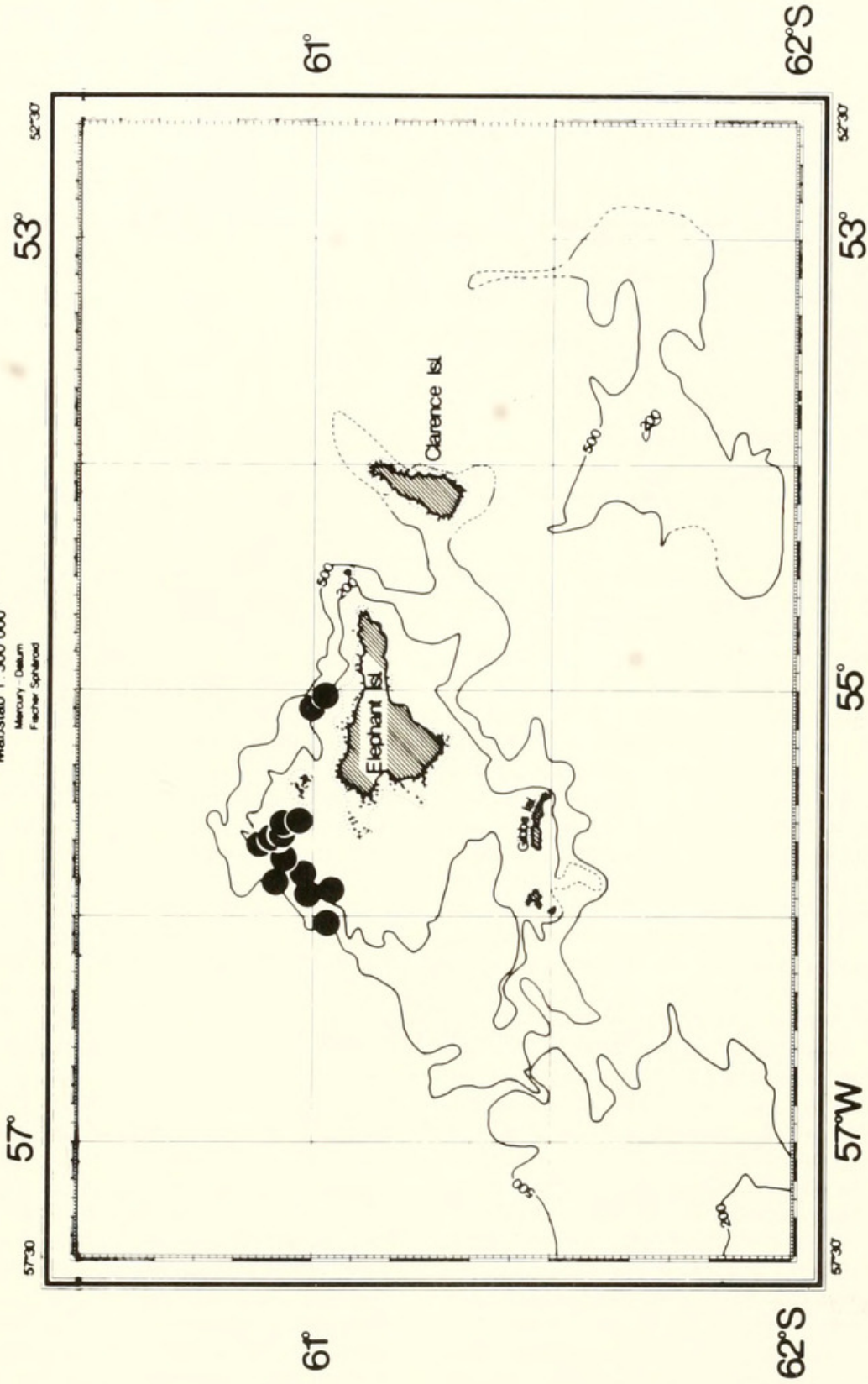
FIG. 1. Map of the study area with locations of the bottom trawl stations of FRV "Walther Herwig."

TABLE 1. Vertical distribution of the *Pareledone* species and *Benthoctopus* sp. off Elephant Island in mid-March, 1981. N denotes abundance in the two depth strata, 50–200 m and 200–500 m, and in the total depth range; D is the percentage abundance.

| Species | Depth strata | | | | | |
| | 50–200 m (n = 6 hauls) | | 200–500 m (n = 6 hauls) | | 50–500 m (n = 12 hauls) | |
	N	D (%)	N	D (%)	N	D (%)
Pareledone charcoti (Joubin, 1905)	63	56.8	51	44.0	114	50.2
Pareledone turqueti (Joubin, 1905)	21	18.9	26	22.4	47	20.7
Pareledone polymorpha (Robson, 1930)	26	23.4	29	25.0	55	24.2
Pareledone sp.	1	0.9	3	2.6	4	1.8
Benthoctopus sp.	0	0	7	6.0	7	3.1
Total	111	100	116	100	227	100

& Knobloch (1983) observed in several octopod species that the stage of egg maturation is indicated by the appearance of striations on the surface of the ova. Boyle & Knobloch (1983) described the formation of this striation as follows: each growing egg is surrounded by a layer of follicle cells that proliferate faster than the growing egg can accommodate them as a single lamina, and so the layer becomes folded. These folds give a longitudinally striped appearance to each egg, obviously externally. In the final phase of egg expansion, the follicle cells are lost and the eggs are smooth and loose in the ovisac. At the same time that the striated ova were observed in the *Pareledone* species, they showed swollen, yellowish ovaries with the oviducts attached closely. Therefore, the striation was used to group female octopods into specimens with only small immature ova and those with large maturing, striated ova. The number of ova of each length class was then pooled for the two groups separately and the percentage frequencies of the ova length classes were calculated from pooled data. The results are given in Fig. 3.

