

## Population biology of the deep-water prawn (*Pandalus borealis*) in Balsfjord, northern Norway: I. Abundance, mortality, and growth, 1979–1983

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The population density, age composition, and ovigerous stock of *Pandalus borealis* (Krøyer) were studied in Balsfjord (ca. 70°N) at about monthly intervals between September 1979 and December 1983. Females generally spawned in September–October, and eggs hatched in the first half of April when maternal prawns were 48 months old. Recruitment was first evident in February at ca. 9 months of age (ca. 7-mm carapace length (C.L.)). An underlying cyclical trend of peaks and troughs was evident, affecting both younger and older prawns, probably indicative of seasonal emigration/immigration. C.L.-at-age varied by 10–50% between year classes, with a general tendency for better growth rates to be associated with periods of warming (from min. 1–2°C to max. 4–5°C) of the bottom waters: this also caused an increase in C.L. of 1–1.5 mm in the spawning stock. A single age class formed more than 90% of the spawning stock in any spawning season. The von Bertalanffy growth function (VBGF) has been fitted in its seasonally oscillating and standard forms to individual year classes and “pooled” data. Length-at-age was similar to that found for *P. borealis* stocks from the Atlantic waters of the southern Barents Sea. Instantaneous rates of total mortality were very high (annual Z of 1.9–2.1), probably owing to the combined effects of predation by cod and the prawn fishery.

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### Introduction

The deep-water prawn (*Pandalus borealis* Krøyer) is an important species, both commercially and ecologically, in boreal seas (see review by Shumway *et al.*, 1985). Although the larger stocks of *P. borealis* have traditionally been heavily fished, there is little doubt that natural mortality is also high. *P. borealis* features significantly in the diet of many fish, squid, and seals (Barr, 1970; Sergeant, 1973; Vinogradov and Noskov, 1979; Pålsson, 1983).

The “Balsfjord project” is a multidisciplinary research programme studying the ecology and productivity of a high latitude fjord system (Hopkins *et al.*, 1989). In Balsfjord, prawns are a major prey of cod (*Gadus morhua*) (Klemetsen, 1982) and previously supported a small fishery (about five boats). In October 1983, because of concern about by-catches of young cod, national legislation was imposed banning prawn fisheries at depths of less than 200 m in fjords throughout Norway.

The prawn population in Balsfjord has been sampled frequently since 1979, and abundance and carapace

length (C.L.) of the various year classes determined. Each year size-related fecundity of ovigerous females has been quantified. Individual and population energy budgets are under construction (Hopkins, 1979; Seiring and Hopkins, 1985). The long-term aim is to build population dynamics and production models (Hopkins, 1987).

This paper describes the demography, spawning and recruitment cycles, and mortality and individual growth of prawns from the Svartnes basin of Balsfjord, from 1979 to 1983. Poorly understood or unknown input parameters (particularly growth and mortality rates) have hampered the quality of Pandalid population models (see Skúladóttir, 1979).

### Materials and methods

#### At sea

Prawns were sampled from the commercial trawling ground near Svartnes (69°21'N 19°06'E) in Balsfjord (Fig. 1). The trawling grounds in the deep basin near Svartnes are a separate entity from the trawling grounds

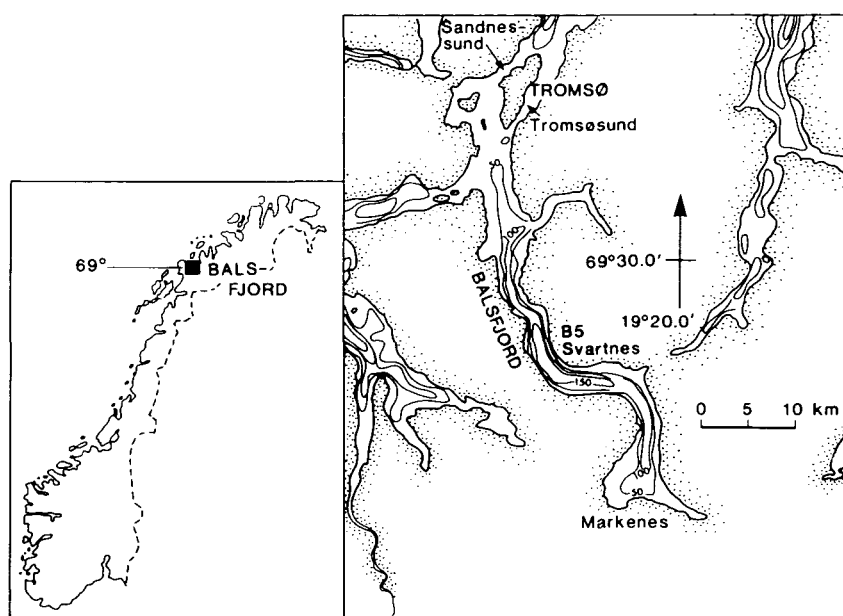


Figure 1. Balsfjord, northern Norway. Location and topography.

near Tennes towards the head of the fjord, the Svartnes ground being delineated by the 150-m depth isoline and having for the most part depths of ca. 180–190 m. The Tennes trawling ground is much shallower, generally around 120 m. The seabed between the two grounds is uneven and trawling is hazardous.

Sampling was carried out using a Norwegian commercial, demersal prawn trawl (Nilssen *et al.*, 1986). Trawling was done by RV “Ottar” (15.5 m, 210 h.p.) of the University of Tromsø, at about monthly intervals between September 1979 and December 1983. Tows were always made within  $\pm 2$  h of the local noon, in order to minimize the effects of vertical migration patterns upon catches. On nearly all sampling dates pairs of tows were made in opposite directions over a distance of 1.0–2.0 nm; the first tow being towards the head of the fjord and the second towards the mouth.

All sampling was standardized so that the results could be quantified and compared. The distance travelled by the trawl over the bottom was measured from radar fixes on standard landmarks ashore at the beginning and end of each tow. The times at which the trawl touched and left the seabed were determined from the resistance and pull in the trawl wires and behaviour of the ship itself. Test measurements of the dimensions of the trawl whilst fishing (the vessel’s motor recording 1100 r.p.m., ca. 1.8 knots ship’s speed), using Scanmar Type DT-300 sensors, have indicated a mean maximum height and width of 3.4 m and 21 m respectively (Nilssen *et al.*, 1986). In the case of a trawled distance of 1.0 nm (1852 m), with an effective trawl width of 20 m, the trawl is considered to have swept a seabed area of 37040 m<sup>2</sup>. In order to standardize results, all prawn data have been expressed as numbers caught per 100000 m<sup>2</sup> of seabed.

On deck, the contents of the by-catch were separated, as far as possible, from the prawns. The by-catch usually consisted of cod (*Gadus morhua* L.), capelin (*Mallotus villosus* Müller), herring (*Clupea harengus* L.), and long rough dab (*Hippoglossoides platessoides* Fabr.). When the catch of prawns was small, all the by-catch was removed and the volume of prawns determined. When the catch of prawns was large and a large by-catch of small-sized fish was also present, a number of 10-l buckets of the “mixed” catch were taken as sub-samples for determining the proportion of prawns compared with by-catch. The total volume of prawns in the catch was then estimated from knowledge of the number of buckets of “mixed” catch in the total catch and proportion prawns:by-catch. Another sub-sample (2–8 l), consisting purely of prawns, was frozen for the determination of carapace length–frequency distributions. When present, known volumes of ovigerous (“berried”) females were also frozen to assist in the separation of cohorts of the older age groups.

Hydrographical data (depth-related temperature, salinity and density) were taken at the Svartnes grounds during the investigation period by RV “Johan Ruud” (University of Tromsø) using a Niel-Brown CTD system. Further details of the CTD and data acquisition system are given by Hopkins *et al.* (1982), while general details of the hydrography and topography of Balsfjord are provided by Eilertsen *et al.* (1981b).

#### In the laboratory

The frozen prawns were thawed, either at room temperature (ca. 22°C) or overnight in a refrigerator, and C.L. measured to the nearest 0.1 mm below (Jocal digital precision caliper gauge) according to the method

