

# Dense aggregations of three deep-sea holothurians in the southern Weddell Sea, Antarctica

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**ABSTRACT:** Spatial distribution patterns of elasipod holothurians from the southern Weddell Sea were studied by analysing underwater photographs and trawl-catch data from 7 stations, ranging in depth from 240 to 1200 m. The 3 investigated species (*Elpidia glacialis*, *Achlyonice violaecuspidata*, *Scotoplanes globosa*) occurred in dense aggregations of differing spatial scale. For the first 2 species, median photographically determined densities within the patches were 17 and 6 ind. m<sup>-2</sup> respectively. The size-frequency distributions of all species were relatively broad. A behavioural communication between individuals assuring the formation and persistence of these aggregations is proposed.

## INTRODUCTION

The benthos of the Antarctic continental shelf and slope is generally known as an ecosystem of high species diversity and high epifaunal biomass (Holdgate 1967, Dayton et al. 1970, Lowry 1975, Knox & Lowry 1977, Jazdzewski et al. 1986, Mühlenhardt-Siegel 1988). The largest proportion is made up of sessile suspension feeders, e.g. sponges, bryozoans, ascidians, and certain echinoderms (Belyaev & Ushakov 1957, Bullivant 1967, Propp 1970, Dayton et al. 1974, Arnaud 1977). At some locations on the continental shelf, which is extremely deep ( $\leq 800$  m) in Antarctica (Picken 1984), the sea floor is completely covered by such organisms (Dayton et al. 1974, Gutt 1988) and biomass estimates may reach 6 kg wet wt m<sup>-2</sup> (White & Robins 1972). In terms of species composition, some authors have noticed an affinity between the Antarctic shelf and the deep-sea (Broch 1961, Bullivant 1967, Dayton & Oliver 1977). Different hypotheses have been proposed to explain this phenomenon in relation to the colonization history of both these biotopes (Menzies et al. 1973, Lipps & Hickman 1982).

For many Antarctic species a circumpolar distribution is assumed (Bullivant 1967, Dell 1972). The composition of the Antarctic benthos, however, is not

uniform. Faunistic investigations in various areas clearly show that there are different assemblages, each with typical features (Bullivant 1967, Gruzov & Pushkin 1970, Hedgpeth 1977, Everitt et al. 1980, Kirkwood & Burton 1988, Voß 1988). For photographic observations see Bullivant (1961), Oliver (1978), Hempel (1986), and Gutt (1988).

During 2 German Antarctic expeditions into the Weddell Sea, underwater photography as well as a dredge (Agassiz trawl) and a bottom trawl were used to study the sparsely investigated bottom fauna of the shelf and slope (see Drescher et al. 1983, Hempel 1983, 1985). Voß (1988), on the basis of the faunistic data obtained by those expeditions, described 3 species assemblages. The 'Eastern Shelf Assemblage' and the 'Southern Shelf Assemblage' correspond to the general picture given above, i.e. they are dominated by suspension feeders, contain intermediate to high species numbers and low evenness. The results presented in this paper, however, refer to a region whose bottom fauna belongs to the 'Southern Trench Assemblage' (sensu Voß 1988). It is poorer in numbers of species as well as individuals, and significantly less diverse. Elasipod grazing holothurians are the most abundant taxon. Their zoogeography and ecology were investigated in more detail by Gutt (1988). For 2 selected species,

*Elpidia glacialis* Théel, 1876 and *Achlyonice violaecuspida* Gutt, 1990, underwater photography was used to quantify densities, small-scale dispersion patterns and length-frequency distributions, and to gain information on their behaviour. For another abundant species, *Scotoplanes globosa* (Théel, 1879), densities and size-frequency distributions were obtained by analysis of bottom trawl samples.

All 3 selected species belong to the order Elasipodida Théel, 1882 which is generally composed of typical deposit-feeding deep-sea holothurians (Pawson 1966a, b). On the basis of present knowledge, *Achlyonice violaecuspida* is considered to be endemic to Antarctica. It has a longish, flattened body of gelatinous consistency with no ossicles in the body wall. The body of *Elpidia glacialis* is oviform and covered by a thin layer of filigrane calcareous ossicles. *Scotoplanes globosa* is similar in shape, but considerably larger. Information on the worldwide distribution of the 2 latter species was compiled by Hansen (1975). The main distribution area of *E. glacialis* is the Arctic Ocean. This species is known as an extremely eurybathic deep-sea form which also occurs in shallow water (Zenkevitch 1963). *S. globosa* has been found mainly in the southern hemisphere. There are several references on the patchy distribution of these two and other related species, which can be best detected by means of underwater photography (Lemche et al. 1976, Pawson 1976, Billet & Hansen 1982, Ohta 1983, Smith & Hamilton 1983).