In *P. charcoti*, the ova length distribution of females with immature ova was characterized by only one distinct peak, at 2 mm, with only a few ovaries containing large eggs up to 11 mm long. In females with maturing ova, the majority of ova varied between 6 and 18 mm long. Only a few females were found with smaller ova present. In *P. polymorpha,*

among females with immature ova only, the highest frequency was recorded at 2 mm but ova up to 10 mm long were also found. The ova length in ovaries bearing maturing eggs ranged mainly from 7 to 14 mm. In the first group of *P. turqueti,* the length of ova varied between 1 and 17 mm with modes at 2 and 10 mm, the latter mode apparently representing a generation of developing ova. A few of these were striated, but the ovaries were not swollen and coloured. The largest maturing eggs (19mm) were observed in *P. turqueti,* but only one female with maturing eggs was investigated. There is evidence that in *P. charcoti* and *P. polymorpha* eggs of more or less equal size begin to mature, whereas in the larger species, *P. turqueti,* egg size at the onset of maturation is also larger (see Fig. 3).

Another estimate of maturity is the gonad index, i.e. the wet weight of the ovary including ducts and glands, or the genital bag expressed as percentage of the total body weight. This index is shown as a function of total length of female *P. charcoti* in Fig. 4; here females were also split into two groups. A total of 29% of females had maturing eggs. They were observed from 5.5 cm ML onwards, corresponding to a wet weight of 43 g. Their gonad index varied between 3 and 20%, indicating that at least partly spent females were present. Indeed, the lowest figures at 3 and 5% represent two females, the ovaries of which contained 60 small and 4 large ova and
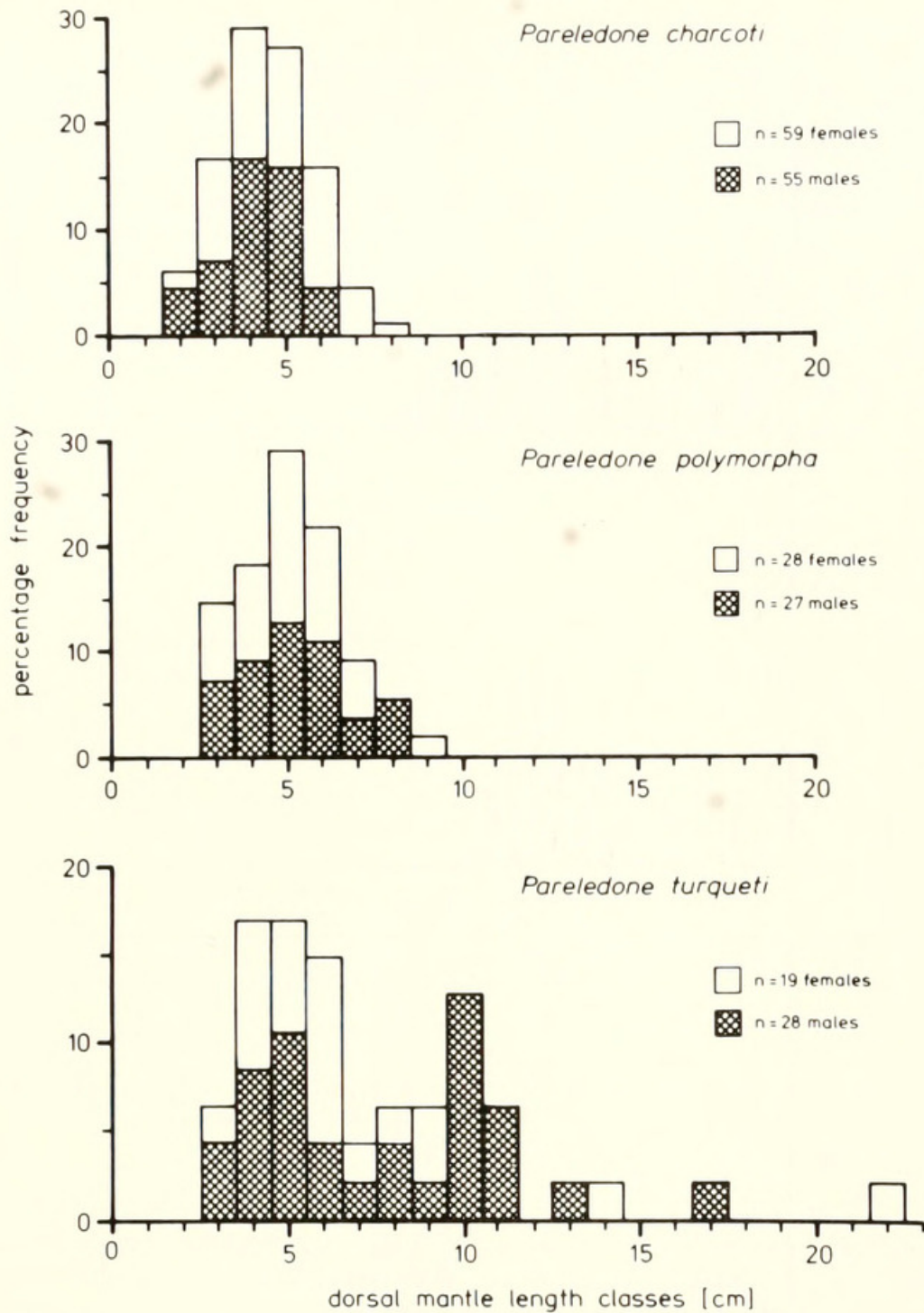
FIG. 2. Length-frequency distributions of *Pareledone charcoti, P. polymorpha* and *P. turqueti.*