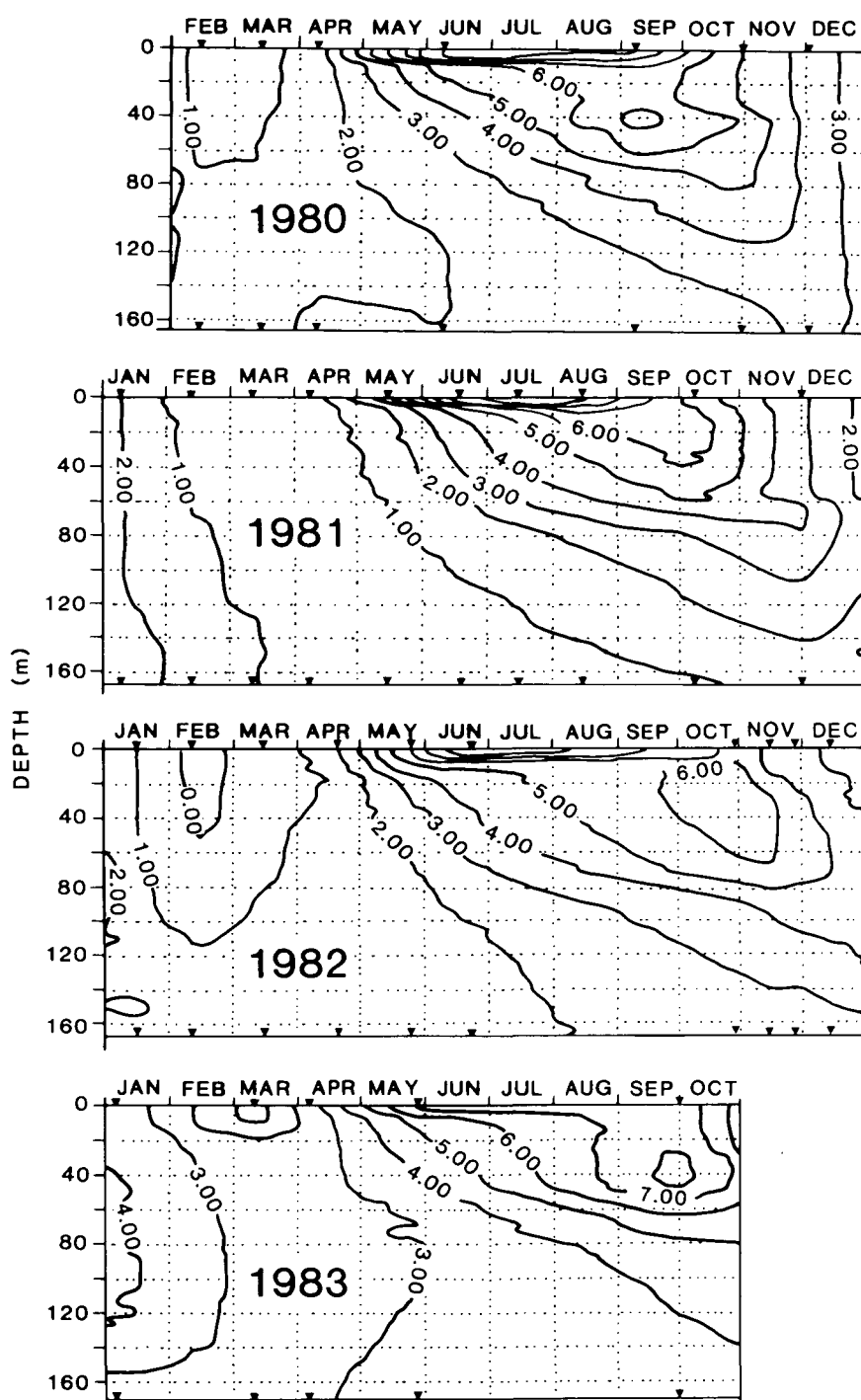


Figure 2. Balsfjord, northern Norway. Depth-related temperature isolines available during the study period.

of Rasmussen (1953). The structure of the first and second pleopods was used to separate males and females (Leopoldseder, 1934; Jägersten, 1936; Allen, 1959; Carlisle, 1959a, b, c). The presence of berried females and females with “head-roë” (i.e. the ovaries clearly visible inside the carapace of the whole prawn) was noted.

Egg numbers as a function of female C.L. were also registered (results not presented here).

#### Statistical treatment

Year classes were separated from length–frequency

polymodal groups using techniques based on normal (Gaussian) distribution theory (see Harding, 1949; Cassie, 1954). An exception to the concept that each modal peak represents a single year class may occur in the case of older prawns. From his investigations in Norwegian waters, Rasmussen (1953, 1969) reported that not all specimens of a given year class necessarily transform from males to females in the same year. Individuals which have transformed have an accelerated growth rate compared with non-transformed individuals, and consequently the year class may eventually comprise two distinct ("fast"- and "slow"-growing) length-frequency modes.

The SYSTAT module NONLIN (Wilkinson, 1988), applying principles related to those described by Abramson (1971), MacDonald and Pitcher (1979), and Schnute and Fournier (1980), was used in the present study to separate presumptive cohorts from length-frequency distributions. The program was used to estimate the numerical abundance, and mean C.L.'s with standard deviations, of prawns from the respective modal length groups, in a non-linear function (non-linear regression, see O'Neill, 1971; Fletcher, 1972; Griffiths and Hill, 1985) describing a polymodal distribution. The derived parameters were checked by using the Bhattacharya (1967) based FAO programs of Sparre (1987). The presumptive age of prawns within a particular mode was prescribed using combined knowledge of the date of sampling, that a single cohort is produced per year, and an average date of egg-hatching in Balsfjord of 15 April (see Results). The age-group system is used to describe the year of life of the prawns; 0-group refers to those in their first year (<12 months old), I-group are those in their second year (12–23 months old), and so on.

Growth in C.L. was described using the von Bertalanffy growth function (VBGF) (von Bertalanffy, 1938; Brody, 1945) modified for seasonal oscillations in growth (Somers, 1988):

$$L_t = L_\infty \{1 - e^{-K(t - t_0) + (CK/2\pi) \cdot \sin(2\pi(t - t_s) - \sin 2\pi(t_0 - t_s))}\}$$

where  $L_\infty$  = asymptotic length,  $K$  = growth constant,  $C$  = constant expressing the amplitude of growth oscillation,  $t_s$  = starting-point of oscillation with respect to  $t = 0$ ,  $t_0$  = origin of the growth curve, and  $L_t$  = length at age  $t$ . This equation reduces to the classic von Bertalanffy function when  $C = 0$ . The parameter  $t_s$  is defined such that  $t_s + 0.5$  = the "winter" point (WP), i.e. the turning-point in time when growth accelerates after seasonal stagnation (Pauly, 1984). The parameters were estimated using the SYSTAT module NONLIN (Wilkinson, 1988). The ELEFAN programs (Gayanilo *et al.*, 1988) were also used by way of comparison.

As  $K$  and  $L_\infty$  are not independent, it follows that estimation and comparison of the parameters in the VBGF is problematical (Bayley, 1977). Gallucci and

Quinn (1972), as an alternative, proposed a new parameter,  $\Omega = KL_\infty$ , which can be estimated directly from a non-linear regression by reparameterization of the VBGF:

$$L_t = \Omega/K\{1 - e^{-K(t - t_0)}\}$$

which has also been calculated in this study.

Catch curves were constructed for investigation of the instantaneous rate of total mortality ( $Z$ ), which is defined by the exponential equation:

$$N_t = N_0 e^{-Zt}$$

where  $N_0$  = number at time 0, and  $N_t$  = number at time  $t$ . In practice the method (Ricker, 1975) consists of plotting the natural logarithm ( $\ln$ ) of the number of individuals in various age groups ( $N_t$ ) against their corresponding age ( $t$ ):

$$\ln N_t = \alpha + \beta t$$

such that  $Z$  is equivalent to the slope  $\beta$  (with sign changed) of the descending right arm of the plot. The "length-converted" catch curve technique, where the absolute age of the individuals is not known, was also used (Jones, 1984):

$$\ln(N_i/\delta t) = \alpha + \beta t_i$$

where  $N_i$  is the number of individuals in the  $i$ th length class,  $t_i$  is the relative age, and  $\delta t$  is the time required to grow through this length class. Having calculated  $Z$ , the probability of capture (retention) curve was fitted using the logistic transformation technique of Sparre (1987).

## Results

### Water temperature

Available temperature isolines in the Svartnes basin as a function of depth and season from February 1980 to October 1983 are given in Figure 2. The bottom temperature was relatively warm (3–5°C; Eilertsen *et al.*, 1981b) in the mid-1970s, but became colder towards the end of the decade. A minimum of <1 to 2°C was reached in 1981 before warming up to 3–4°C in 1983 (Fig. 2).

### Variations in catch

The monthly catch of prawns in litres per standardized area (i.e. per  $10^5 \text{ m}^2$ ) in the Svartnes basin from 1979 to 1983 is shown in Figure 3. A clear cycle is seen with peaks, about 150 l, present from about February to June. Troughs, about 10–20 l, are present from about August to November.

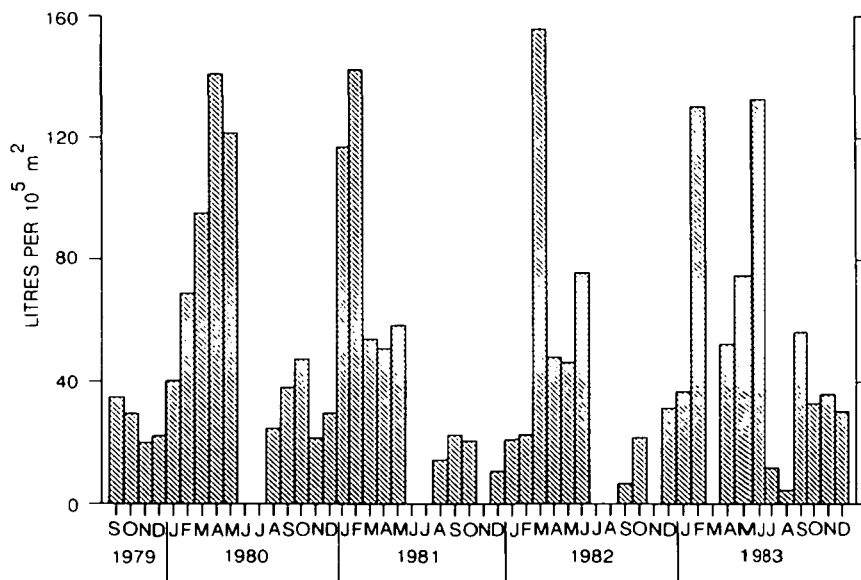


Figure 3. *Pandalus borealis*, Balsfjord. Fluctuations in volume (litres) of prawns caught each month by demersal trawl near Svartnes between Sept. 1979 and Dec. 1983.