#### STUDY SITE, MATERIALS AND METHODS

Specimens were collected in the southernmost part of the Weddell Sea during the German Antarctic Expeditions ANT I/2 and ANT III/3 with RV 'Polarstern' in 1983 and 1985 (Fig. 1). Underwater photography was used at 4 stations; one (307) is situated in the central part of the Filchner Depression in a depth of 1175 m, the others (301, 302, and 303) in Gould Bay in 240 to 445 m. Bottom trawl catches were made at 5 stations on the western edge of the Filchner Depression at 640 to 700 m depth.

A cyclonic circulation of very cold water ( $-1.9^{\circ}\text{C}$ ) known as 'Western Shelf Water' (Carmack & Foster 1975, see Hellmer & Bersch 1985 for review) leads to a southward flow under the ice shelf east of the Filchner Depression and a northward outflow west of it. Robin et al. (1983) described another cyclonic circulation west of the Gould Bay which is superimposed by tidal currents with velocities of up to  $0.4\text{ m s}^{-1}$ . They calculated a net northward outflow from areas under the ice shelf for the region between ca 40 and  $49^{\circ}\text{W}$  (see also Carmack & Foster 1975, Foldvik et al. 1985). Due to these oceanographic conditions there are only weak bottom currents in the Filchner Depression and, subsequently, the sea bottom at Stn 307 consists mainly of soft, fine substrate. Coarser sediments, however, were found at the edges of the Filchner Depression. The shelf area of the Gould Bay is generally characterized by sandy bottoms (Melles pers. comm.).

Square photographs were taken with a 70 mm underwater camera (Gutt 1988). The camera was triggered at a constant distance to the sea floor; therefore the size of the vertically photographed area ( $1.2\text{ m}^2$ ) could be calculated (see also Hersey 1967, Heezen & Hollister 1971, George et al. 1985). A small variation in area photographed may have occurred owing to the trigger weight sinking deeper into softer sediments. However, pictures in which the weight was photographed show that the camera was also triggered immediately on soft bottoms. It is thus assumed that the areal underestimate is 10 % at most (i.e.  $\leq 0.12\text{ m}^2$ ). The distance between the positions of the first and the last pictures in a run depended on the drift speed of the ship. Since successive pictures did not overlap, and the time intervals between shots varied from 12 to 20 s, the distance must be at least 80 m for a film of 60 exposures. Assuming a maximum horizontal drift of  $0.5\text{ m s}^{-1}$  the maximum distance between the first and the 60th photograph is 600 m.

On each photograph, individuals of the 3 selected species were counted. It was easy to identify *Achlyonice violaecuspida* due to the typical violet colour of its tentacles and foot tips. In the study area it was also found in considerable numbers in trawl catches. The

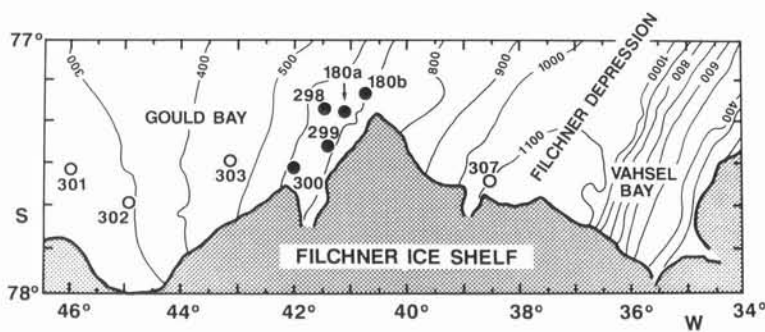


Fig. 1. Station map. Depth contours after Melles (unpubl.). (●) Stations with trawl catch data; (○) stations with photographic observations

holothurians visible on the photographs from Stn 307 in the Filchner Depression were identified by B. Hansen (Zoological Museum, Copenhagen, Denmark) as *Elpidia glacialis*. This species, however, was not found in any of the numerous trawl catches obtained during 3 expeditions of RV 'Polarstern' (ANT I, ANT II, and ANT III) in the Weddell Sea. Only one specimen of the third species, *Scotoplanes globosa*, which differs from *E. glacialis* in having 2 instead of 3 or more dorsal papillae and in the shape of the anterior body, was found in the photographs. This species was present in high numbers, however, in the 5 trawl catches at the western edge of the Filchner Depression.

