

## Seasonality and spatial variability in the reproduction of two Antarctic holothurians (Echinodermata)

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**Summary.** Seasonality in the reproduction of *Ekmocucumis steineni* and *Psolus dubiosus* (Holothuroidea) from the Antarctic shelf was investigated. The material was collected in spring (October/November) and autumn (mainly February) in the southeastern Weddell Sea. For *E. steineni* differences between both seasons in relative female fecundity and relative gonad weight were found in both sexes. Large yolky oocytes (0.3–1.0 mm in diameter) forming 1–3 cohorts were present in spring, nearly none in autumn. A delayed or prolonged spawning is possible, depending on the locality. No seasonal differences were found in *P. dubiosus*, a brood-protecting species with a lower fecundity and larger eggs ( $\leq 1.5$  mm in diameter). A longer spawning phase in *P. dubiosus* than in *E. steineni* (October to January) is suggested. Both species are suspension feeders and their intestines were more filled with organic material in autumn than in spring. However, the occurrence of mature oocytes was not directly linked with the seasonal availability of food. The size-frequency distribution of the entire material in the study area was heterogeneous, indicating differences in long-term environmental conditions. The data show an evolutionarily more evolved high Antarctic mode of reproduction in *P. dubiosus* with a prolonged reproductive period than in *E. steineni* which has a distinct annual spawning cycle.

### Introduction

This study describes aspects of the reproductive biology of two species of holothurians from the Weddell Sea, Antarctica. This region belongs to the zone of permanent pack-ice (Hempel 1985) with high Antarctic environmental conditions, which greatly influence the whole ecosystem. During summer primary production might be most intense and shortest in the southernmost parts, near the continent and near sea-ice edges (Hart 1942; Nöthig 1988). Information on dynamic processes in the benthos is

scarce, although most parts of the Antarctic shelf belong to this kind of environment.

This study investigates how the intensive seasonal signal in the euphotic layer is reflected in the benthos and whether regional differences exist. Two dendrochirote holothurians were chosen as representative organisms for this ecosystem: *Ekmocucumis steineni* (Ludwig, 1898) and *Psolus dubiosus* (Ludwig and Heding, 1935). Reproduction of benthic invertebrates can be synchronized with trophic factors (Pearse 1965; Bregazzi 1972; Arnaud 1977; Luxmoore 1982). However, in the Antarctic, the local food availability is less predictable (White 1984). Recent investigations on the seasonality of benthic processes in the Southern Ocean are mostly from the more northern zone of seasonal pack-ice. White (1977) has introduced a classification of marine Antarctic poikilotherms, belonging to different types of reproduction. They range from an aseasonal mode, e.g. for the giant isopod *Glyptonotus antarcticus* (White 1970), to different kinds of cyclic types that are dependent on primary production. Generally, a trend towards few large yolky eggs per female and a non-planktonic development with increasing latitudes (Thorson 1950; Pearse 1965; Picken 1980, 1985), known as "Thorson's rule" (Clarke 1979), is typical only for some taxa of the Antarctic benthos (Pearse et al., 1991).

In the area under study the extent of sea-ice varies to a large degree from year to year (Zwally et al. 1983), and this has a direct influence on the temporal and spatial occurrence of phytoplankton blooms. The area of open water in the southernmost Weddell Sea was larger in 1984 than long-term average. Therefore, at the time of sampling, mainly in February, an important part of the yearly flux of organic material to the bottom must already have occurred. In October 1986, an extraordinary Secchi depth between 70 and 80 m was measured on the western shelf of the Weddell Sea (Gieskes et al. 1987), indicating that primary production had not yet started. The same result were obtained by sediment traps in this area showing a clear pre-phytoplankton-bloom situation in October/early November 1989 and a decreasing bloom in February 1990 (Arntz et al., in press). Thus both periods of

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sampling must be regarded as being from two significantly different seasons, here defined as "spring" and "autumn". The large spatial extent of the study area also made it possible to investigate the variability of seasonal processes depending on different localities.

The investigations were carried out on *E. steineni* and *P. dubiosus* because these mostly sessile suspension feeders can be regarded as representative benthos organisms of this area. Several details of their life history and spatial distribution in the Weddell Sea are known (Gutt 1991a). The species belong to the Dendrochirotrida, an order preferring in general the continental shelves. They were sampled during faunistic surveys in the Weddell Sea at high abundances and presences (Gutt 1991a), mainly in the "Southern Shelf Community" and "Eastern Shelf Community" sensu Voß (1988). *E. steineni* is known from the continental shelf of the Antarctic, the Subantarctic and the Antarctic islands whereas *P. dubiosus* was found only in the East Antarctic and the Weddell Sea. Differences exist in their preference of spatial microniches and in characteristics of their morphology. *P. dubiosus* is bilaterally symmetrical, with a conspicuous sole on the functional ventral side and a dorsal mouth and anus. It is adapted to live on a plane substratum mostly consisting of stones, but can also occur on solitary ascidians or similar biotic structures. The dorsal body surface consists of a solid calcareous test. The brooding behaviour in two different seasons was analyzed from material used in the present study (Gutt 1991b). *E. steineni* shows plesiomorph pentamerous symmetry, reducing the endoskeleton during ontogenesis. It lives in two different micro-habitats, between fan-shaped bryozoans several centimeters above the bottom or with the posterior body half burrowed in the sediment. This plastic behaviour has been discussed as the

main reason for the highest abundance of this species among all Weddell Sea holothurians (Gutt 1991a).

The investigation of the size-frequency structure and the weight of the intestine at different stations was to provide additional information about temporal and spatial variability of dynamic processes in the benthos.