### Size distribution and demography

The length–frequency distributions of prawns caught, expressed as numbers between September 1979 and December 1983, are shown in Figure 4a–d. The identification of tentative age groups (Roman numerals) using SYSTAT NONLIN are also shown. The population sampled with the trawl comprised between three and four modal length groups. In the majority of cases each modal length group is considered to be equivalent to a year class/age group. In some instances, particularly in the case of III- and IV-groups, the suffixes A and B have been added to define the presence of presumptive “slow”- and “fast”-growing modal groups from the *same* year class (see Materials and Methods). 0-group individuals were generally first recorded in February (about 7 mm C.L.), but this could be as early as January (e.g. 1981). Few IV-group individuals were found after September.

The abundance of individuals per 10<sup>5</sup> m<sup>2</sup> estimated from cod-end catches between 1979 and 1983, subdivided into component year classes (1976–1982), are shown in Figure 5. The periodicity earlier seen from the catch in litres (Fig. 3) is also clearly apparent in Figure 5. Throughout the study, the decrease in numbers seen at the peaks (defined as the peak value from February to May/June) compared to the troughs (defined as the peak value from August to October) regularly represents a relative change of about –80%. This trend is particularly easily seen in the annual decrease of II- and III-group prawns between April (24 and 36 months old respectively) and October (30 and 42 months old respectively); the change is on average between about –80% and –90%. The numbers of animals of the same age class generally increase again in the autumn.

### Growth

The mean C.L. of the year classes comprising the population as a function of the time of sampling is shown in Figure 6a. Mean individual growth is followed from young males to the point that males mature and the growth curve splits into separate components for females and males, i.e. the two sexes are identifiable on the basis of their original unimodal length-distribution into individual growth components for “slow”-growing (male) and “fast”-growing (female) prawns (see Materials and Methods for details). The comparative growth of the respective year classes is most clearly shown by the males until they reach the age at which they develop “head-roe” (i.e. have turned into females with ovaries visible inside the carapace) and their growth slows (Fig. 6b). There is a general trend for increasing growth from the 1976 year class through to the 1982 year class.

VBGFs using the seasonally oscillating modification (Somers, 1988) have been fitted by NONLIN (using data for “male” prawns) individually for the 1977 to 1981 year classes (Table 1). Estimates of the VBGF parameters using “pooled” data (all data from the 1977–1981 year classes) are also included for comparative purposes. In all cases the best fit was obtained using the seasonally oscillating VBGF (measured by lowest residual sum of squares), although C varied from 0.15 (1978 year class) to 0.58 (1979 year class). The “winter” point (WP) is relatively stable (0.86–1.07), indicating a change-over from stagnated growth to high growth again in late March to early April. The plotted seasonal VBGFs are shown in Figure 7, and clearly show the steadily increasing size-at-age attained by prawns from the 1978 (least) to 1981 (greatest) year classes. None of

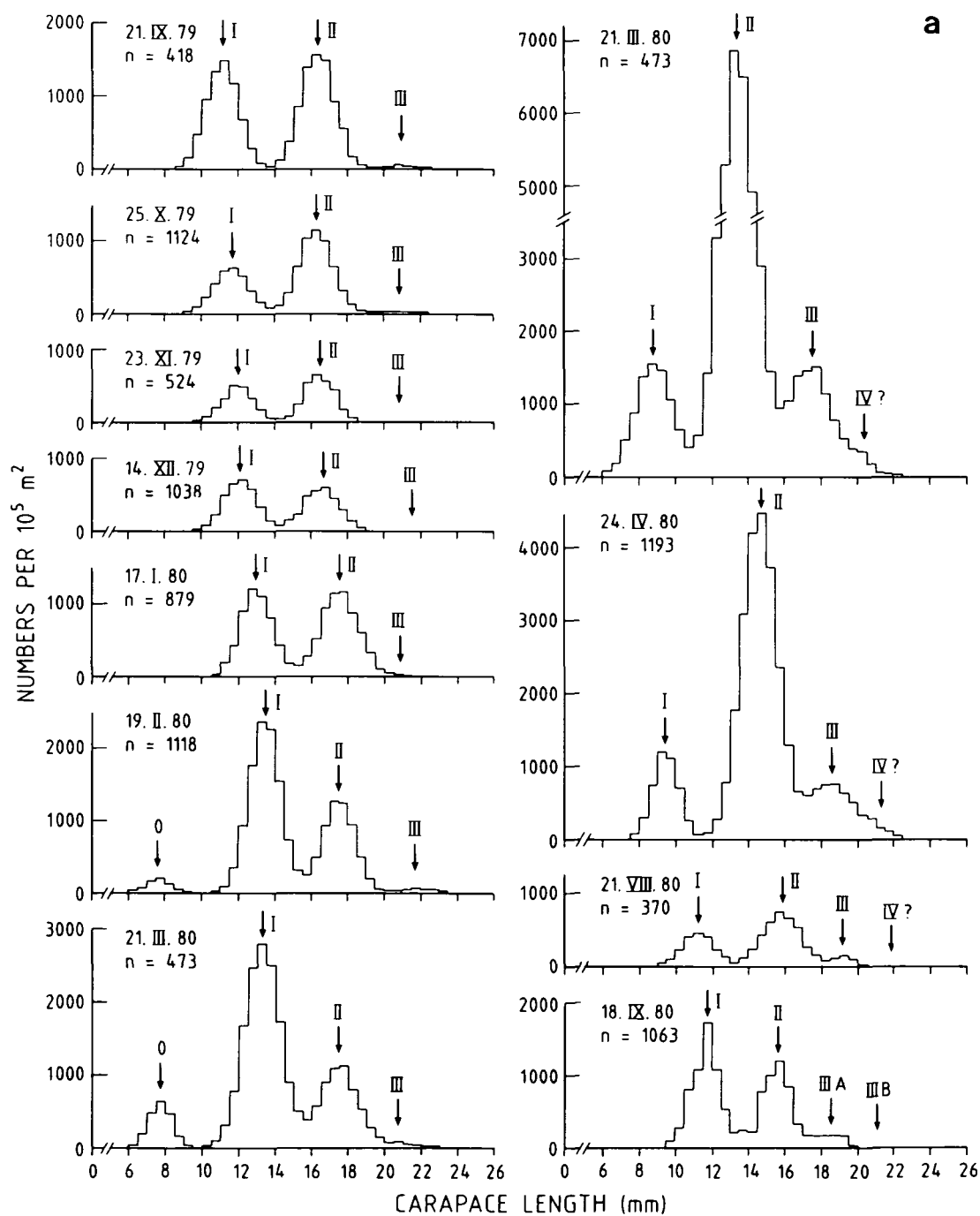
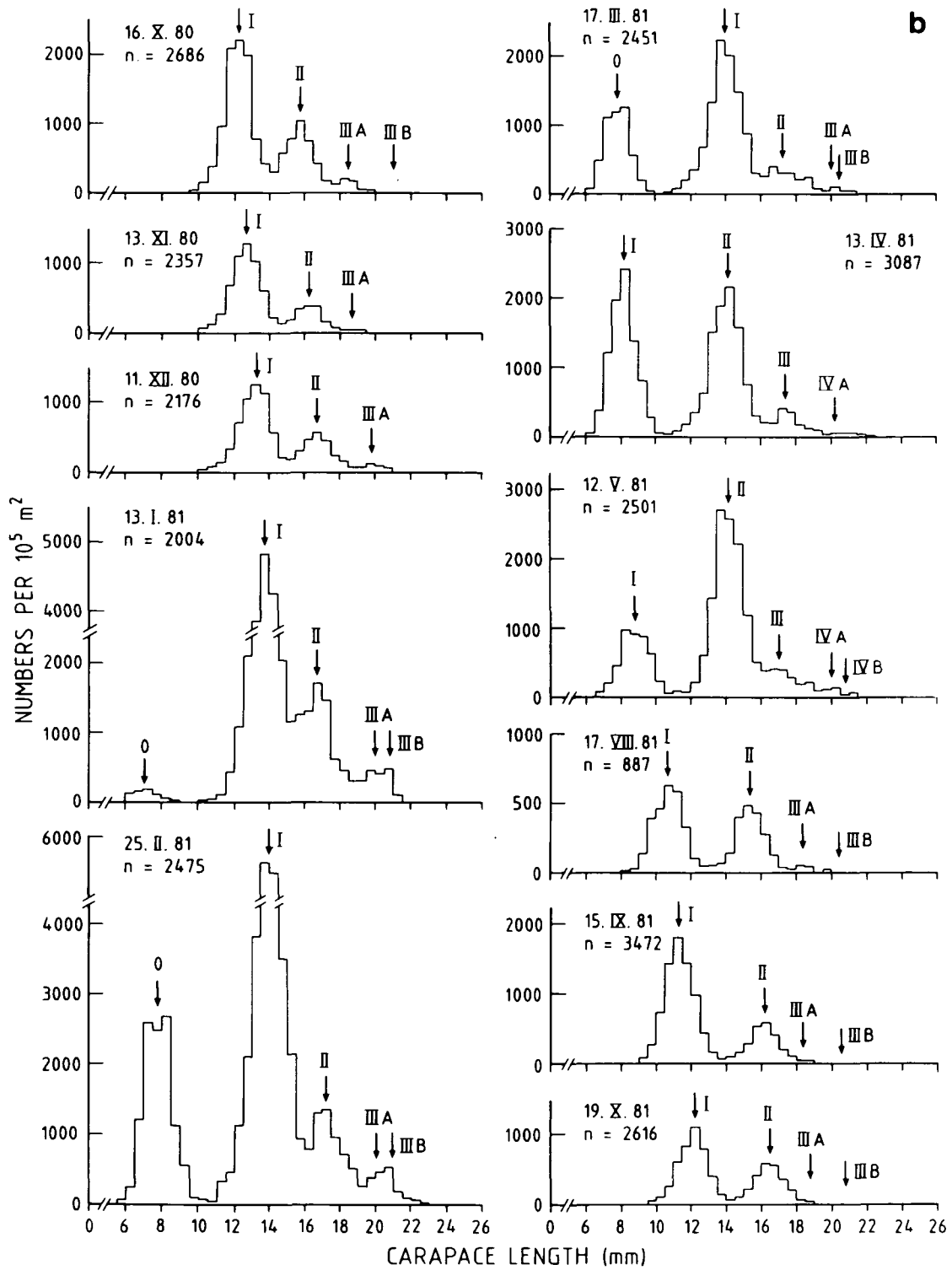
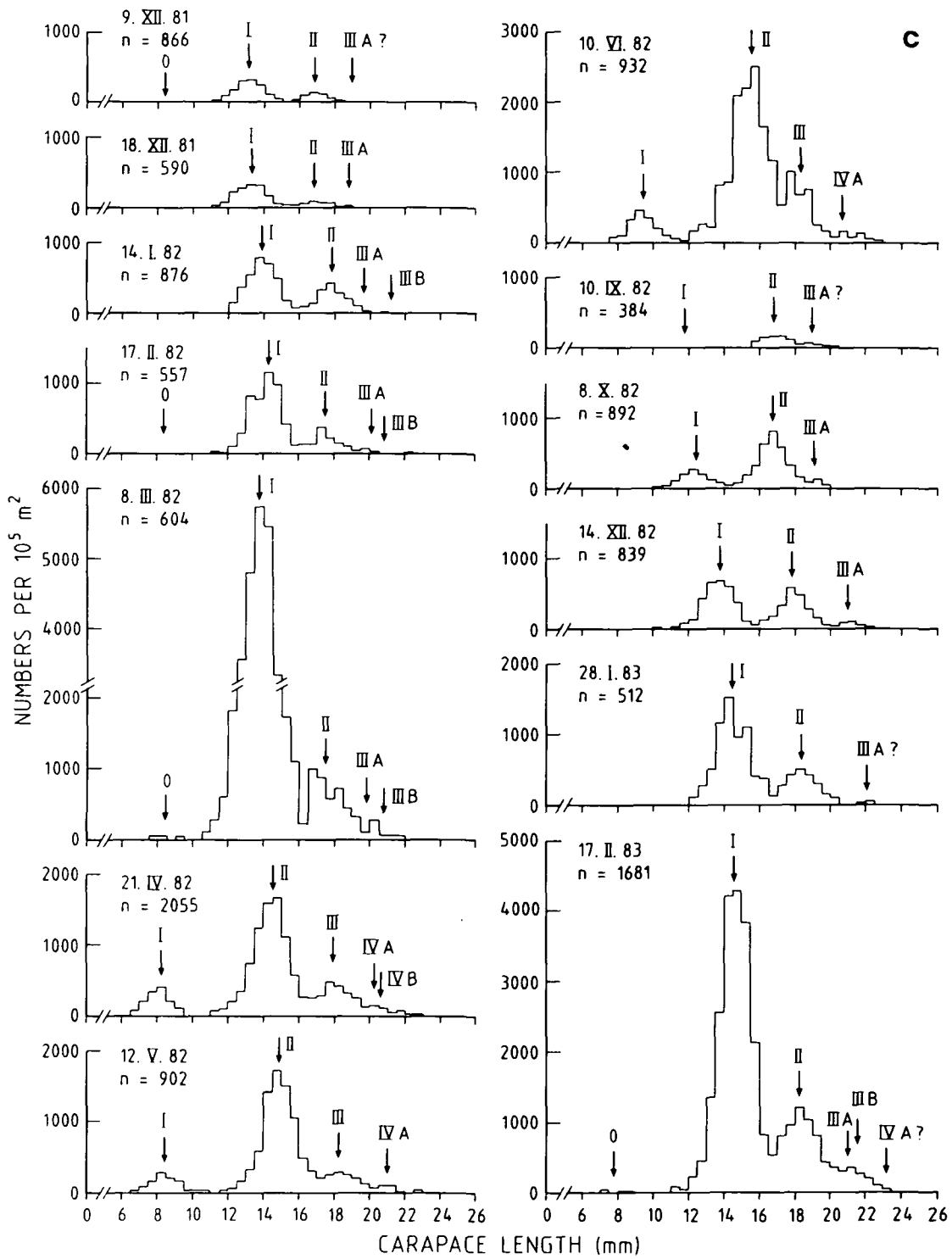