21 large ova, respectively. As in *P. charcoti,* the gonad index varied considerably in female *P. polymorpha,* ranging from 0.8 to 15% in specimens bearing maturing ova (Fig. 5). These occurred from 5 cm ML upward; 9 out of a total of 25 females had maturing eggs (36%). In *P. turqueti,* the available number of specimens was too low to present results adequately and would not even permit a preliminary analysis, because the size range was much broader in this species. The one female with striated ova had a mantle length of 6.6 cm at a wet weight of 68.9 g.

The developmental stage of maturation was not investigated in males. Only the presence or absence of spermatophores in
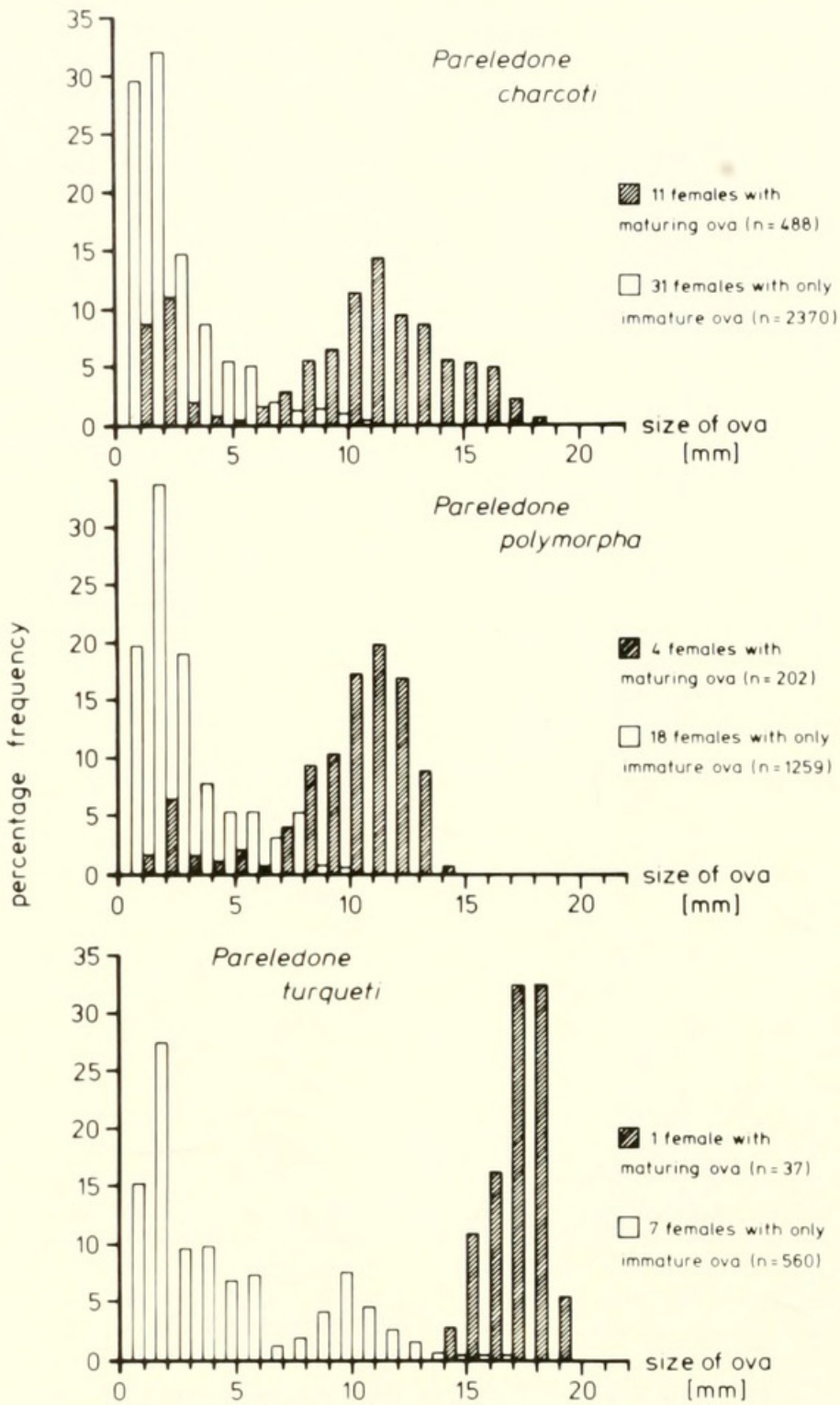
FIG. 3. Frequency distributions of ova lengths in *Pareledone charcoti, P. polymorpha* and *P. turqueti,* grouped by females with maturing ova and females with immature ova only. Pooled data (see text).