In the following the term 'small-scale' refers to the spatial extent of one station (see above), i.e. each photograph is regarded as one sample unit. For the statistical description of the spatial pattern we used the measure of patchiness  $m'/m$  proposed by Lloyd (1967) where  $m$  denotes the sample mean and  $m'$  the index of mean crowding (the mean number, per individual, of other individuals in the same sample unit):

$$\text{Index of mean crowding: } m' = m + V/m - 1$$

$$\text{Measure of patchiness: } m'/m = 1 + V/m^2 - 1/m$$

where  $V$  = sample variance. A 2-tailed chi-square statistic tests the significance of departure from randomness ( $m'/m = 1$ ). An aggregated dispersion is indicated by  $m'/m > 1$ , whereas for a value less than unity a uniform dispersion is indicated. In contrast to the hitherto more popular variance-to-mean ratio ( $V/m$ ) the measure of patchiness is independent of the mean and thus more useful when comparing samples of different abundances (Elliott 1971).

The lengths of individual *Elpidia glacialis* and *Achlyonice violaescuspida* were estimated from the underwater photographs. Because of the easily deformable body of *Scotoplanes globosa*, weight is a more appropriate parameter for size classification of trawl specimens. Only externally intact specimens were weighed. The orientation of the holothurians in the photographs was registered as the angle between body axis and picture vertical, measured clockwise. The true compass orientation of the camera, and thus also of the holothurians, was not known; however, at Stn 301 it was possible to measure the orientation of *A. violaescuspida* to the current. The current direction was detectable by the direction in which the tentacles of actinians, present on each photograph, were pointed. For *E. glacialis* the anterior body ends could not be distinguished from the posterior ones. Therefore only the angle of the body axis to the picture vertical was determined.

The bottom trawl used was a commercial 140 ft (43 m) version with a cod-end mesh of 15 mm. The net

opening was ca 22 m. The along-bottom haul time was 30 min except for Stn 180b (60 min).

## RESULTS

The numbers of specimens per photograph arranged in exposure sequence are presented in Fig. 2. In Table 1 the specimen counts per photograph are converted to density figures ( $\text{ind. m}^{-2}$ ).

### *Achlyonice violaescuspida*

This species was present with 231 specimens on the first 30 photographs from Stn 301 (Fig. 2). No further specimens were found on the remaining photograph of the sequence (66 photos). Counts range from 1 to 32 specimens per photograph; the maximum represents a density of 26  $\text{ind. m}^{-2}$  (Fig. 3a). At Stns 302 and 303, 26 and 52 km respectively from Stn 301, *Achlyonice violaescuspida* was absent. Further calculations of these data are listed in Table 1. The dispersion index is calculated for all 66 photographs as well as for only those 30 on which specimens are present. In both cases the calculated coefficients indicate clumped spatial distributions (Table 1; chi-square test,  $p < 0.001$ ).

The lengths of *Achlyonice violaescuspida* ranged from 3.5 to 8.5 cm (median 6.25 cm), with few specimens  $< 5.0$  cm (Fig. 4). The length-frequency distribu-

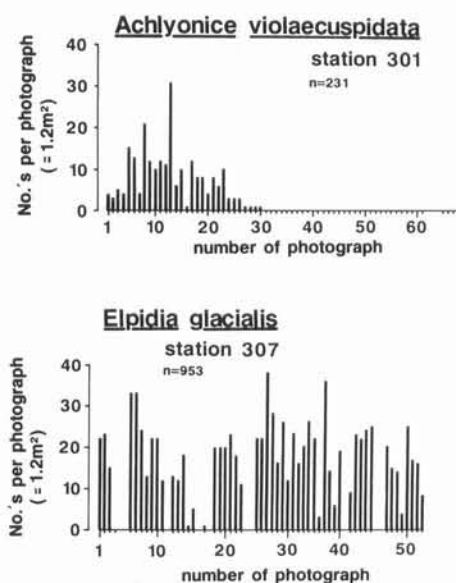


Fig. 2. *Achlyonice violaescuspida* (Stn 301) and *Elpidia glacialis* (Stn 307). Densities and small-scale distribution analysed by underwater photography. Numbers of specimens per photo arranged in exposure sequence. Distances between single photos are represented ideally by equal intervals. Missing values, i.e. unusable photos, are indicated by spaces