Figure 4. *Pandalus borealis*, Balsfjord. Length–frequency distributions of prawns caught by demersal trawl near Svartnes between Sept. 1979 and Dec. 1983. (a) Sept. 1979 to Sept. 1980. (b) Oct. 1980 to Oct. 1981. (c) Dec. 1981 to Feb. 1983. (d) Apr. 1983 to Dec. 1983. Arrows and Roman numerals denote age groups (e.g. III), ‘A’ and ‘B’ denote “slow” and “fast” growing components of an age group, ‘+’ indicates probable presence of older age groups, ‘?’ indicates age group which is difficult to prescribe (too few individuals).







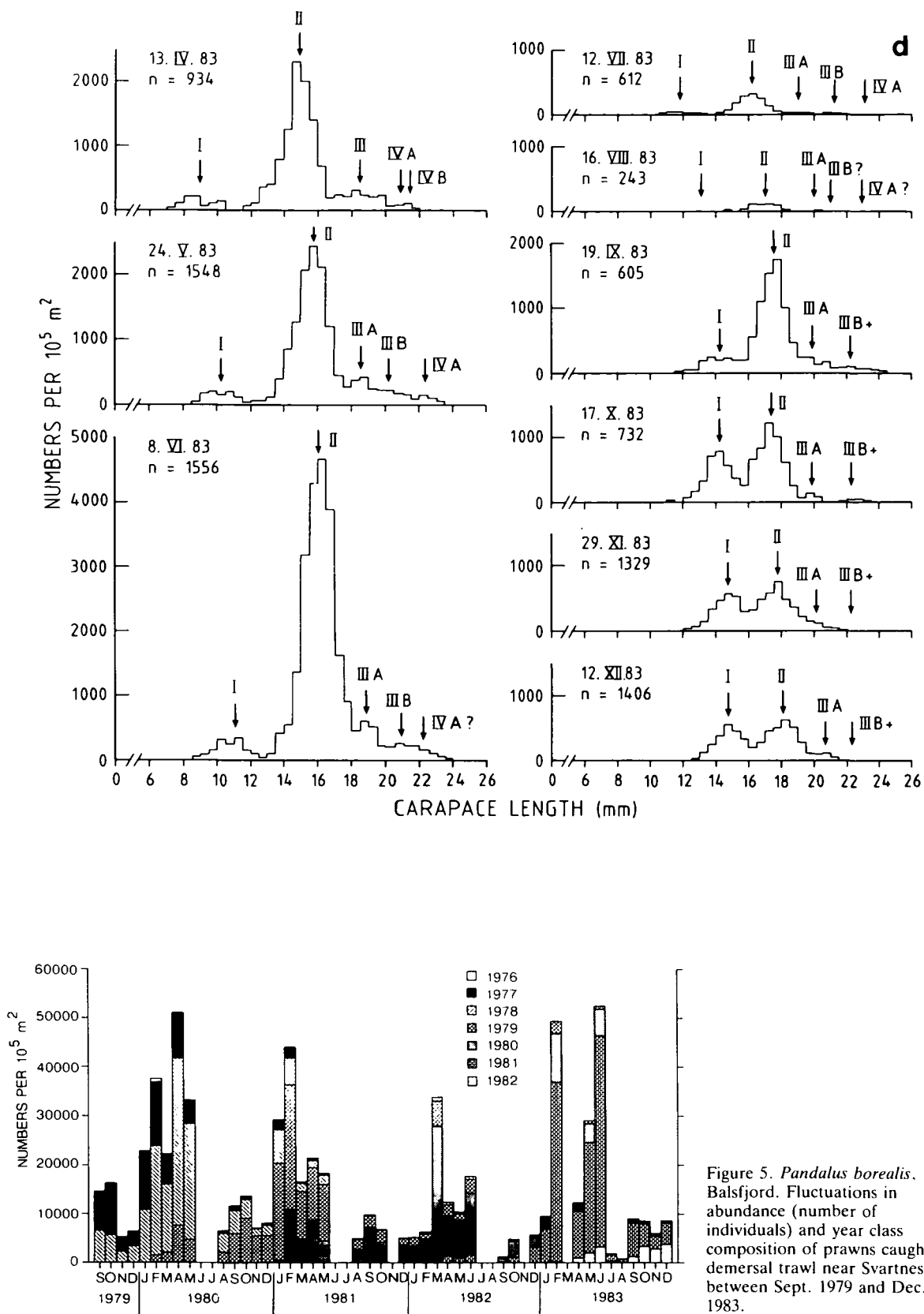


Figure 5. *Pandalus borealis*, Balsfjord. Fluctuations in abundance (number of individuals) and year class composition of prawns caught by demersal trawl near Svartnes between Sept. 1979 and Dec. 1983.