## Materials and methods

The material is from three expeditions with RV Polarstern to the eastern and southern Weddell Sea. The first two cruises, ANT I (1983) and ANT II (1984), took place from late January to early March, here defined as "autumn". Most of the material from the third cruise, ANT V, is from the middle of October to the middle of November 1986, here defined as "spring". Total numbers of specimens per sample with additional information about the stations are listed in Table 1 and shown in Fig. 1. For complete station lists and cruise reports see Hempel (1983), Drescher et al. (1983), Kohlen (1984) and Schnack-Schiel (1987). The animals were captured by an Agassiz or bottom trawl and preserved in buffered formaldehyde. Since fecundity must be referred to the size of the specimens, an appropriate parameter for the latter had to be found. Length, width or total wet weight are inadequate for these holothurians because of unpredictable body contraction and loss of body fluid due to catch and preservation. The dry weight is assumed to be theoretically the best dimension for the individual size of these animals. As its determination is time-consuming, the gutted wet weight was chosen for further investigations after it could be proven that it is highly correlated with the dry weight. Therefore the gutted animals of a subsample were dried for 36 h at 70°C. The term "gutted weight" refers to the weight of the whole animal without intestine and gonads.

Sex was determined by eye. If no classification was possible, the specimens were regarded as juveniles. The measurements were made by using a microscope with 40× magnification. For *Ekmocucumis steineni*, oocytes  $\geq 0.300$  mm, for *Psolus dubiosus*, oocytes  $\geq 0.075$  mm were counted. The yellowish opaque colour of the larger

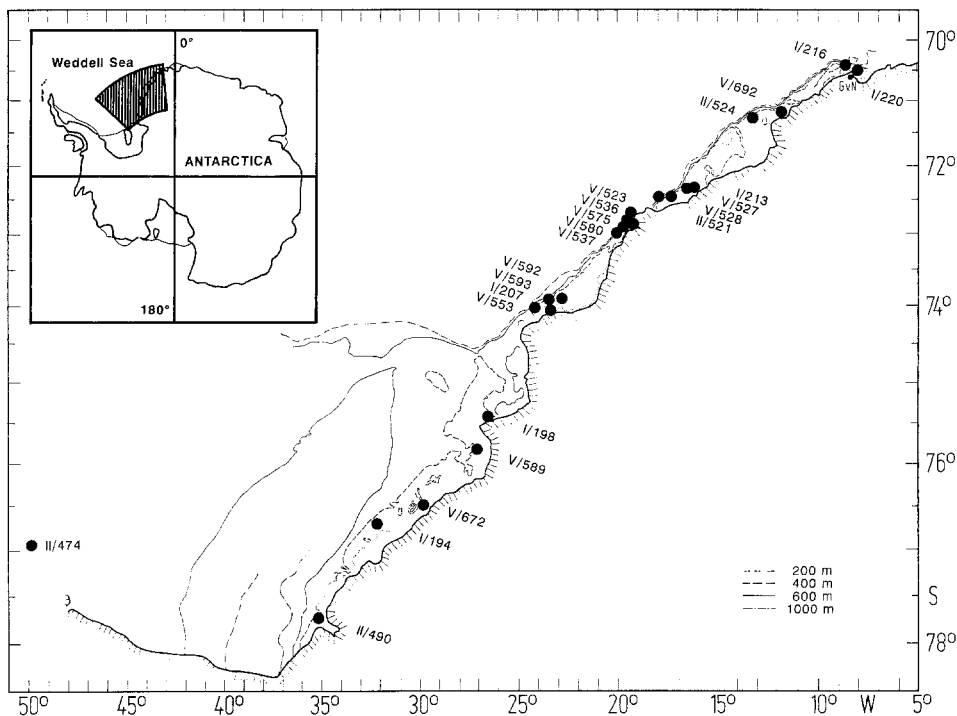


Fig. 1. Station map

**Table 1.** List of stations with cruise number, station number, depth, date of sampling, and numbers of sampled specimens of *Ekmocucumis steineni* and *Psolus dubiosus*, separately listed for the sexes and juveniles (juv)

Cruise no. (ANT)	Stn no.	Depth (m)	Date (dd.mm.yy)	Material							
				<i>E. steineni</i>				<i>P. dubiosus</i>			
				♀♀	♂♂	juv	Σ	♀♀	♂♂	juv	Σ
<b>Spring-group</b>											
V/3	523	840	21.10.86					35	26	6	67
V/3	527	315	22.10.86					3	1	0	4
V/3	528	290	22.10.86	1	7	1	9				
V/3	536	595	24.10.86	1	4	1	6	2	2	0	4
V/3	537	420	24.10.86	18	14	2	34				
V/3	553	350	31.10.86	5	0	0	5				
V/3	575	670	07.11.86					8	5	0	13
V/3	580	710	08.11.86	3	2	0	5	1	1	0	2
V/3	589	318	12.11.86	2	4	1	7				
V/3	592	211	14.11.86	2	5	0	7				
V/3	593	343	14.11.86	4	2	3	9	4	3	0	7
Σ				36	38	8	82	53	38	6	97
<b>Autumn-group</b>											
V/4	672	266	12.01.87					0	4	1	5
V/4	692	189	25.01.87					8	9	1	18
II/4	474 <sup>a</sup>	220	14.02.84	see below				10	5	0	15
II/4	474 <sup>b</sup>							4	9	0	13
II/4	490	395	20.02.84					2	2	0	4
I/2	194	270	22.02.83					1	2	0	3
I/2	198	230	23.02.83	11	9	0	20	3	7	0	10
I/2	207	260	24.02.83					1	1	0	2
II/4	521	780	25.02.84					3	10	0	13
II/4	524	325	25.02.84					4	0	0	4
I/2	213	220	26.02.83	see below				0	6	0	6
I/2	216	330	01.03.83	10	10	0	20	16	14	1	31
I/2	220	262	01.03.83	25	24	1	50	3	1	0	4
Σ				46	43	1	90	55	70	3	128
II/4	474	220	14.02.84	79	70	8	157	see above			
I/2	213	221	26.02.84	15	13	8	36	see above			
Σ(total)				176	164	25	365	108	108	9	225

<sup>a</sup> Regular sample

<sup>b</sup> Additional material of specimens with above average size, only considered for fecundity studies

oocytes indicated the vitellogenesis, in contrast to the smaller, whitish translucent oogonia. For *E. steineni*, approx. 300 oocytes were measured of each specimen. In *P. dubiosus*, a mean diameter for the oocytes per gonadal tube was estimated by eye on the basis of single measurements, because of the unimodal size distribution (see "Results"). Their size frequencies and further calculations are based on these values. Measurements were made by 0.025 mm graduation marks. Sizes were combined to classes of two marks.