Table 1. *Achlyonice violaecuspidata* and *Elpidia glacialis*. Statistical analysis of densities and dispersion patterns. Values in brackets represent only those pictures in which *A. violaecuspidata* is present. Significant departures of dispersion from randomness tested by chi-square statistic; \*  $p < 0.05$ ; \*\*\*  $p < 0.001$

	<i>A. violaecuspidata</i>	<i>E. glacialis</i>
Station	301	307
Depth (m)	240	1175
Number of photographs	66 (30)	53
Total no. of specimens	231 (231)	953
Median of abundance ( $m^{-2}$ )	— (6)	16.6
Interquartile range	— (3–11)	10.4–19.2
Dispersion coefficient	3.73*** (1.63***)	1.18*

tion is positively skewed and not normal (Anderson-Darling test,  $p < 0.05$ ; see Theodorsson 1988).

Orientation was examined for 229 individuals (Fig. 5). The frequencies of the measured angles show a normal distribution (Anderson-Darling test,  $p < 0.05$ ) with a range of  $220^{\circ}$  to  $40^{\circ}$ , a mean of  $300^{\circ}$ , and a standard deviation of  $47.6^{\circ}$ . The orientations coincide with the direction of the current, i.e. the holothurians faced down-stream (Fig. 5).

### *Elpidia glacialis*

A total of 953 specimens of this species were counted on the 53 photographs examined from Stn 307 (Fig. 2). Individuals are present on nearly every photograph, with counts ranging from 1 to 38. One example is given in Fig. 3b. The maximum value represents a density of  $32 \text{ ind. m}^{-2}$ . The median density is  $16.6 \text{ ind. m}^{-2}$  (Table 1). The dispersion coefficient indicates a clumped distribution of the individuals (see Table 1, chi-square test,  $p < 0.05$ ).

Body lengths ranged from 0.5 to 6.0 cm with a median of 1.75 cm (Fig. 4). Their frequency distribution is not normal (Anderson-Darling test;  $p < 0.05$ ).

Analysis of the orientation of 953 specimens shows relatively even distribution (Fig. 5). For 284 individuals the anterior body pole could be determined. From these no significant preference for any particular orientation is detectable, either with regard to all photographs or to a single picture.

### *Scotoplanes globosa*

Table 2 shows the numbers of specimens of this species caught in bottom trawls at the 5 stations in Gould Bay. The abundances ranged between 201 and 2760 individuals per 30 min trawl. The weight-frequency distributions at Stns 298, 299, and 300 (Fig. 6) are significantly different from each other (Kruskal-Wallis test,  $p < 0.05$ ; see Sachs 1984). At Stn 299 relatively large individuals were caught, whilst many small individuals were found at Stn 298. The maximum between-station distance of 30 km is that between Stns 298 and 300.

## DISCUSSION

In the Weddell Sea the 3 investigated holothurian species are restricted to the 'Southern Trench Assemblage' (Gutt 1988). In regions colonized by the 'Southern Shelf Assemblage' and 'Eastern Shelf Assemblage' sessile suspension feeders such as sponges, bryozoans, and ascidians cover up to 100 % of the sea floor. Conditions are therefore unsuitable for motile deposit feeders.

*Achlyonice violaecuspidata* was present on the whole continental shelf of the southern and eastern Weddell Sea between 225 and 785 m (Gutt 1988). High abundances, however, were detected only at one location in Gould Bay. Ohta (1983) mentioned maximum densities of 7900 ind. per 1000  $m^2$  for the closely related *Peniagone japonica* off Japan.