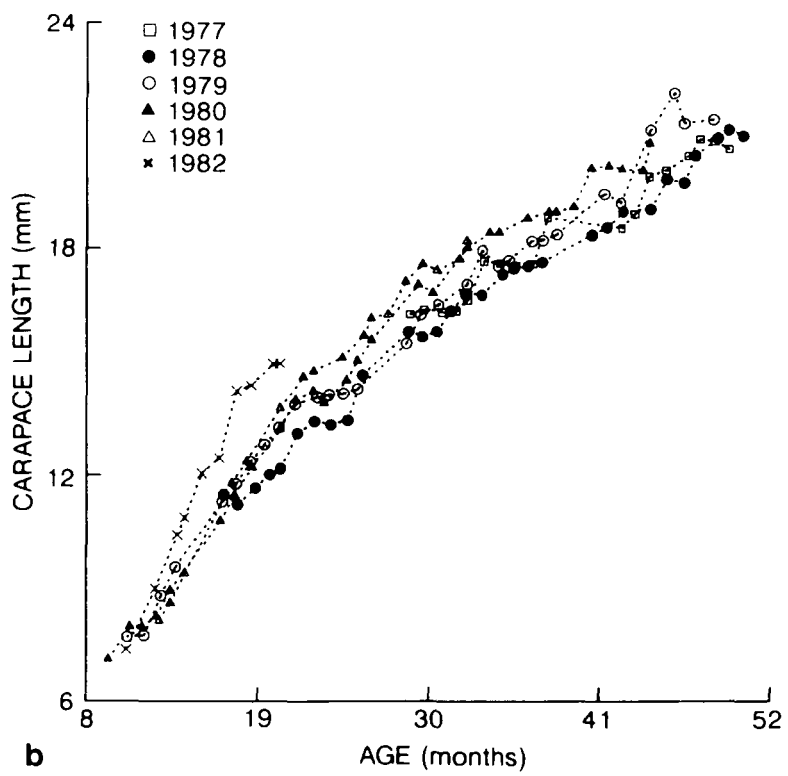
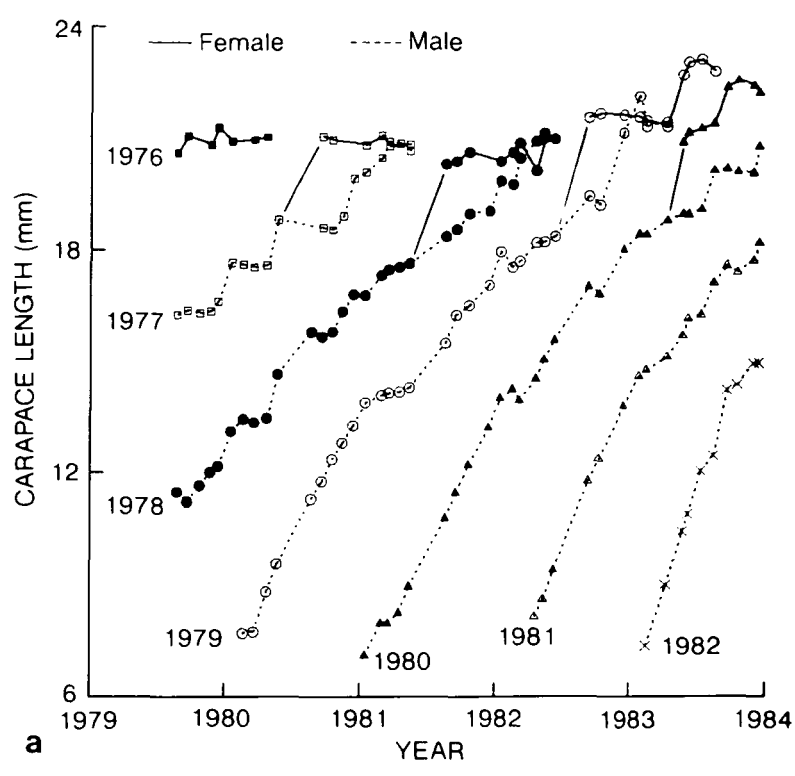


Figure 6. *Pandalus borealis*, Balsfjord. (a) Mean carapace length (C.L., mm) of the 1976–1982 year classes registered during the study period. Unbroken line = females, dotted line = males. (b) Comparison of growth in C.L. (mm) of prawns of the 1977–1982 year classes, presented for males until the time that they change sex, develop head-roë, and their growth stagnates.

Table 1. *Pandalus borealis*, Balsfjord. Parameters of the seasonally oscillating von Bertalanffy growth function (VBGF; Somers, 1988) fitted by the NONLIN (Wilkinson, 1988) technique, and Gallucci and Quinn's (1972)  $\Omega$ , for individual year classes and for "pooled" year classes (1977–1981). Data are for males until they exhibit stagnating growth. "N" = normal, i.e. without seasonal oscillation, "S" = with seasonal oscillation.

Parameter	1977	1978	1979	1980	1981	Pooled	
						N	S
$L_{\infty}$	25.29	27.51	30.47	28.95	35.53	26.56	26.81
K	0.40	0.32	0.29	0.34	0.26	0.37	0.36
$t_0$	-0.08	-0.12	-0.25	-0.06	-0.10	-0.07	-0.09
WP	0.86	1.07	0.93	0.96	0.95		0.89
C	0.45	0.15	0.58	0.28	0.35		0.21
$\Omega$	10.21	8.91	8.79	9.73	9.28	9.91	9.73

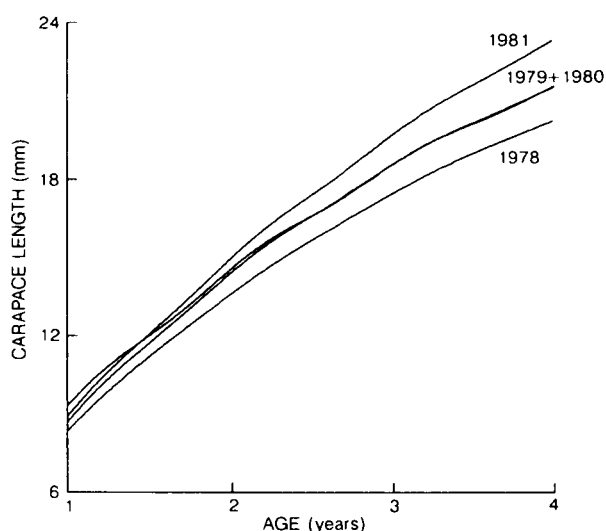


Figure 7. *Pandalus borealis*, Balsfjord. Plot of the seasonally oscillating von Bertalanffy growth function (Somers, 1988) for 1978–1981 year classes.

the parameters  $L_{\infty}$ , K or  $\Omega$  provide simple descriptions of "growth" as seen in Figure 7.

The VBGF parameters, with and without seasonal oscillations, and Gallucci and Quinn's (1972)  $\Omega$ ,

obtained using the NONLIN (non-linear regression) and ELEFAN techniques, on pooled data ("males" and "males + females" fitted separately) for the 1976–1982 year classes are presented in Table 2. There is no significant difference in the lengths-at-age between the two techniques ( $p > 0.05$ ). The WP values were similar, although the C-values of the NONLIN estimates were greater than those estimated by ELEFAN.

The percentage frequency distributions of C.L. of berried females samples from the Svartnes grounds between the autumn of 1979 and the spring of 1984 are shown in Figure 8a–f. Berried females during this period ranged from a minimum size of ca. 17.5 mm to a maximum of ca. 25.9 mm (Fig. 8f). The mean values for C.L. were relatively stable for the period autumn 1979 to spring 1982 (Fig. 8a–c), but increased steadily thereafter (Fig. 8c–e). A plot of the percentage coefficient of variation (CV%) within various C.L. classes during the period studied (Fig. 8g), seen in conjunction with the data presented in Fig. 8f, indicates that those females which dominated the spawning stock with the least degree of variability were found in the range 20 to 22 mm.

The cumulative (%) distributions of C.L. for berried females from the five year classes presumptively designated 1976 to 1980 are plotted in Figure 9. These year

Table 2. *Pandalus borealis*, Balsfjord. Comparison of parameters of the von Bertalanffy growth function (VBGF), and Gallucci and Quinn's (1972)  $\Omega$  fitted to "pooled" year classes (the complete data, 1976–1982) for "males" (m) and "males + females" (m + f) (see Results for definitions) using the NONLIN (Wilkinson, 1988) and ELEFAN (Gayaniolo *et al.*, 1988) techniques. "S" = with seasonally oscillating VBGF (Somers, 1988). "N" = normal, i.e. without seasonal oscillations.

Parameter	NONLIN				ELEFAN			
	m		m + f		m		m + f	
	N	S	N	S	N	S	N	S
$L_{\infty}$	25.77	26.43	28.00	29.43	27.01	26.95	26.75	26.80
K	0.40	0.36	0.35	0.31	0.39	0.40	0.41	0.40
$t_0$	-0.08	-0.11	-0.09	-0.12				
WP		0.79		0.73		0.69		0.65
C		0.37		0.56		0.15		0.20
$\Omega$	10.22	9.8	9.8	9.1	10.64	10.78	10.83	10.72