The gonad index is defined as gonad wet weight × 100 (g) per gutted wet weight (g). The relative fecundity is the number of oocytes per gutted wet weight (g). The relative intestinal weight is the wet weight of the filled intestine posterior to the muscular stomach × 100 (g) per gutted wet weight (g).

## Results

### Wet weight-dry weight relationships

To find an appropriate parameter for the individual size of the specimens, the linear regression model for the correla-

tion between gutted wet weight (called "wet weight" in the following) and dry weight was calculated for stn 474. The summed up data for males, females and juveniles are given in Table 2. In both species the variances of the dry weight can be explained by the gutted wet weight, as can be seen from the high and significant correlation coefficients. The wet weight-dry weight ratio is lower for *Psolus dubiosus* than for *Ekmocucumis steineni*, which is also visible in the two linear regression models.

### Wet weight of the specimens

Before investigating local differences in the populations, the mean sizes of the sexes were compared statistically. Only stations with ≥ 9 specimens per sex were considered (Table 3). For *E. steineni*, at 50% of the 6 analyzed stations there were significant differences between the mean weights of the sexes. At two stations (220, 474) the males

**Table 2.** *Ekocucumis steineni* and *Psolus dubiosus*. Linear regression model for the correlation between wet weight (x) and dry weight (y) on stn 474. Correlation coefficients are significantly different from 0 ( $p \leq 0.05$ , two-sided)

	<i>Ekocucumis steineni</i>		<i>Psolus dubiosus</i>	
	wet wt (g)	dry wt (g)	wet wt (g)	dry wt (g)
Linear regression	$y = 0.15x - 0.01$ $n = 93; r = 0.969$		$y = 0.13x + 0.23$ $n = 20; r = 0.855$	
Mean	3.48	0.51	2.84	0.61
Standard deviation	1.68	0.26	0.76	0.12
Range	0.707–8.87	0.07–1.32	1.72–4.04	0.42–0.87
Wet wt/dry wt ratio	6.82		4.66	

**Table 3.** *Ekocucumis steineni* and *Psolus dubiosus*. Wet weights per sex and stations with at least 9 specimens with significant differences between males and females

Stn		<i>Ekocucumis steineni</i>		<i>Psolus dubiosus</i>	
		♂♂	♀♀	♂♂	♀♀
198	median	5.76	5.77		
	interquartile range	4.41–6.48	4.33–7.23		
	range	1.62–8.95	3.92–10.61		
	<i>n</i>	9	11		
	difference <sup>a</sup>	not significant			
213	median	3.60	4.26		
	interquartile range	2.96–3.70	3.72–5.72		
	range	1.88–4.15	1.11–8.21		
	<i>n</i>	13	15		
	difference <sup>a</sup>	significant			
216	median	6.82	6.60	2.05	1.50
	interquartile range	4.90–7.37	5.23–7.05	0.92–7.22	0.79–5.70
	range	4.13–8.96	3.13–9.11	0.37–10.46	0.42–8.71
	<i>n</i>	10	10	14	16
	difference <sup>a</sup>	not significant		not significant	
220	median	5.81	4.67		
	interquartile range	5.04–6.42	3.79–5.78		
	range	2.02–8.77	1.03–8.64		
	<i>n</i>	24	25		
	difference <sup>a</sup>	significant			
474	median	3.94	3.22		
	interquartile range	2.59–5.26	1.90–4.36		
	range	0.87–10.17	0.59–6.92		
	<i>n</i>	70	79		
	difference <sup>a</sup>	significant			
523	median			2.98	2.83
	interquartile range			1.77–4.23	2.09–3.81
	range			0.79–6.85	1.09–7.54
	<i>n</i>			26	35
	difference <sup>a</sup>			not significant	
537	median	3.52	3.36		
	interquartile range	2.73–4.01	3.15–4.35		
	range	1.35–6.32	2.48–6.79		
	<i>n</i>	14	18		
	difference <sup>a</sup>	not significant			
Σ <sup>b</sup>	median	4.16	3.91	2.85	2.28
	interquartile range	2.97–5.75	2.73–5.21	1.54–4.26	1.26–3.69
	range	0.87–10.17	0.59–10.61	0.37–12.16	0.26–11.25
	<i>n</i>	140	158	108	108
	difference <sup>a</sup>	not significant		not significant	

<sup>a</sup> Mann-Whitney test,  $P \leq 0.05$ , two-sided

<sup>b</sup> *E. steineni*: for above listed stations

*P. dubiosus*: for the whole used material listed in Table 1

were heavier than the females and at stn 213 the situation was vice versa. In *P. dubiosus* the males are heavier than the females, however, no significant difference was found at the separate stations. So in both species the representatives of one sex are generally not heavier than those of the other. Also the medians of the wet weights per sex and station (Table 3) were compared statistically. No significant differences between the sexes were found (Mann-Whitney test,  $P \leq 0.05$ , two-sided). The total samples for both species show no deviations from the 50:50 sex-ratio (see Table 1).

To get information on the variability in the population structures for the above-considered stations, weight-frequency distributions were plotted (Figs. 2, 3). The mean weights, with some additional material for *P. dubiosus*, were compared statistically. Weights of males, females, and juveniles were summed up. The results are given in Table 4. For *E. steineni*, 60% of all 15 stations combinations show significant differences. Also the medians for the weights of *P. dubiosus* have a broad range, but only few significant differences could be detected. Combinations with stn 216 were not calculated because of the bimodal size-frequency distribution with peaks at approx. 1 and 8 g wet weight.