Needham's sac was taken as indicative of maturity; in some cases in *P. charcoti,* spermatophores were encountered in the penis and diverticulum. The portion of mature males was 76% of the total population. Spermatophores were recorded in specimens from 3 cm ML upwards, corresponding to a wet weight of 9 g. Also in males, the high variation of the gonad index suggests that spawning had already commenced (Fig. 6). However, the number of spermatophores is not related directly to spawning since they can be stored
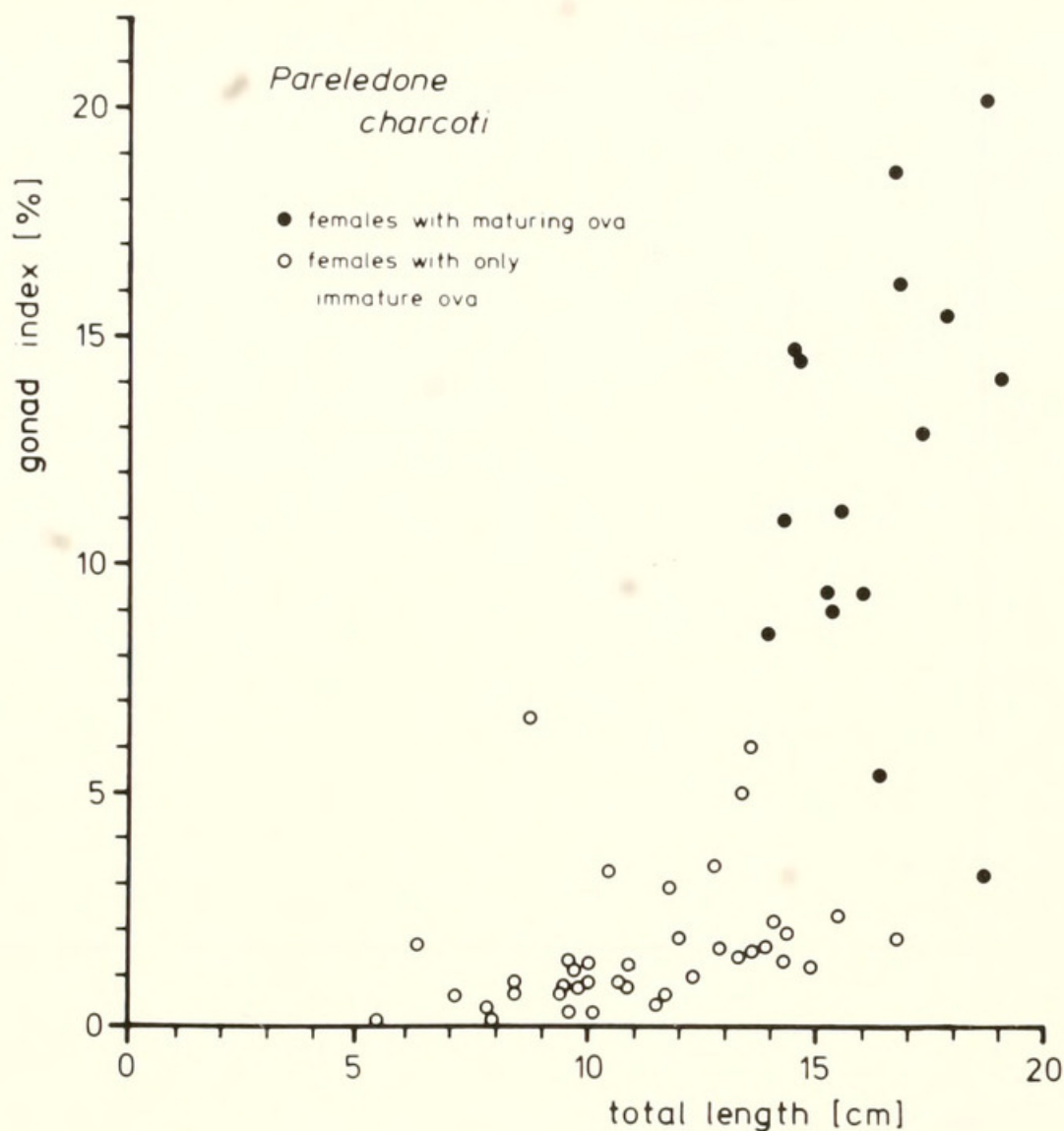
FIG. 4. *Pareledone charcoti*. Gonad index of females as a function of total length.

in Needham's sac and new ones are likely to be produced. This is reflected by the number of spermatophores counted in *P. charcoti* over the total wet weight range (Fig. 7). Although a rather consistent tendency of increase in number with wet weight is apparent, there is a considerable overlap of weight ranges at a given number of spermatophores. This means also that males of equal size may have one to five spermatophores. In male *P. polymorpha*, spermatophores were observed from 4 cm ML upward. They were present in 20 of 27 males (74.1%). The smallest male *P. turqueti* in which spermatophores were observed was 4.3 cm ML, weighing 21.4 g. The maximum recorded number and length of

spermatophores differed considerably among species. In *P. charcoti* (max. number = 7), they were up to 8.5 cm, while in *P. polymorpha* (max. number = 5), maximum length was 6.9 cm. Spermatophores were largest in *P. turqueti* (max. number = 9) with a maximum of 16.5 cm.