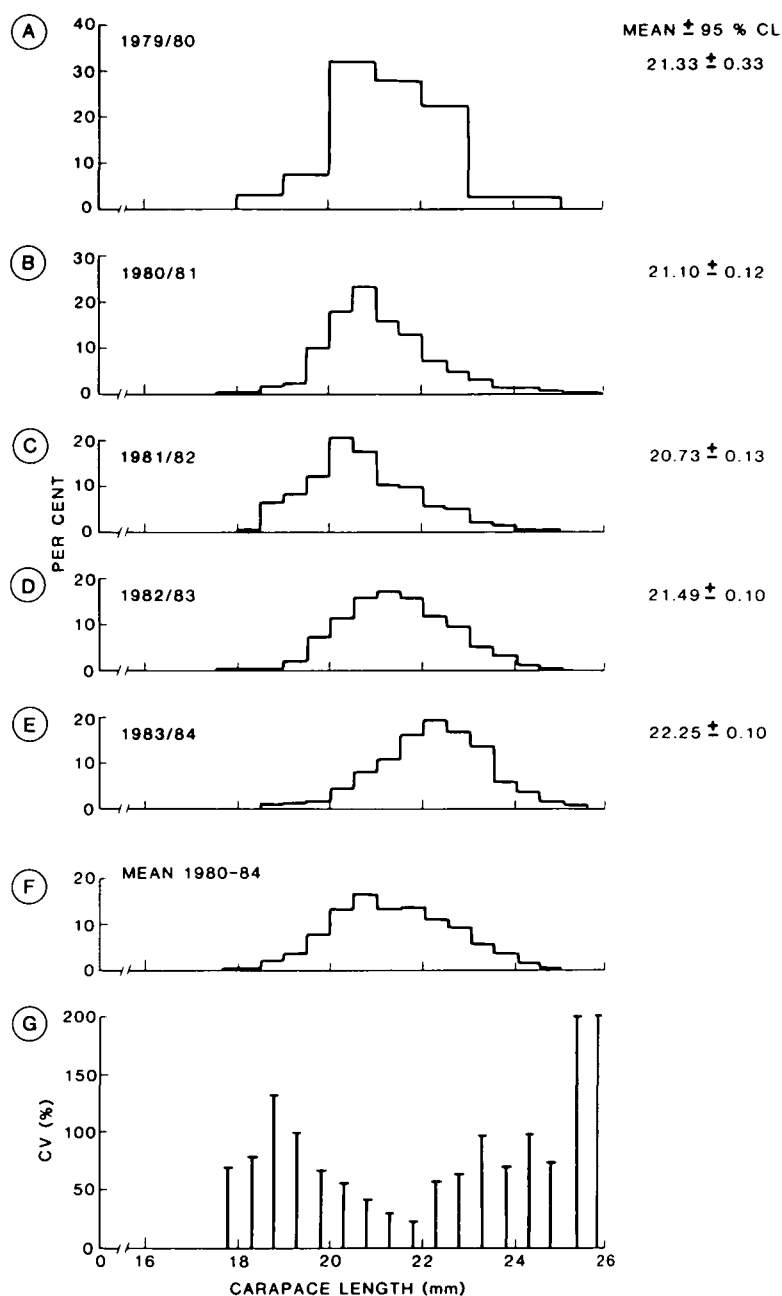


Figure 8. *Pandalus borealis*, Balsfjord. Length-frequency distributions (per cent) of berried females caught by demersal trawl near Svartnes. (a) Autumn 1979 to spring 1980. (b) Autumn 1980 to spring 1981. (c) Autumn 1981 to spring 1982. (d) Autumn 1982 to spring 1983. (e) Autumn 1983 to spring 1984. (f) Mean for a-e. (g) Coefficient of variation (CV) within each length class during the period a-e. Each autumn to spring period stretches from spawning to hatching (generally Oct. to Apr. inclusive).

classes comprised the core of the spawning stock from the autumn 1979/spring 1980 to the autumn 1983/spring 1984 respectively. The plots confirm the general impression of normal distributions seen in Figure 8a-d. Use of Kolmogorov-Smirnov tests for goodness-of-fit (Sokal and Rohlf, 1981) did not detect any departures from normality (two-tail,  $p > 0.05$  in all instances). These data indicate that the spawning population is primarily composed, at any one time, of a single year class. The general trend of increasing 50% (cumulative) C.L. of ovigerous females is clearly seen; amounting to

ca. 1.8 mm from the 1977 to 1980 year classes. It is noteworthy that the slopes of the cumulative percentages are essentially parallel for all the year classes.

#### Recruitment, mortality, and mesh retention

A catch curve of numbers of individuals caught from the various year classes (1976-1982) as a function of their age (in months) is plotted on a logarithmic scale in Figure 10a-c. It is evident that recruitment started at about 10 months of age and the average maximum

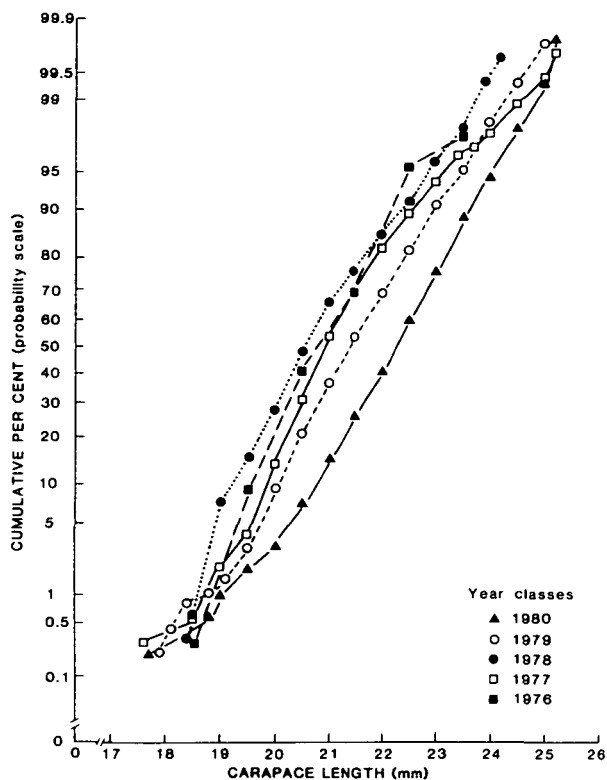


Figure 9. *Pandalus borealis*, Balsfjord. Cumulative frequency distributions of carapace length of berried females of various year classes (1976–1980) caught by demersal trawl near Svartnes.

lifespan was about 50 months. The catch curve peaks at about 25 months of age, which corresponds to about 14 mm C.L. (cf. Fig. 7). The cyclical trend of alternating troughs and peaks seen in Figure 5 is reflected to a greater or lesser extent in Figure 10, confirming that the cycle is essentially independent of year class or age of prawn. Generally the peaks are present at about 10–15, 22–27, 33–37, and 43–50 months of age. The relatively poor recruitment of I-group individuals seen in 1982 and 1983 (Fig. 5) is evident from the extremely low density of the I-group prawns of the 1981 and 1982 year classes compared with those of the 1979 and 1980 year classes; the order of magnitude difference in recruitment seen at 12 months of age, however, is no longer clearly evident after 24 months of age (Fig. 10c).

Survival curves fitted individually for the 1977–1979 year classes and for combined data for the 1980 + 1981 year classes are shown in Figure 11a. The fits are all highly significant ( $p < 0.001$ ), and  $Z$  (annual instantaneous rate of total mortality) estimated from the slopes decreases from 2.12 to 1.89 from the 1977 year class onwards (Table 3). An analysis of covariance (ANCOVA), however, indicated that these estimates of  $Z$  for the various year classes (seen in the slopes of Fig. 11a) were not significantly different ( $p = 0.97$ ).

The elevations, however, were statistically different ( $p < 0.05$ ) due to the especially high abundance of the 1977 year class.

A length-converted catch curve (for 13.9–24.8 mm C.L.; assuming the ELEFAN solution of Table 2,  $L_{\infty} = 27$ ,  $K = 0.39$ ) using all the available data for the 1976–1982 year classes, yielded an annual  $Z$  of 1.83 (Fig. 11b). The derived retention curve has a  $L_{50}$  of 13.2 mm at 1.7 years, and a  $L_{75}$  of 14.4 mm at 2.0 years (Fig. 11b).

A plot of the numbers (logarithmic scale) of berried females per  $10^5 \text{ m}^2$  in each sampling month is shown in Figure 12. The presence of berried females delimits the period from spawning through to hatching; in Balsfjord the former was first apparent in August while the latter had taken place by the middle of April. After October, when the majority of females had spawned, there was a tendency for the density of berried females to decrease to a minimum level about December. Thereafter, numbers tended to rise, resulting in peak densities of berried females in February and March.

## Discussion

In the present study data were collected on *P. borealis* at the Svartnes trawling grounds in Balsfjord at intervals of about 1.2 months (at least 43 cruises) over a period of 52 months. The study is one of the rare examples to date where a population of this species has been followed over such a long time scale with any degree of frequent and regular sampling (see, however, Skúla-dóttir, 1981). As such, it allows conclusions about the regularity and periodicity of life-cycle phenomena to be drawn with greater conviction than is generally the case from a single year's study, or those where sampling has been relatively fortuitous.

### Recruitment and migration

Data for catch in litres (Fig. 3) and numbers of individuals (Fig. 5) indicate a clear seasonal cycle that recurs annually. Increased abundances (peaks) were always present from early in the calendar year until late spring (i.e. about February to May), while decreased abundances (troughs) were present from the summer until the end of the year (i.e. July/August to December). The same general periodicity is present in the catch curve representing numbers of individuals from the various year classes examined as a function of their age in months (Fig. 10). The apex of the winter abundance agrees well with the recruitment of the previous year's year class, which is first apparent in February. The reduction in abundance which soon follows is related to a general reduction in the abundance of prawns of all ages from about 12 months of age upwards (see Fig. 10). The selection ogive of the research trawl used has an  $L_{50}$  of 13.2 mm cpx length, corresponding to