### Reproduction

The gonads of both species consist of two tufts of  $\geq 50$  tubes in adult specimens. In *E. steineni* oocytes of all developmental stages can be present in one tube, whilst in *P. dubiosus*, only one stage was found in one tube. In this species, there were more small oocytes per tube (approx. 35) than larger ones (approx. 15).

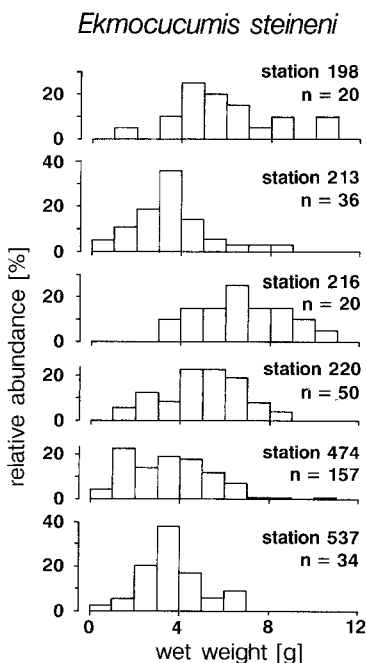


Fig. 2. *Ekmocucumis steineni*. Weight-frequency distributions for males, females, and juveniles at those six stations with more than 19 specimens

To obtain data sets large enough for statistical analyses, several samples from same seasons were combined as listed in Table 1. The relative numbers of mature oocytes and their size frequencies were checked by eye on differences between the single samples to ensure that no stations were combined which were different from each other. As a result of the check by eye the samples of *E. steineni* from stns 474 and 213, both from autumn, are treated separately from the spring and autumn-group.

In order to compare subsamples of approximately the same size range and to exclude an influence of immature specimens, only specimens  $\geq 1.5$  g,  $\leq 8$  g (*E. steineni*) and  $\geq 1$  g,  $\leq 9$  g (*P. dubiosus*) wet weight were considered. For this material the medians, interquartile ranges and ranges of wet weights are shown in Fig. 4. No significant differences in size between the subsamples could be found except for *E. steineni* between the autumn-group and those from stn 474.

*Ekmocucumis steineni*. The gonad indices have similar average values for both sexes (Fig. 4). They comprise approx. 15% in the spring group and at stn 474 whereas they account for half of it in the autumn-group and at stn 213. The relative fecundity (Fig. 4) shows an average of approx. 400 oocytes at stn 474, approx. 300 oocytes in the spring group and only 73 oocytes at stn 213. 3–15% of these females were without oocytes. In the autumn group the ovaries were empty except for a small residual number of mature oocytes in 25% of the specimens.

The statistical tests on differences between stn 474, the spring and the autumn groups show that the results for all investigated parameters (relative fecundity of the females, gonad index and relative intestine weight of both sexes) are equal: between the spring and autumn groups the differences are significant. Although sampling at stn 474 took place in autumn no significant differences from the spring group could be detected but from the autumn group. Stn 213, also sampled during autumn shows no differences from the autumn group, but to the spring-like stn 474. Between the spring group and stn 213 there are no significant differences except in the gonad index of the females.

Summarized and individual size frequencies of mature oocytes for the above considered station groups are shown

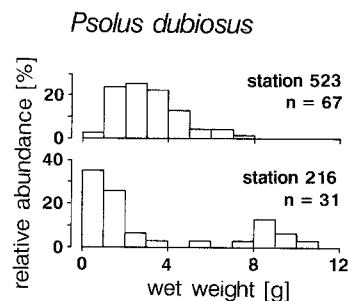


Fig. 3. *Psolus dubiosus*. Weight-frequency distributions for males, females, and juveniles at those two stations with more than 19 specimens

**Table 4.** *Ekmocucumis steineni* and *Psolus dubiosus*. Wet weights on stations with at least 9 specimens per sex (*E. steineni*) and for at least 10 specimens per sample (*P. dubiosus*) with significant differences between the stations

<i>Ekmocucumis steineni</i> (males, females and juveniles)							
Stn	198	213	216	220	474	537	
213	sig.						
216	n. sig.	sig.					
220	n. sig.	sig.	n. sig.				
474	sig.	n. sig.	sig.	sig.			
537	sig.	n. sig.	sig.	sig.	n. sig.		
Median interquartile	5.73	3.69	6.71	5.10	3.37	3.48	
Range	4.30–7.03	2.24–4.25	4.92–7.32	4.96–6.35	1.94–4.83	2.73–4.16	
Range	1.62–10.61	0.57–8.21	3.13–9.11	1.03–8.77	0.55–10.17	0.53–6.79	
N	20	36	20	50	157	34	

<i>Psolus dubiosus</i> (males, females and juveniles)							
Stn	198	216	474	521	523	575	692
216	a						
474	sig.	a					
521	n. sig.	a	n. sig.				
523	sig.	a	n. sig.	n. sig.			
575	n. sig.	a	n. sig.	n. sig.	n. sig.		
692	sig.	a	n. sig.	n. sig.	n. sig.	sig.	
Median interquartile	6.69	1.49	2.22	3.27	2.82	4.26	1.26
Range	5.90–7.19	0.73–6.27	1.73–2.95	2.86–4.33	1.83–3.97	3.49–5.32	0.82–1.48
Range	4.02–9.47	0.37–10.46	1.49–4.05	1.62–5.47	0.79–7.54	2.85–7.78	0.37–12.16
N	10	31	15	13	67	13	17

<sup>a</sup> Not tested because of the bimodal size distribution on stn 216

Kruskal-Wallis test and comparison of independent samples according to Nemenyi (Sachs 1988),  $P \leq 0.05$ , two-sided