To obtain an estimate of fecundity, the number of eggs was considered from females with maturing ova. It is assumed that, with the possible exception of *P. turqueti*, the immature ova will not have been spawned in the same season. This means that in *P. charcoti* only ova between 6 and 18 mm length were included, and in *P. polymorpha* between 7 and 14 mm. Then the absolute fecundity
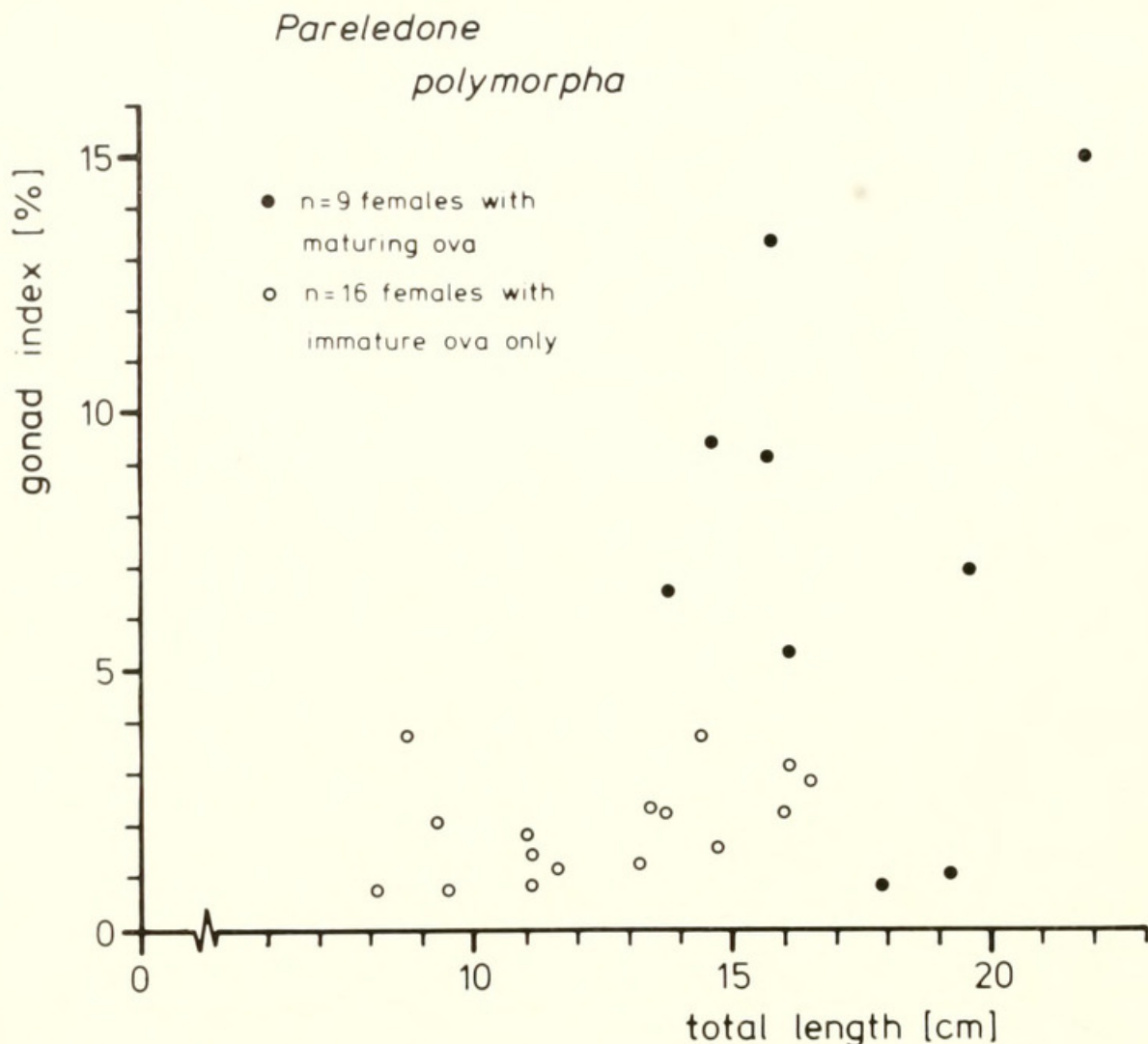
Pareledone
polymorpha

FIG. 5. *Pareledone polymorpha.* Gonad index of females as a function of total length.

varied between 21 and 58 in *P. charcoti* of wet weights 49.2 and 136.1 g. The relative fecundity, i.e. the number of ova per g total body weight, was 0.4 to 0.8 (mean 0.5 ± 0.2) for this species. In *P. polymorpha* of 44.6 to 164.6 g wet weight, the number of ova ranged from 34 to 65 with a relative fecundity of 0.4 to 0.9 (mean 0.7 ± 0.2). The one female of *P. turqueti* contained 37 ova, of 0.5 per g wet weight.

DISCUSSION

Two of the species recorded off Elephant Island are known to have a circumantarctic distribution: *Pareledone charcoti* and *P. turqueti* (Dell, 1972). The first has been found previously at depths from the upper eulittoral zone down to 1500 m, whereas *P. turqueti* has been reported from shallow waters to the

upper continental slope at about 550 m (Joubin, 1905, Palacio, 1978). This is corroborated by the present findings. However, for *P. polymorpha,* both the vertical and geographical distributions can be extended widely through our samples. This species has so far only been observed off South Georgia at a depth of 273 m (Robson, 1930; Palacio, 1978). However, the present results show that off Elephant Island, *P. polymorpha* has the same vertical range of occurrence as the other two species, and hence can also be termed eurybathic. The geographical distribution of *P. polymorpha* is not limited to South Georgia. During the German Antarctic Expedition in 1985, all three species were recorded in the Weddell Sea (Kuehl, in preparation), suggesting that the geographical distribution of *P. polymorpha* may extend even farther along the continental coast.