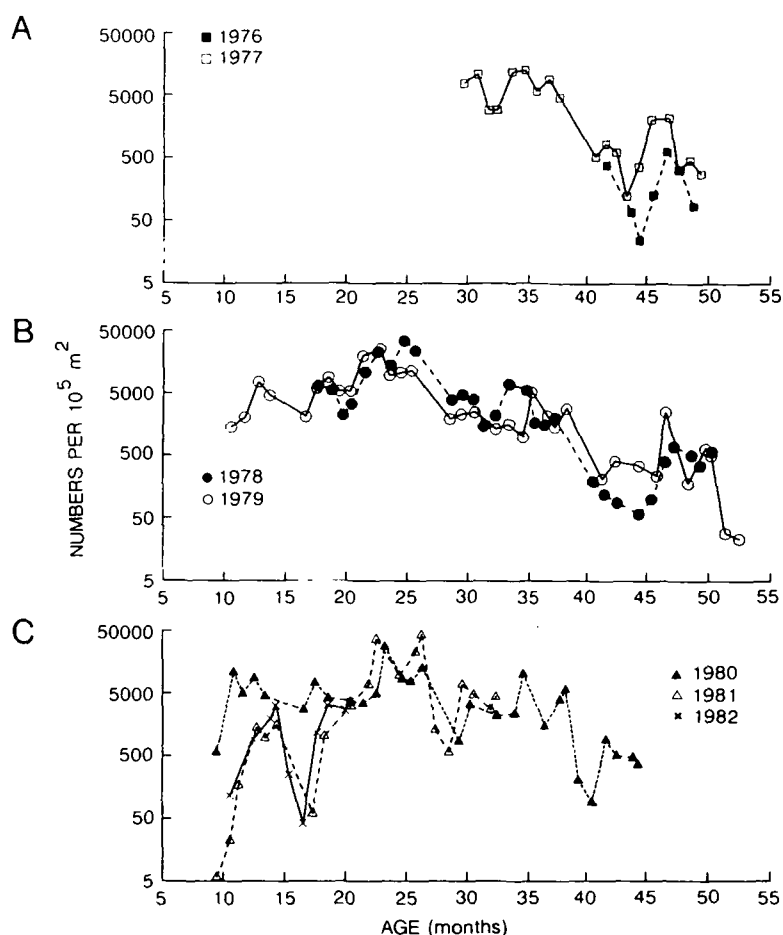


Figure 10. *Pandalus borealis*, Balsfjord. Fluctuations in density (number of individuals) as a function of age: (a) 1976 and 1977 year classes, (b) 1978 and 1979 year classes, (c) 1980–1983 year classes. Data extracted from Fig. 5.

an age of about 21 months (Fig. 11b). An approximately constant annual commercial fishing effort (about five 50-foot trawlers operating at both the Svartnes and Tennes trawling grounds) was effective during the study period, with the fishing season mainly confined from February/March to July (Hopkins, unpubl.). As the trawls used in the north Norwegian prawn fishery have a large  $L_{50}$  of about 16 mm C.L. (Thomassen and Ulltang, 1975), it is obvious that the periods of reduced prawn abundance, affecting both small and large prawns alike, are not due to fishing pressure.

The major predator of the post-recruitment prawns at Svartnes is cod (*Gadus morhua* L.) (Pearcy *et al.*, 1979; Klemetsen, 1982; Eliassen and Grotnes, 1985). Seasonal information on the diet of cod (*ibid.*) and on multispecies modelling involving the cod as apex predator in Balsfjord (Bax and Eliassen, submitted) does not indicate significantly increased predation pressure at the time of the seasonal decreases in prawn abundance. The evidence thus suggests that there is either a concerted emigration of prawns from the Svartnes trawling grounds or a change in their behaviour (e.g. vertical distribution), thereby reducing catchability. The return again of prawns of the same year

classes, in numbers that are generally more similar to those seen at the previous peaks than at the troughs, clearly indicates that increased mortality is not the causal factor. Preliminary investigations of diel and seasonal patterns of availability of prawns to the trawl have been started in Balsfjord (Nilssen *et al.*, 1986).

### Spawning

One of the best known examples of emigration/immigration of specific fractions of prawn populations is

Table 3. *Pandalus borealis*, Balsfjord. Values of the annual instantaneous rate of total mortality ( $Z$ ) fitted to individual year classes (1977–1979, and 1980 + 1981). SE = standard error;  $n$  = number of months fitted;  $r^2$  = coefficient of determination;  $P$  = level of probability.

	1977	1978	1979	1980 + 1981
$Z$	2.12	1.99	1.89	1.89
SE	0.41	0.34	0.36	0.36
$n$	18	21	24	29
$r^2$	0.63	0.60	0.73	0.51
$P$	<0.001	<0.001	<0.001	<0.001

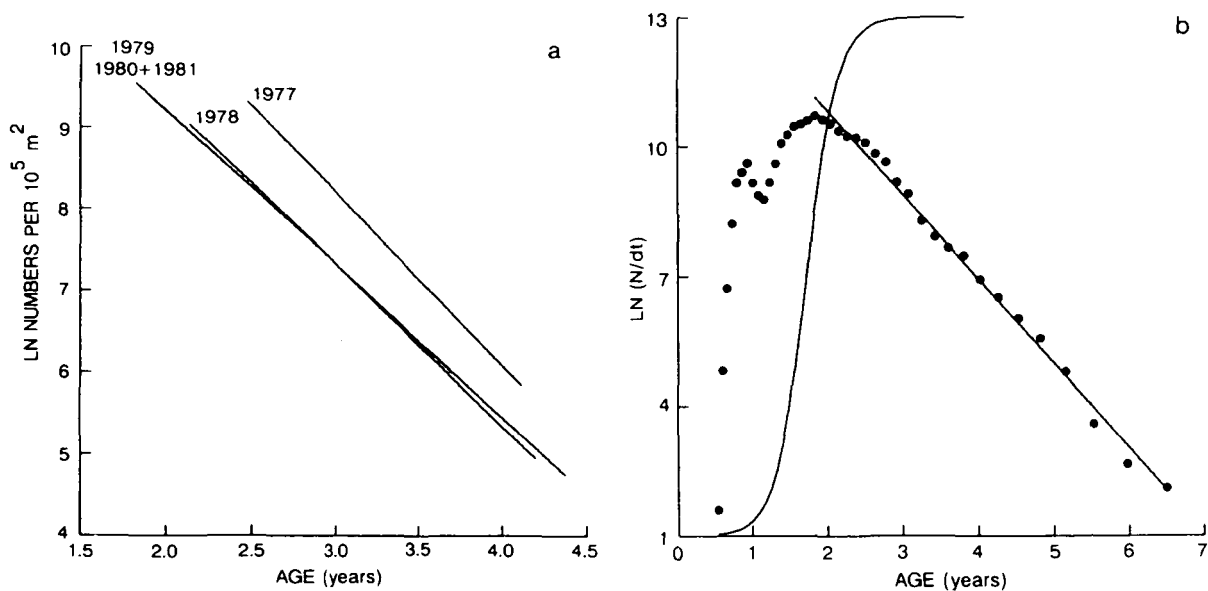


Figure 11. *Pandalus borealis*, Balsfjord. (a) Fitted survival regressions for individual 1977–1979 year classes, and for combined 1980 + 1981 year classes. (b) Length-converted catch curve for carapace (C.L.) length 13.9–24.8 mm, based on data pooled for 1977–1981 year classes (assuming  $L_x = 27$ ,  $K = 0.39$ ), with superimposed retention curve. The fitted survival regression is also shown.

associated with the movement of ovigerous females into shallower regions before hatching of eggs (e.g. Wollebæk, 1903; Hjort and Ruud, 1938; Scattergood, 1952; Horsted and Smidt, 1956; Haynes and Wigley, 1969; Apollonio *et al.*, 1986). Our data for population density of ovigerous females at Svartnes (Fig. 12) indicate a clear downward trend in numbers after spawning until about January/December, before increasing again to March. This trend would be consistent with emigration from the Svartnes grounds after spawning. Despite the resumption of fishing effort from the end of January, there is a clear increase in the abundance

of ovigerous females again on the Svartnes grounds commensurate with their return before hatching of eggs in April. There is, however, a tendency for the abundance of ovigerous females on the grounds just prior to hatching to be significantly higher than at the height of spawning (Fig. 12); this may be indicative of a net accumulation of females on the Svartnes grounds from some surrounding areas. The presence of large numbers of spent females on the Svartnes grounds at the end of April also supports the belief that hatching of eggs occurs on the Svartnes grounds. Our findings here are partly at odds with the interpretation of *P. borealis*

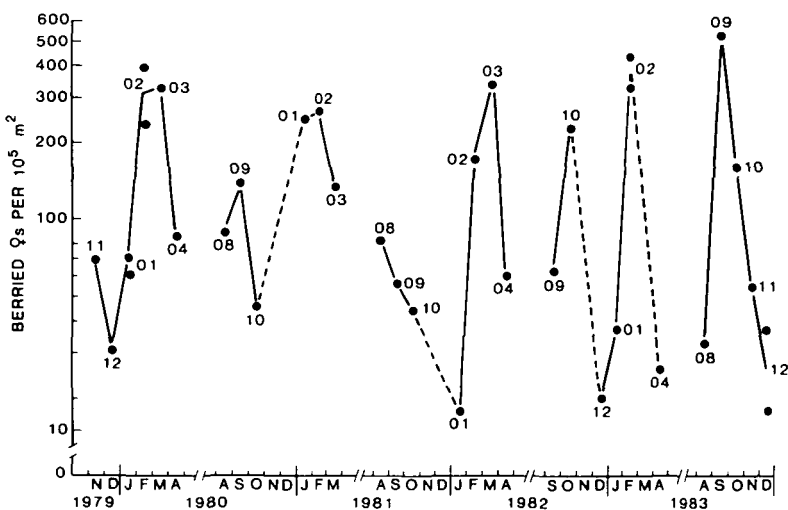


Figure 12. *Pandalus borealis*, Balsfjord. Fluctuations in density (number of individuals) of berried prawns caught by demersal trawl near Svartnes between Sept. 1979 and Dec. 1983. 01 = Jan., 02 = Feb., etc.

biology from some other areas of its distribution, which suggests a spawning migration with its associated hatching of eggs inshore (cf. Berkeley, 1930; Stickney, 1981).