Table 2. *Scotoplanes globosa*. Bottom trawl catch data

	180a	180b	Station 298	299	300
Haul time (min)	30	60	30	30	30
Depth (m)	690	700	650	690	640
Captured specimens per 30 min haul	2760	1381	2200	272	201



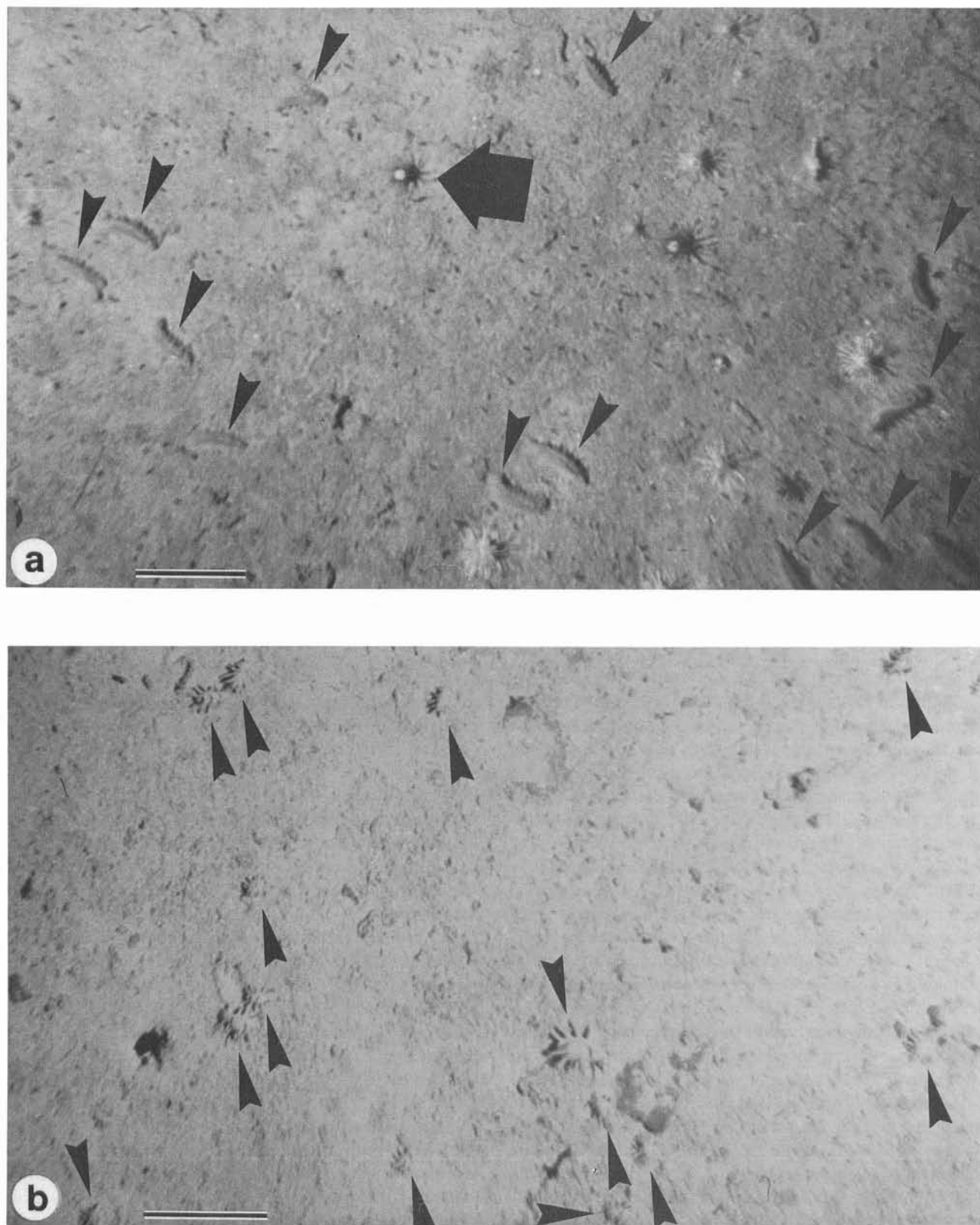


Fig. 3. Underwater photographs. Bars = 3 cm. (a) *Achlyonice violaecuspadata*, in a 0.45 m<sup>2</sup> section of photograph no. 13 at Stn 301 with 13 specimens (small arrows). Large arrow indicates direction of the current determined by the bending of actinian tentacles. (b) *Elpidia glacialis*, in a 0.32 m<sup>2</sup> section of photograph no. 37 at Stn 307 with 14 specimens (arrows)