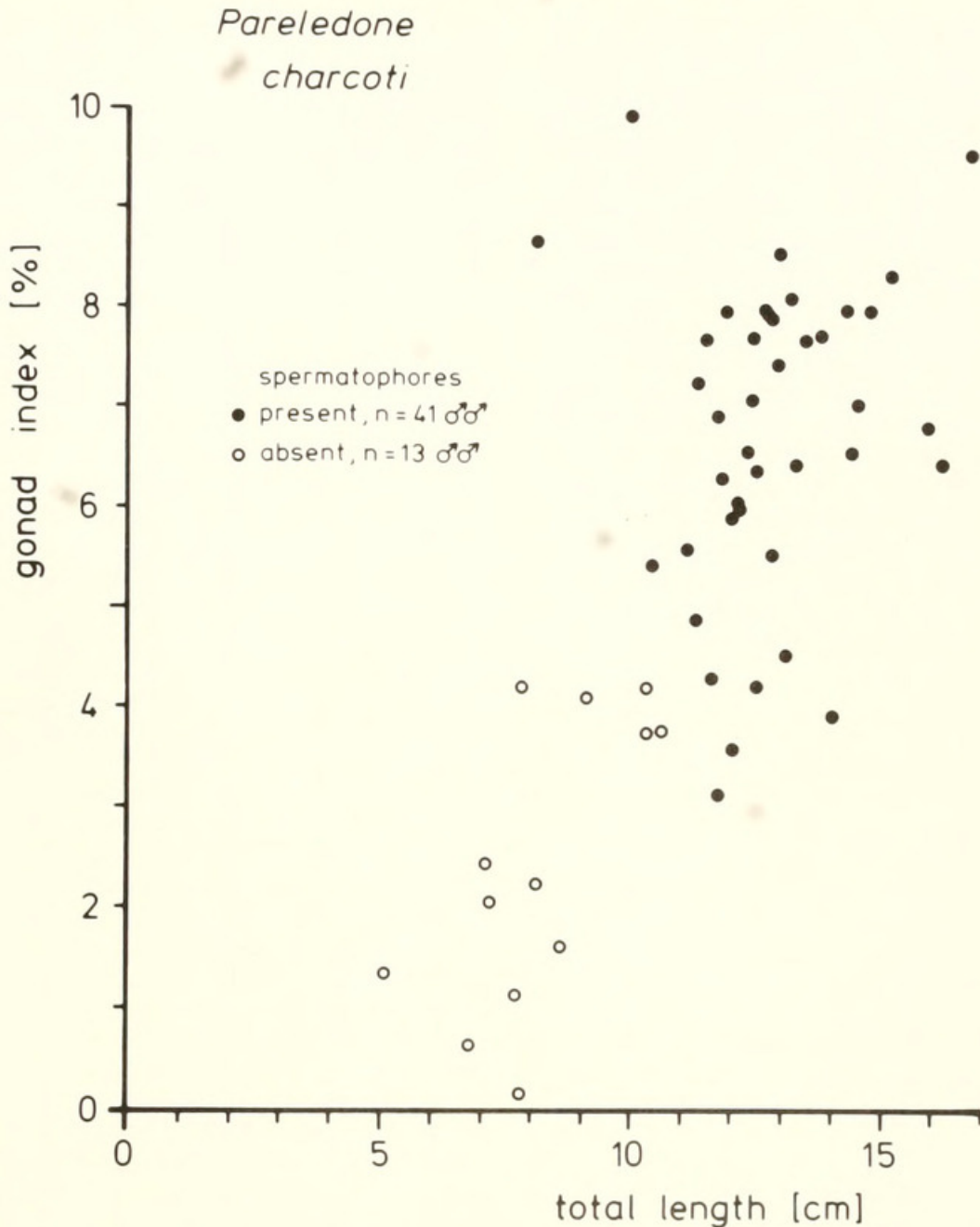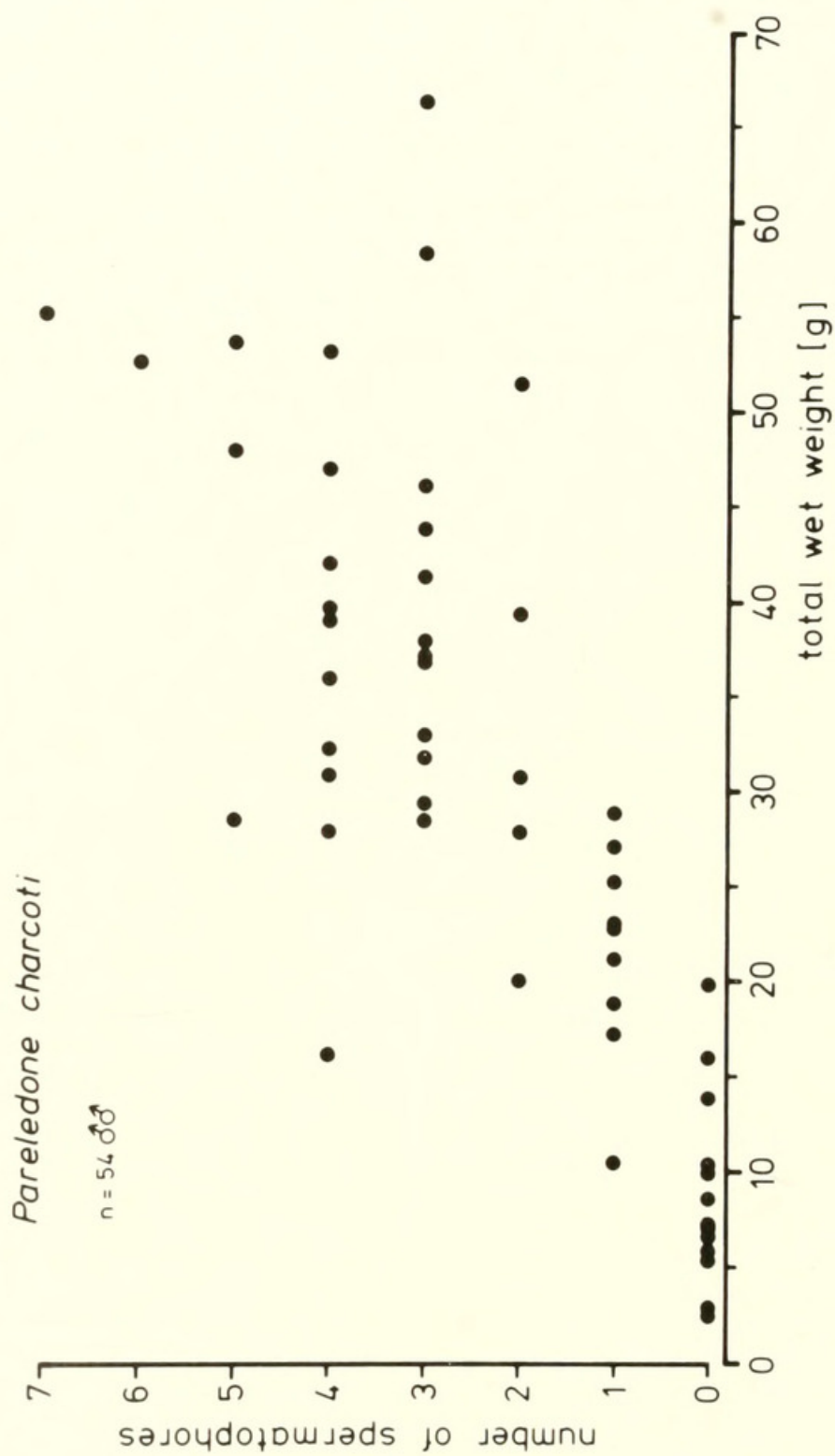Males and females were present in equal