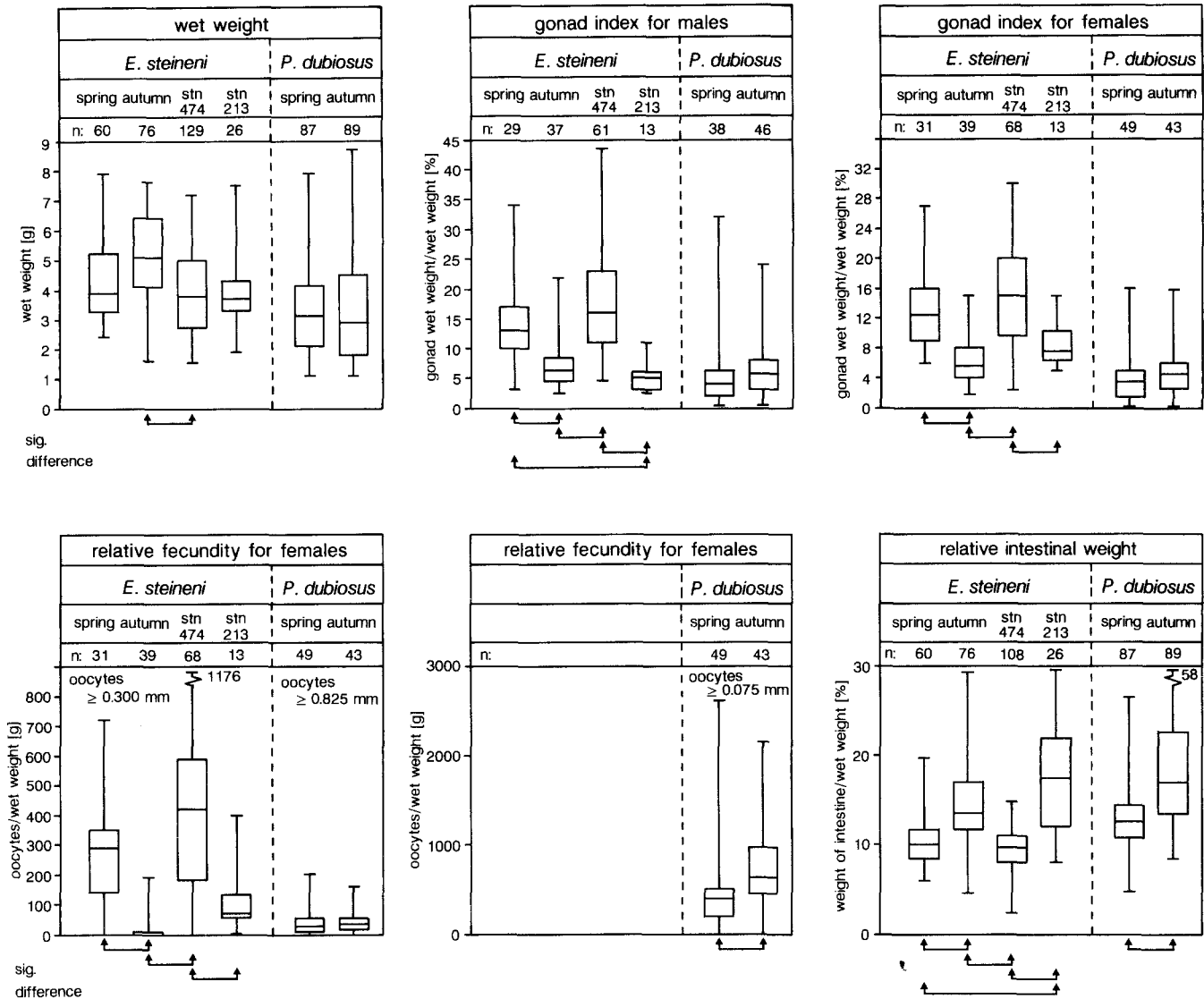
in Figs. 5–8. At stn 474 these results are from a representative subsample of 16 specimens; here one cohort of large oocytes was found. Bimodal size frequencies for stn 213 and the spring group have peaks around 0.45 and 0.75 mm. They represent the individual oocyte size frequencies of the total sample although there are a few individuals either with the smaller or the larger fraction. In the autumn group, a few oocytes in a few specimens at stns 198 and 220 also show two peaks in their size distribution, each peak belonging to one of the two stations. At the third stn 216, belonging to the autumn group, no mature oocytes were found.

*Psolus dubiosus*. The gonad index of the males, approx. 5%, is slightly higher than that of the females (approx. 4%) mainly because of higher maximum values (Fig. 4). The relative fecundity of mature oocytes ( $\geq 0.825$  mm) varies between 26 and 37 oocytes in the spring and autumn groups, respectively (Fig. 4). Significant differences between the two seasons for these parameters could not be found. The percentages for females without mature oocytes are 16% and 22% in the spring and autumn groups, respectively. The number of oocytes per wet weight, 0.075–1.440 mm in diameter, was significantly higher in autumn (640) than in spring (400) (Fig. 4).

Oocyte size frequencies for the autumn and spring groups are similar to each other (Figs. 9, 10). They are dominated by the fraction with a diameter  $\leq 0.800$  mm. The cohort of oocytes 0.825–1.400 mm in diameter has an approx. normal distribution where the mean diameter of the autumn-group (1.20 mm) is slightly larger than that of the spring group (1.00 mm). The graphs for selected typical single specimens in Figs. 9, 10 show the fraction of many small immature oocytes. In most specimens a less distinct peak of a next larger oocyte group approx. 0.475–0.725 mm in diameter, is visible. In both seasons, the cohort of the large oocytes has one peak with average diameters ranging from 0.925 to 1.175 mm.