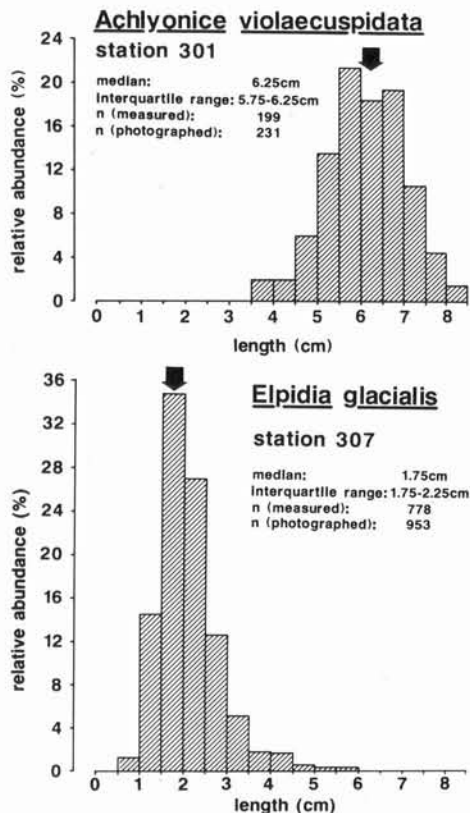


Fig. 4. *Achlyonice violaecuspidata* (Stn 301) and *Elpidia glacialis* (Stn 307). Length-frequency distributions analysed by underwater photography. Arrows indicate medians

We found *Elpidia glacialis* in the Weddell Sea only at Stn 307 (1175 m) in the Filchner Depression. It was not found elsewhere during extensive benthos collections in 1983, 1984, and 1985 either in trawl catches or on underwater photographs. Rich trawl catches of *Elpidia* sp. in the South Sandwich and South Orkney Trenches were described by Andryashev et al. (1974). Lemche et al. (1976) photographed 1 to 10 ind. *E. glacialis* per 100 m<sup>2</sup> north of Australia. These values are significantly lower than those from the Filchner Depression (1 to 32 ind. m<sup>-2</sup>). This species mainly inhabits the deep sea of the Arctic Ocean, but there are also several subspecies in the southern hemisphere (Hansen 1975). Although *E. glacialis* must be considered as a typical deep-sea form, it is the most eurybathic species among the Elasipodida with a depth range of 70 to 9800 m (Hansen 1975).

In the southern Weddell Sea *Scotoplanes globosa* occurred in high abundances at a few stations (especially at Stns 180a, 180b, and 298) in Gould Bay between 640 and 768 m (Gutt 1988), but only sporadically at other stations on the shelf. Barham et al. (1967) reported densities of 15 ind. m<sup>-2</sup> in the San Diego Trough (off California, USA), but the species has been found mainly in the southern hemisphere (Hansen 1975). Its ambulation has been analysed by means of

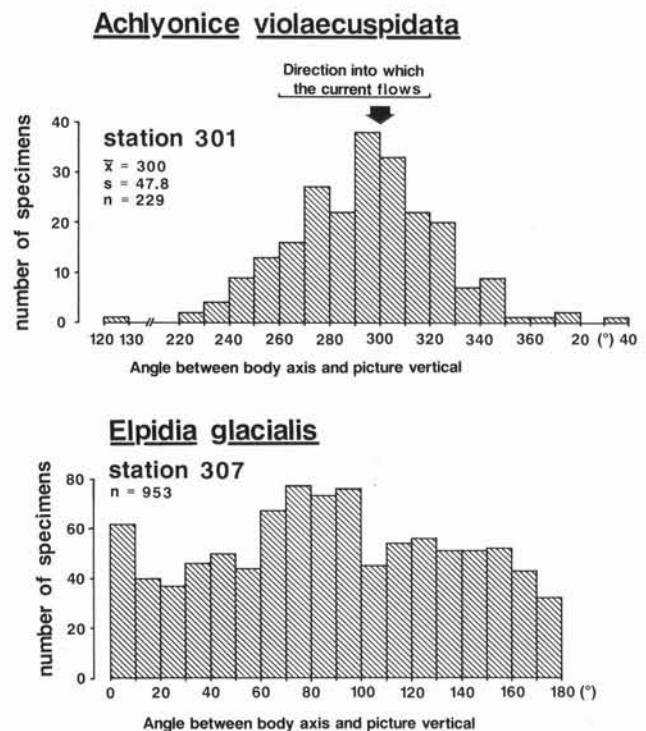


Fig. 5. *Achlyonice violaecuspidata* (Stn 301) and *Elpidia glacialis* (Stn 307). Orientation analysed by underwater photography, measured as angle between body axis and picture vertical for *A. violaecuspidata* (potential range: 0 to 360°), and for *E. glacialis* (potential range: 0 to 180°). Arrow indicates mean of orientation

underwater photography (Hansen 1972). Lafond (1967) calculated for *Scotoplanes* sp. in the San Diego Trough a speed of motion of 0.6 cm min<sup>-1</sup>, observed in situ for 44 min.