FIG. 6. *Pareledone charcoti*. Gonad index of males as a function of total length.

numbers in *P. charcoti* and *P. polymorpha;* none of the two depth strata was preferred. In these two species, there was strong evidence that spawning had already commenced. In contrast, the portion of males was much higher in *P. turqueti*. If the striking lack of large females is because they occur usually in deeper waters, then this could indicate a spawning migration into the shelf area, with males preceding females. Such a migration pattern was observed in *Octopus vulgaris* from the Mediterranean, although the vertical depth range there was much less extended (Mangold & Boletzky, 1973).

Fecundity is extraordinarily low and egg size is large in these antarctic species when compared with figures from other regions. Comparable values of number of eggs are reported for many octopods (cf. Boyle, 1983), including *Bathypolypus sponsalis* (Mangold-Wirz, 1963) and *Bathypolypus arcticus* (O'Dor & Macalaster, 1983). O'Dor & Macalaster (1983) observed 20 to 80 eggs per female of 9–14 mm in length in *Bathypolypus arcticus,*

FIG. 7. *Pareledone charcoti*. Numbers of spermatophores plotted versus total body wet weight.

whose geographical distribution extends into arctic waters. Among the *Pareledone* species, differences in fecundity and egg size were obvious; the number of eggs was higher (both absolute and relative) and eggs smaller in *P. polymorpha* than in *P. charcoti*. Largest eggs were observed in *P. turqueti;* since there is an inverse relationship between egg size and number (Voss, 1983), *P. turqueti* can be expected to have the lowest fecundity of the three species.

The length distribution of ova and variation of the gonad indices suggest that the spawning season extends over a considerable period of time. The long spawning period is due to the variation of gametogenesis in individual females as manifested by the wide range of maturing ova in *P. charcoti*, and possibly to repeated spawning events in individual females. This was indicated by the peak of small ova co-occurring with a few large ripening ones in *P. charcoti* and *P. polymorpha*. However, resorption or degeneration of ova after spawning is completed may occur (see Van Heukelem, 1973). Multiple spawning within one season would mean that fecundity is underestimated in the two species. The question is still open as to whether the females with only immature ova arrive at the spawning stage during that spawning season. In other words: how much time does it take the eggs to develop? As can be seen from Figs. 4 and 5, most females are much smaller than females with maturing ova. Hence it seems unlikely that they would have attained spawning condition in the same season. However, the overlap in size distribution of ova between the two groups of females indicates that at least the larger immature females may do so. Thus, there are two possibilities. The first is that spawning occurs more or less continuously due to smaller females subsequently entering maturity; thus there would be no distinct seasonality in the spawning period. The second is that the immature females attain sexual maturity not until the following year and this would mean that gametogenesis takes longer than one year and that spawning is seasonal. In *Bathypolypus arcticus*, no indication of a seasonal reproductive cycle was noted (O'Dor & Macalaster, 1983).

The period of this investigation was in March, i.e. austral autumn. At this time of year, pack ice drifting out of the Weddell Sea appears in the region and sea ice starts forming. Due to their large size, incubation time of eggs is probably long and extends over the winter months. In *Bathypolypus arcticus*, eggs developed over eleven months at temperatures between 10 and 3°C (O'Dor & Macalaster, 1983). However, *B. arcticus* is not endemic to arctic waters, and only extends its distribution that far N. The *Pareledone* species are endemic and hence are probably stenothermal. Therefore, incubation times are probably on the same order of magnitude or even less, despite the lower environmental temperatures. Many antarctic benthic invertebrates show a seasonal reproductive cycle, timed so that the offspring are released during spring and summer at the time of maximum food availability (White, 1977). Thus, the adaptive significance of the octopod spawning season in austral autumn might be to provide maximum chances of survival for the brood, e.g. when young crustaceans or molluscs of suitable sizes are abundant.