#### Intestine content

The intestine contents were quantitatively investigated to enable a direct comparison of nutrition in the two observed seasons with the results of the reproductive study. Therefore the same classification of stations for both species was used (Table 1). In *E. steineni*, a larger amount of intestine content in the autumn group than in the spring group and at stn 474 is indicated by higher values of the



**Fig. 4.** *Ekmocucumis steineni* ( $\geq 1.5$  g,  $\leq 8.0$  g) *Psolus dubiosus* ( $\geq 1.0$  g  $\leq 9.0$  g). Wet weights for specimens considered in the investigation of reproduction, gonad indices, relative fecundities, and relative intestinal weights with analyses on statistical differences

between subsamples (indicated by bars with arrows). Kruskal-Wallis test and comparison of independent samples according to Nemenyi (Sachs 1988),  $P \leq 0.05$ , two-sided

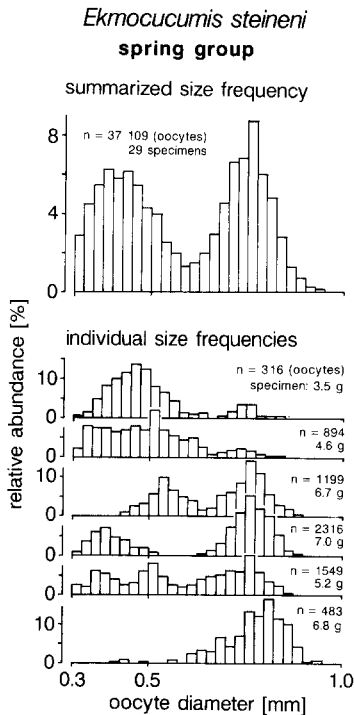
relative weight of the intestine (Fig. 4). Statistically significant differences are similar to those of the fecundity studies. However, one exception is an extremely high value of 17% at stn 213. Thus, concerning the intestine content this station has no intermediate position between the spring and autumn groups as in the reproduction results, but the value is higher than that of the autumn group. Also in *P. dubiosus* the relative weight of the intestine of the autumn group is significantly higher than in the spring group.

**Discussion**

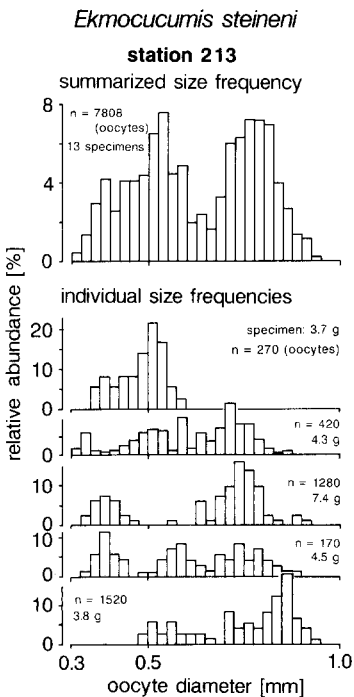
Our investigations revealed similarities in seasonal and spatial aspects of the reproductive biology of *Ekmocucumis steineni* and *Psolus dubiosus*, as well as differences between single specimens within one station and season.

The wet weight was shown to be a reproducible parameter for the size of the specimens because of the significant correlation coefficient between this parameter and the dry weight. Thus the wet weight was used in the calculations for both species. The lower value for the wet weight-dry weight ratio in *P. dubiosus* is due to the calcareous test covering the whole functional dorsal surface. In contrast *E. steineni* has a muscular body wall.

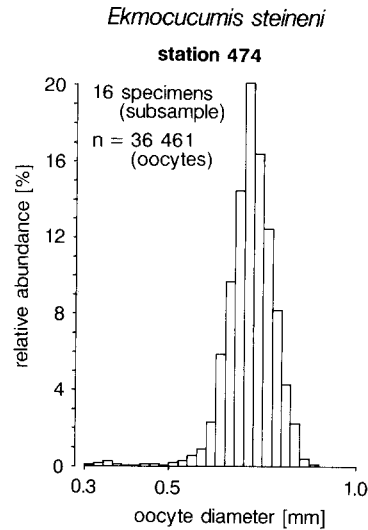
The population structures of both species showed significant differences in mean body sizes between different localities. No detectable relationship was obvious between population size structure and latitude or depth. Therefore differences in unknown spatial small-scale but long-term effective environmental processes must have led to these heterogenous results, if they are not exclusively due to short-term colonization events. Such environmental factors probably influence the reproductive biology although no general direct correlation between population structure



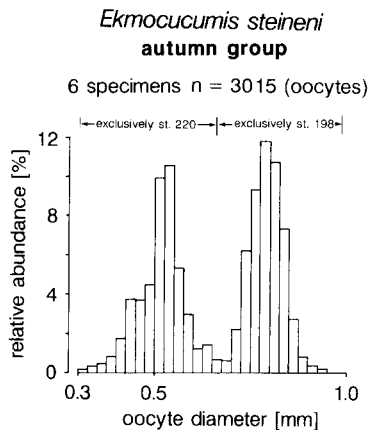
**Fig. 5.** *Ekmocucumis steineri* (spring group). Summarized size-frequency distributions of all oocyte-carrying females with selected size-frequency distributions of single specimens, characteristic for the entire material. *N* indicates numbers of oocytes. Weights given at individual size frequencies refer to wet weight of females



**Fig. 6.** *Ekmocucumis steineri* (stn 213). Summarized size-frequency distributions of all oocyte-carrying females with selected size-frequency distributions of single specimens, characteristic for the entire material. *N* indicates numbers of oocytes. Weights given at individual size frequencies refer to wet weight of females



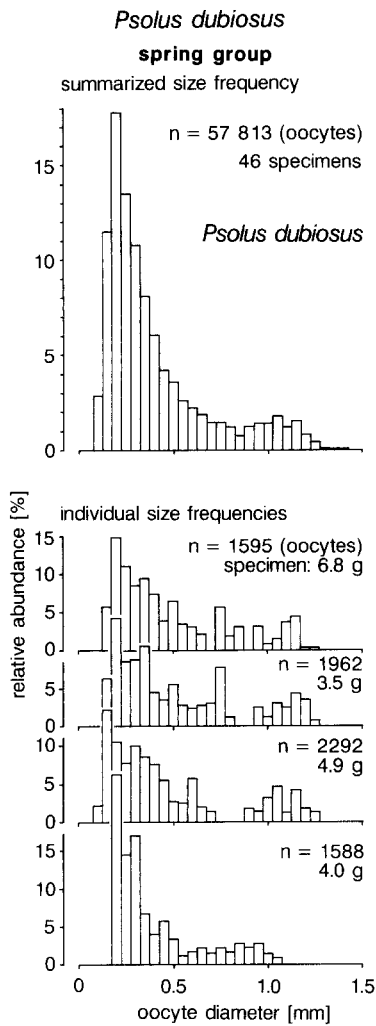
**Fig. 7.** *Ekmocucumis steineri* (subsample of stn 474). Summarized size-frequency distribution for oocytes