A sharply defined patch with a 1-dimensional extent of roughly 100 m is evident in the small-scale distribution of *Achlyonice violaecuspidata* at Stn 301 in Gould Bay (Fig. 2). The individuals were distributed in clumps within this aggregation. *Elpidia glacialis* was present, in contrast, over the entire photographed field at Stn 307 but exhibited a clumped distribution within it.

The length-frequency distribution of *Achlyonice violaecuspidata* occurring in the sharply defined patch at Stn 301 shows that there were no specimens < 5 cm. In contrast, the lengths of *Elpidia glacialis* from Stn 307 ranged from very small specimens to those of about the maximum size for this species, suggesting several cohorts were present in the observed patch. Thus, the patchy occurrence of *E. glacialis* is probably not due to a single synchronized recruitment. A similar pattern is seen in the weight-frequency distributions of *Scotoplanes globosa* caught at Stns 298, 299, and 300. The frequency distributions are, however, significantly different from each other, indicating that distinct 'herds' of *S. globosa* are present within a radius of ca 30 km. These aggregations may mix, but almost cer-

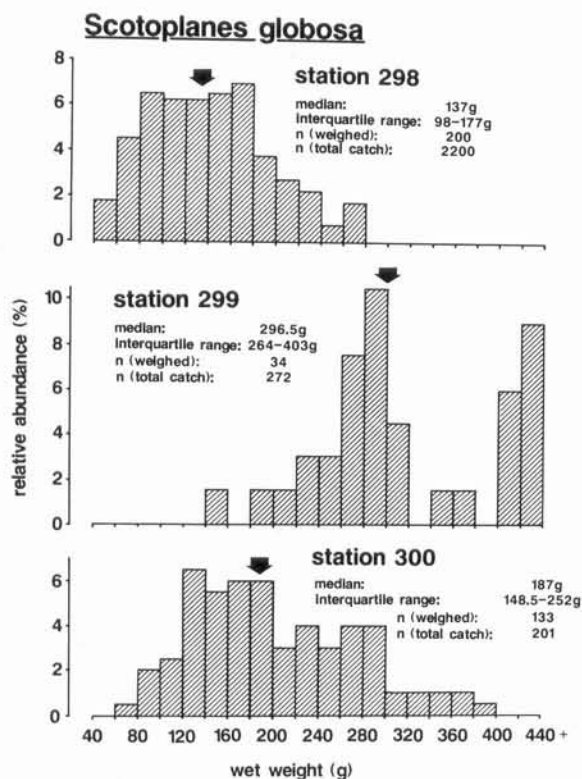


Fig. 6. *Scotoplanes globosa*. Weight-frequency distribution at 3 stations in Gould Bay. Arrows indicate medians

tainly contain more than one age group. Smith & Hamilton (1983) found densities of up to 3 ind. m<sup>-2</sup> in dense aggregated clumps from 25 to 96 m diameter in the Santa Catalina Basin off California.

Most specimens of *Achlyonice violaescupidata* photographed at Stn 301 were oriented with the current, whereas those of *Elpidia glacialis* from Stn 307 were not. The phenomenon of deep-sea holothurians facing, and presumably also migrating, in the same direction is reported by several authors. Billet & Hansen (1982) discovered it at one of 6 stations of *Kolga hyalina*, a species closely related to *E. glacialis*. Similar observations for other species were made by Barham et al. (1967) (for *Scotoplanes globosa*), Heezen & Hollister (1971), Pawson (1976), and Ohta (1983). The observed individuals were mostly moving against the current whilst in the present study *A. violaescupidata* moved with the current. The feet of *A. violaescupidata* are more densely packed in the posterior half of the body than in the anterior half, thus aiding an efficient foothold on the substrate for the body pole facing the current. Consequently, the whole specimen may act like a 'flag in the wind'. The area of the body exposed to the current is minimised when it moves parallel to rather than perpendicular to the current, decreasing flow-induced stress. This point is less important for the oviform *E. glacialis* and *S. globosa*. Ohta (1983, 1985)

found downstream orientation for some elasipod holothurians, e.g. *Achlyonice monactinica*, *Peniagone japonica* and *Enypniastes eximia*, in the bathyal zone of Suruga Bay, central Japan.