ACKNOWLEDGEMENTS

LITERATURE CITED

BERRY, S.S., 1917, Cephalopoda. *Australasian Antarctic Expedition 1911–1914; Scientific Reports,* Seri. C. *Zoology and Botany,* 4(2):1–38.

BOYLE, P.R., ed., 1983, *Cephalopod Life Cycles, Species accounts.* Vol. 1. Academic Press, London, 475 p.

BOYLE, E.R. & KNOBLOCH, D., 1982, Sexual maturation in the octopus *Eledone cirrhosa* (Lamarck). *Malacologia,* 25: 189–196.

BOYLE, E.R. & KNOBLOCH, D., 1983, The female reproductive cycle of the octopus, *Eledone cirrhosa. Journal of the Marine Biological Association of the United Kingdom,* 63: 71–83.

CLARKE, M.R. & MACLEOD, N., 1982a, Cephalopods in the diet of elephant seals at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin,* 57: 27–31.

CLARKE, M.R. & MACLEOD, N., 1982b, Cephalopod remains in the stomachs of eight Weddell seals. *British Antarctic Survey Bulletin,* 57: 33–40.

DELL, R.K., 1972, Antarctic benthos. *Advances in Marine Biology,* 10: 1–216.

EVERSON, I., 1977, *The Living Resources of the Southern Ocean.* FAO GLO/SO/55/1, Rome: 156 p.

HEMPEL, G., KOCK, K.H. & STEIN, M., 1982, Antarctic Expedition 1981 of the FRG with FRV "Walther Herwig," Fahrtverlauf. *Archiv für Fischereiwissenschaften,* 33: 17–26.

JOUBIN, L., 1905, Déscription de deux Eledones provenant de l'Expédition du Dr. Charcot dans l'Antarctique. *Memoires Societe Zoologique Francaise,* 18: 22–31.

KOCK, K.H., 1985, Fish and Squid. *Environment International.* Pergamon Press, in press.

LU, C.C. & MANGOLD, K., (1979), Cephalopods of the Kerguelennian Province of the Indian Ocean. *Proceedings of the International Symposium on Marine Biogeography and Evolution in the Southern Hemisphere, Auckland, New Zealand 17–20 July 1978:* 567–574.

MANGOLD-WIRZ, K., 1963, Biologie des Céphalopodes benthiques et nectoniques de la Mer Catalane. *Vie et Milieu,* Suppl. 13: 1–285.

MANGOLD, K. & BOLETZKY, S.V., 1973, New data on reproductive biology and growth of *Octopus vulgaris. Marine Biology,* 19: 7–12.

MASSY, A.L., 1916, Mollusca. Part II. Cephalopods. *British Antarctic "Terra Nova" Expedition 1910: Zoology,* 2, no. 7: 141–175.

O'DOR, R.K. & MACALASTER, E.G., 1983, *Bathypolypus arcticus. In:* Boyle, P.R. ed., *Cephalopod Life Cycles,* Vol. 1, *Species Accounts.* Academic Press, London: p. 401–410.

PALACIO, F.J., 1978, *Vosseledone charrua,* a new Patagonian cephalopod (Octopodidae) with notes on related genera. *Bulletin of Marine Science,* 28: 282–296.

ROBSON, G.C., 1930, Cephalopoda, I. Octopoda. *Discovery Reports,* 2: 371–402.

ROBSON, G.C., 1932, *Monograph of the Recent Cephalopoda. Part II. The Octopoda (excluding the Octopodinae).* British Museum (Natural History). Oxford University Press, London. 352 p.

ROPER, C.F.E., 1981, Cephalopods of the Southern Ocean region: potential resources and bibliography. In: Biomass, selected contributions to the Woods Hole Conference on Living Resources of the Southern Ocean, 1976, 2: 99–105.

ROPER, C.F.E. & VOSS, G.L., 1983, Guidelines for taxonomic discriptions of cephalopod species. *Memoires of the Natural Museum of Victoria,* 44: 49–63.

TAKI, I., 1961, On two new eledonid octopods from the Antarctic Sea. *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University,* 3(2): 297–316.

VAN HEUKELEM, W.F., 1973, Growth and life span of *Octopus cyanea* (Mollusca: Cephalopoda). *Journal of Zoology,* London, 169: 299–315.

VOSS, G.L., 1968, The biology and bathymetric distribution of deep sea cephalopods. *Studies of the Tropical Oceanographic Institute of Marine Science, University of Miami,* 5: 511–535.

VOSS, G.L., 1976, Two new species of octopods of the genus *Graneledone* (Mollusca: Cephalopoda) from the Southern Ocean. *Proceedings of the Biological Society of Washington,* 88(42): 447–458.

VOSS, G.L., 1983, A review of cephalopod fisheries biology. *Memoires of the National Museum of Victoria,* 44: 229–241.

WHITE, M.G., 1977, Ecological adaptations by Antarctic poikilotherms to the polar marine environment. In LLANO, G.A., ed., *Adaptations within Antarctic ecosystems.* Gulf Publishing Company. Houston, Texas, p. 197–208.