**Fig. 8.** *Ekmocucumis steineri* (autumn group). Summarized size-frequency distribution for oocytes

and reproductive behaviour could be found. One exception might be the results for *E. steineri* at stn 474. In this southernmost part of the Weddell Sea, the coastal polynya is usually narrower than elsewhere and does not occur each year (Zwally et al. 1983). Therefore a generally reduced and delayed availability of food is expected. This is indicated by the lower weights of intestinal contents in *E. steineri* from stn 474, similar to those of the spring group. As a result, the smaller average size and the delay in reproduction can be explained. Wägele (1987) found a latitudinal variation in the reproductive biology of the isopod *Ceratoserolis trilobitoides* in the same area of investigation. Hendler (1979) emphasized the complexity of interrelationships between environmental factors and reproductive biology. He could not find that productivity was the prime factor determining reproductive cycles for Atlantic and Pacific ophiuroids. Clarke (1985), however, discussed a delicate tuning of the reproductive cycle to the

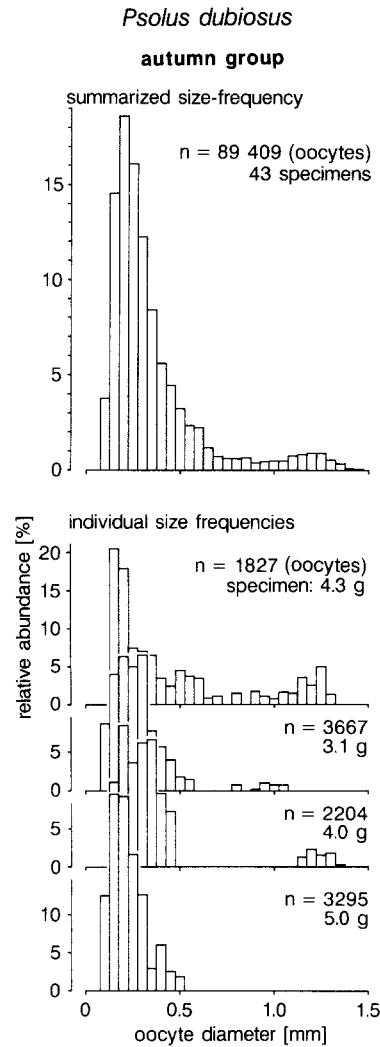




**Fig. 9.** *Psolus dubiosus* (spring group). Summarized size-frequency distributions of all oocyte-carrying females with selected size-frequency distributions of single specimens, characteristic for the entire material.  $N$  indicates numbers of oocytes. Weights given at individual size frequencies refer to wet weight of females

pattern of primary productivity for Antarctic marine invertebrates. A sexual dimorphism in size or a deviation from a 50:50 ratio between the sexes, affecting the general population structure, was not found.

The main seasonal similarity between the two species is the presence of large, yolky oocytes. For *E. steineni* the main bulk of these was found in spring (October/November). In that season the mean gonad index for both sexes and the relative fecundity of the females are high compared to most of the other samples. The two size classes of oocytes are either of the same magnitude or one of them is underrepresented or absent in some specimens. This may be the result of a discontinuity in cycles of oogenesis with a high variability between individuals. The absence of the larger fraction may also be due to an already finished spawning. Thus, this entire sample from spring must be considered as to be within a long-term spawning phase, consisting of individual short-term spawning events. Such behaviour in Antarctica has also been observed in the pelagic krill, *Euphausia superba* (Cuzin-Roudy 1987). A



**Fig. 10.** *Psolus dubiosus* (autumn group). Summarized and individual size-frequency distributions for oocytes.  $N$  indicates numbers of oocytes. Weights given at individual size frequencies refer to wet weight of females

major spawning activity in early summer is known for the dendrochirote holothurian *Thyone briareus* around Japan (Colwin 1948). The Subantarctic echinoid *Abatus cordatus* shows highest gonad indices at the end of march, during austral summer (Magniez 1983). In *E. steineni* most specimens from autumn have a low gonad index and no oocytes are present in the ovaries. Therefore it can be concluded that *E. steineni* has a yearly reproductive cycle, with a spawning phase from at least October to February. During one cycle different batches of ova will be developed and spawned. This interpretation partly corresponds and is partly in contrast to results for the high Antarctic asteroid *Odontaster validus* and the echinoid *Sterechinus neumayeri*. In both species 1–3 cohorts of oocytes have been observed by Pearse (1965) and Pearse and Giese (1966), respectively. Both species spawn in winter, approx. from June to November, and have well-defined reproductive periodicities. The authors estimate a time of 18–24 months for the oogenesis on the basis of a material sampled throughout the whole year. However, both species are restricted to

shallow water and therefore are scarce in the Weddell Sea. For the Antarctic crinoid *Promachocrinus kerguelensis*, which mainly spawns in November and December, McClintock and Pearse (1987) came to similar conclusions for the time of oogenesis. Yakovlev (1983) called the 18–24 month duration of oocyte growth for *Sterechinus neumayeri* “erroneous” and suggested one year. Two cohorts of oocytes in February and May are also known from the North Atlantic dendrochirote holothurian *Aslia lefevrei* (Costelloe 1985). Kühl (1988) gave two alternative interpretations for her data on the reproduction of Antarctic octopods: spawning throughout the year and seasonal spawning with gametogenesis that takes longer than one year.