Aggregations in the distribution of elasipod holothurians, so-called 'herds' or 'clumps', are well known. Photographic observations of different species were shown by Barham et al. (1967), Heezen & Hollister (1971), Menzies et al. (1973), Grassle et al. (1975), Pawson (1976, 1982) and Ohta (1983). Billet & Hansen (1982) reported mean densities of 4 to 50 ind. m<sup>-2</sup> for *Kolga hyalina* in the deep-sea west of Ireland. The coefficients of dispersion (Lloyd's index) ranged from 1.1 (random dispersion) to 11.9 (clumped dispersion). This heterogeneity in the distribution pattern was supposedly due to temporal aggregations (Billet & Hansen 1982). Ohta (1983) records *Peniagone japonica* as the dominant faunistic element in different depths between 514 and 3290 m with densities up to 7907 ind. per 1000 m<sup>2</sup>, providing up to 98.5% of the numerical abundance of the megabenthos of Suruga Bay.

Explanations given for the observed aggregations of grazing elasipod holothurians include synchronized reproduction events and/or ameliorated food conditions, since they often occur in submarine trenches, troughs or canyons (Barham et al. 1967, Stanley & Kelling 1968). Some of these areas are characterized by increased spatial and temporal heterogeneity, and by a possibly higher instability of the sedimentary environment. Rowe (1971, 1972) and Haedrich et al. (1980) described typical canyon faunas quite different from those of adjacent areas. The motile life style of the characteristic species of these assemblages is thought to permit them, with their grazing manner of feeding, to take advantage of a spatially and temporally patchy detritus supply (Haedrich et al. 1980).

The genus *Elpidia*, for instance, has a general affinity to trenches and/or highly productive regions (Hansen 1975). Thus, it is not surprising to find *E. glacialis* in the southern Weddell Sea on soft bottom with grain sizes similar to those of deep-sea sediments. There is, however, no previous evidence for intermittent sediment slumping or turbidity currents in the Filchner Depression. *Scotoplanes globosa*, or its close relative *S. clarki*, are also reported to occur mainly in canyons (see Hansen 1975), where the generally high organic content of sediments offers favourable food conditions. *Peniagone*, a genus related to *Achlyonice*, has been emphasized as a canyon indicator by Rowe (1972). However, Stn 301 with the densest aggregation of *Achlyonice violaescupidata* in the southern Weddell Sea is on a plain at about 250 m. The bottom consists of well-sorted sandy sediments (Rex et al. 1970) covered by a thin, yellowish-green layer visible on the photographs. This layer is probably composed of organic

material deposited recently. Thus, it is likely a food resource of high nutritional value for deposit-feeding holothurians, and probably accounts for the mass occurrence of *A. violaceuspidata* in Gould Bay.

Our data indicate that the presence of this yellowish-green layer probably consisting of organic material does not explain the patchy distribution of the investigated species. If the individuals continued to move in the same directions as when they were photographed (regardless of whether they exhibited the directionality of *Achlyonice violaceuspidata* or that of *Elpidia glacialis*), the once dense aggregations would be dispersed. Moreover, the yellowish-green layer is rather uniformly distributed over an area larger than that covered by the 'herds'. It was also present in areas (Stns 302 and 303, 26 and 52 km respectively from Stn 301) where no specimens of *A. violaceuspidata* were found (see Fig. 1). It seems, therefore, that the herding can only be explained by 'communication' between individuals which causes the persistence and/or formation of the aggregations.

Herring (1974) found bioluminescence in all 6 elasipod holothurian species he studied. Although bioluminescence was not considered a medium of intraspecific communication by Herring (1974), we propose that it is likely to aid the cohesion of the observed aggregations.

Important questions concerning aggregations of holothurians to be studied in the future are: How do they form, and how long do they persist? Are there any kinds of special spawning aggregations? What is the influence of tides and the subsequent rhythmic current changes on the migration direction of aggregations? Answers to those questions would greatly advance knowledge of the ecology of grazing holothurians which are important components of the bottom fauna of the southern Weddell Sea and of deep-sea ecosystems generally.

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