### Temperature and growth

The bottom temperature is considered to be an important factor influencing the biology and population parameters of *P. borealis* (see review by Shumway *et al.*, 1985). Apollonio *et al.* (1986) have plotted the relationship between the average annual bottom temperatures and the ages of first spawning of *P. borealis* throughout its geographical range, and concluded that age at maturity in females increases with decreasing temperature. At 2°C the regression of Apollonio *et al.* (1986) provides an estimate of age at first spawning of about five years, while temperatures of 4–5°C are associated with age at first spawning of 4 years. The present data, as well as those of Thomassen (1976, 1977) and Hopkins (1979), show that female maturity in Balsfjord has been constant (42 months when calculated as maternal age at spawning and 48 months calculated as maternal age at egg hatching) from 1975 to 1983, despite the occurrence of warm (ca. 4–5°C) as well as cold (ca. 1–2°C) periods. Although not disputing the gross correlations between age at first spawning and ambient temperature in *P. borealis* involving different localities on a latitudinal basis, the Balsfjord data suggest that there are more important overriding factors than temperature *per se* at any one locality.

Over its latitudinal range *P. borealis* has a variable ovigerous period (period between spawning and egg hatching), with water temperature appearing to be a steering factor (Haynes and Wigley, 1969; Shumway *et al.*, 1985). This period ranges from about 4.5 months at 8°C in the North Sea to 9–11 months at close to 0°C in the waters of west Spitsbergen, Jan Mayen, and west Greenland in the Arctic (see Rasmussen, 1953; Horsted and Smidt, 1956; Allen, 1959; Butler, 1964; Haynes and Wigley, 1969). The time of spawning in *P. borealis* in Balsfjord was variable, starting as early as August (1980,

1981, 1983) or as late as the end of October/early November. Hatching of eggs always occurred in April, the peak month of the spring phytoplankton bloom (Eilertsen *et al.*, 1981a; Eilertsen and Taasen, 1984). The ovigerous period in Balsfjord prawns of 6 to 8 months, at about 1–4.5°C bottom temperature, is therefore generally intermediate between that cited for populations from the colder temperate regions and the high-arctic localities (see Shumway *et al.*, 1985).

Rasmussen (1953) has described the growth of *P. borealis* at several localities along the Norwegian coast, including Balsfjord. General comparisons of length-at-age between Balsfjord *P. borealis* and populations investigated by Hjort and Ruud (1938) and Rasmussen (1953) from southern Norway to Spitsbergen, show that the growth of Balsfjord prawns is slightly faster than the growth of those from Spitsbergen but slower than those from southern Norway. Thomassen's (1976) study of Balsfjord prawns provides similar C.L.-at-age values to those found in the present study. Growth of Balsfjord *P. borealis* is similar to that of Teigsmark's (1983) so-called "4–1" stock (first spawning at 4 years old, with subsequent annual spawning) from the southern, Atlantic dominated waters (range 1–3°C, bottom temperature) of the Barents Sea, but slower than that of Teigsmark's (1983) "5–2" and "6–2" stocks (first spawning at 5 and 6 years old respectively, biennially thereafter) of the relatively cold (0–1.5°C) north and eastern Barents Sea. Relevant growth parameters for these populations are summarized in Table 4.

There are few studies examining differences in growth between year classes of *P. borealis* at a specific locality. Skúladóttir (1981) found up to 40–50% differences in C.L.-at-age of slow-growing and fast-growing year classes from the cold (<2°C bottom temperature) Arnarfjörður of northwestern Iceland. Length-at-age of prawns in Balsfjord was appreciably greater than found in Arnarfjörður. Our data indicate a range of about 10–20% in length-at-age between the slowest- and fastest-growing year classes from 1 to 4 years of age. However, the exceptionally fast-growing 1982 year class, followed

Table 4. Summary of carapace length (C.L., mm)-at-age and parameters ( $L_{\infty}$ ,  $K$ , and  $t_0$ ) of the von Bertalanffy growth function (VBGF) for *Pandalus borealis* populations from fjords of Norway and Spitsbergen (Isfjord), and from the Barents Sea. Authors: (A) Teigsmark, 1983; (B) Rasmussen, 1953; (C) Thomassen, 1976; (D) Hopkins and Nilssen, this study; (E) Hjort and Ruud, 1938. VBGF parameters estimated from authors (B) and (E) original data. Further details in Discussion.

Author/site	Age (years)						VBGF		
	1	2	3	4	5	6	$L_{\infty}$	$K$	$t_0$
(A) B. Sea (6–2)	6.3	10.7	14.2	17.0	19.2	20.9	27.4	0.2	-0.10
(A) B. Sea (5–2)	7.6	12.3	15.9	18.5	20.6	22.1	26.7	0.3	-0.19
(A) B. Sea (4–1)	9.5	14.5	18.0	20.4	22.0	–	25.6	0.4	-0.24
(B) Spitsbergen	7.6	12.9	16.8	19.8	22.1	–	29.6	0.3	-0.10
(C) Balsfjord	8.9	15.3	19.6	22.4	24.3	–	28.2	0.4	0.05
(D) Balsfjord	9.4	15.1	18.9	21.5	23.2	–	26.7	0.4	-0.08
(E) Oslofjord	13.6	19.8	23.3	25.1	–	–	27.4	0.6	-0.14



to about 2 years old at the end of this study period, grew up to 50% faster than the slowest-growing 1978 year class.

Ranking of growth rates in Balsfjord shows a steady increase in length-at-age from the 1978 (slowest-growing) to the 1982 (fastest-growing) year classes. The 1978 year class developed at a time when the bottom temperature of the fjord was steadily decreasing from 3–4°C to its lowest in 1981 (<1 to 2°C), while the 1981 and 1982 year classes developed when the temperature began to rise again to 3–4°C. This general picture of better growth rates being associated with periods of warming is also supported in the data describing C.L. of the spawning stock of *P. borealis* in Balsfjord. The 1976 and 1977 year classes, comprising the spawning stock during the season autumn 1979/spring 1980 and autumn 1980/spring 1981 respectively, grew up during a period when temperatures were falling (4–5°C in the mid-1970s falling to 1–2°C in 1981: Eilertsen *et al.*, 1981b, and this study). They had a mean C.L. at spawning of about 20.5 mm, which was 1–1.5 mm less (see Fig. 9) than that of the 1979 and 1980 year classes, which comprised the spawning stock during the season autumn 1982/spring 1983 and autumn 1983/spring 1984 respectively. The 1979 and 1980 year classes had relatively rapid growth as temperatures increased.

According to Pauly and Gaschütz (1979) use of the seasonally oscillating fit to the VBGF will provide biologically more realistic estimates of  $L_{\infty}$ . One general drawback of the ELEFAN technique is that it is based on the key assumption that growth is similar from one year to the next, i.e. there are no factors inducing any strong changes in growth between years (Gayanilo *et al.*, 1988). The present data clearly show that the various year classes have indeed exhibited appreciable differences in growth. ELEFAN, in its present version, thus does not perform quite as well as NONLIN on our data.

In the present study the seasonally oscillating VBGF provided a better fit (reduced error sum of squares) than the “standard” version. The fits obtained using NONLIN appear intuitively realistic, as the winter point WP (the turning-point in time when the seasonally stagnated growth terminates and the growth rate becomes elevated again) is relatively stable (0.86–1.07), indicating a turn-over from stagnated growth to high growth again in late March to early April, when the spring bloom is generally associated with the onset of the crustacean growth season in Balsfjord (Hopkins *et al.*, 1989). The parameter  $C$ , a measure of the degree of sinusoidal growth (Pauly, 1982), varied from 0.15 (1978 year class) to 0.58 (1979 year class). Pauly (1984) has postulated that  $C$  is extremely well correlated with the difference between annual minimum and maximum temperatures (°C) of the water masses inhabited by aquatic animals. The  $C$ -values recorded here for *P. borealis* correspond to temperature differences of about

2–4°C predicted by Pauly (1984), almost identical to the range in ambient bottom temperatures registered in Balsfjord.

Food and temperature account for most of the growth variation in a given species (Beverton and Holt, 1957). However, as  $L_{\infty}$  and  $K$  are negatively correlated (see also Tables 1 and 2), simple comparisons of growth based on one of these parameters are problematical (Bayley, 1977). Although the seasonally oscillating VBGF provides the most realistic and best fit (see above), comparisons of Figure 7, and the values of the parameters, including Gallucci and Quinn's (1972)  $\Omega$ , clearly demonstrate that there is no simplistic parameter describing the dynamics of the growth curve.

### Mortality

The instantaneous rates of total mortality (annual  $Z$  of 1.8–2.1) of Balsfjord *P. borealis* recorded in this study are similar to those recorded by Thomassen (1976) in the mid-1970s, and are among the highest recorded in the literature (cf. Fréchette and Labonté, 1981; Fréchette and Parsons, 1981; Teigsmark, 1983: annual  $Z$  of 0.4 to 1.1; Rinaldo, 1981: annual  $Z$  of 1.0 to >2.0). These very high total mortality rates in Balsfjord are without doubt due to the combined effects of predation from the fjordic cod stock and fishing by the local prawn trawlers. In the local fish markets prawns from Balsfjord are referred to as “small”; there is, however, little evidence that this is due to poor growth; it is more likely that the high mortality rate reduces the relative proportion of “large” prawns in the catch. High total mortality rates also explain the lack of survival of large prawns to become second time spawners.

A forthcoming paper (Nilssen and Hopkins, in prep) will examine the changes in abundance and population dynamics that occurred after October 1983, when a ban on commercial prawn trawling was imposed in the fjord.

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