In *E. steineni* deviations from the above-discussed general results are possible. At the end of February most of the females at stn 213 and 6 females from the autumn group still had mature oocytes in the ovaries. The size distribution of the oocytes was similar to that of the spring specimens, however, the relative gonad weight and female fecundity were lower. If the oocytes of the smaller size group were spawned later than the larger ones, at stn 213 spawning continued after the time of sampling. First the batch of ova with the larger diameter will be released and after a period of oocyte growth the rest will be spawned before the end of this reproductive cycle is reached. Stn 474 from February (autumn) shows a different situation. All oocytes belong to one size class, and the gonad indices are similar to those of the spring samples although the female fecundity was higher. As the spring group is interpreted to be at the beginning or within a reproductive cycle, it may be that at stn 474 all observed oocytes are released in one batch and that the main spawning event had not been taken place in mid-February. This also can explain the highest relative fecundity in this group. Thus a delayed spawning phase must be stated. At stn 213 however, spawning appears to have begun at the same time in spring as at adjacent stations, e.g., stns 537 and 593, which means that the whole spawning period has been prolonged. A “breakdown” of oocytes or an increase in gonad index caused by environmental factors has also been observed in *Sterechinus neumayeri* by Pearse and Giese (1966). Pearse (1965) found regional differences in oocyte growth in *Odontaster validus* to be due to suboptimal conditions.

In *P. dubiosus* the similarities between results from the two seasons are more evident. Generally the mature oocytes belonged to one size class but the average diameter may vary individually. Averaging the whole investigated material, this cohort of oocytes is approx. of the same magnitude in autumn as in spring although spawning appears to have occurred throughout the entire period of investigation. The distinct separation of the large yolky oocytes from the smaller transparent ones, however, indicates a cyclic oogenesis. Whether this periodicity is coupled to annual environmental changes cannot be concluded from these data. No periodicity was observed in the spawning events even though the material is from two completely different seasons. Thus a non-synchronous spawning throughout the year might exist regarding the population as a whole, with single specimens reproducing discontinuously. This interpretation is supported by the

fact that *P. dubiosus* is brood-protecting without a detectable seasonality in the size structure of the early life stages (gutt 1991b). This result is in accordance with the generally formulated relationship between species with a non-pelagic development and aseasonal or prolonged spawning period (Picken 1980). A significant difference between specimens from spring and autumn was found in the numbers of the smallest oocytes, where an increase in number from spring to autumn indicates a next reproductive cycle. As specimens collected in autumn contain ten times as many small oocytes/oogonia as mature ones, most of these must be regarded as nutritive cells. Similar observations have also been made for the two above mentioned echinoderm species *Odontaster validus* and *Sterechinus neumayeri* (Pearse 1965; Pearse and Giese 1966; Yakovlev 1983). An intermediate generation of oocytes, slightly larger than the cohort of numerous small oocytes, is visible in the size distributions for several single specimens. As they do not show a seasonality like the small ones these oocytes of intermediate size probably belong to a new generation to be spawned, rather than nutritive cells. Thus, in *P. dubiosus* oogenesis appears to take approx. two years from the first appearance of the main bulk of smallest oocytes to the time of their spawning. For West Pacific, coastal asteroids Farmanfarmaian et al. (1958) found one asteroid species, *Patiria miniata*, which spawned throughout the year and other species which had a well defined annual reproductive cycle. In the deep sea, which shows a general faunistic affinity to the Antarctic shelf (Bullivant 1967; Dayton et al. 1974; Andriashev 1977; Lipps and Hickman 1982), three holothurians have been reported to have an aseasonal reproduction in the north-east Atlantic: *Ypsilothuria talismani* (Dendrochirotida) (Tyler and Gage 1983), *Laetmogone violacea* and *Benthogone rosea* (both Elaspodida) (Tyler et al. 1985). Schoener (1968) found seasonal and aseasonal reproduction in deep-sea ophiuroids.

The results of the investigations on the intestine weight should render information on the seasonality in the nutrition conditions for these holothurians; nothing was previously known about this. For the detritivorous irregular echinoid *Abatus cordatus*, Magniez (1983) found no obvious seasonality in the ratio between gut weight and body weight. Because of the passive filter-feeding behaviour the investigated holothurian species could be used as quasi natural sediment traps. In spring only small amounts of material were found in the intestine of *P. dubiosus* and *E. steineni*, indicating that a major flux of organic substance had not taken place at the moment of sampling. As the period of primary production in autumn is short in Antarctica, no important amount of food for the investigated holothurians could have been available before this period of sampling (October/November). In autumn, stn 213 included, the significantly higher values of intestine contents show that the animals are in a more successful feeding phase. However, because oogenesis in both species is long compared to the annual period of the phytoplankton bloom, no direct correlation between feeding and spawning phase exists. The mature oocytes, ready to be released, are already present before the main feeding period in autumn. A second generation of oocytes to be

spawned next year was not even found in specimens of *E. steineni* which had finished spawning and had well-filled intestines. Such as intermediate size class was found in *P. dubiosus* in both seasons. In this species, however, the significant increase of the smallest oocytes between the two investigated seasons coincides with the summer flux of organic material to the bottom, which possibly triggers their development.

In general *Ekmocucumis steineni* differs from the brood-protecting *Psolus dubiosus* in having a higher relative fecundity and a smaller diameter of mature oocytes. Since *E. steineni* has a more northern limit of distribution than *P. dubiosus* only occurring in high Antarctic regions, this evolutionary development is in accordance with Thorson's rule. The trend to a more advanced evolutionary stage is also present in the external morphology: *E. steineni* shows the more primitive pentamerous and *P. dubiosus* the more recently developed bilateral symmetry. A similar observation has been made by Ekau (1991) for several high Antarctic fish species. It can also be observed in some deep sea asteroids (Tyler et al. 1983).

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