

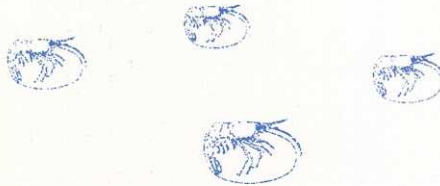
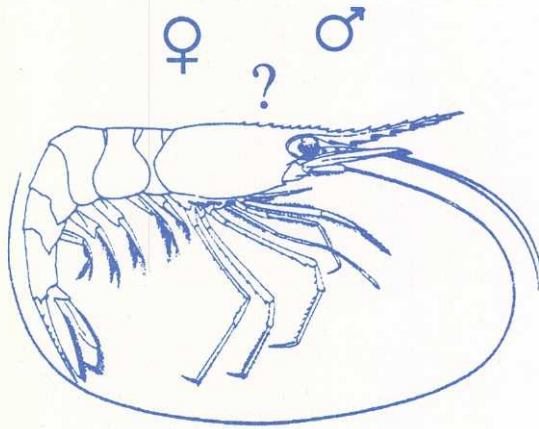
Det här verket har digitaliserats vid Göteborgs universitetsbibliotek. Alla tryckta texter är OCR-tolkade till maskinläsbar text. Det betyder att du kan söka och kopiera texten från dokumentet. Vissa äldre dokument med dåligt tryck kan vara svåra att OCR-tolka korrekt vilket medför att den OCR-tolkade texten kan innehålla fel och därför bör man visuellt jämföra med verkets bilder för att avgöra vad som är riktigt.

This work has been digitized at Gothenburg University Library. All printed texts have been OCR-processed and converted to machine readable text. This means that you can search and copy text from the document. Some early printed books are hard to OCR-process correctly and the text may contain errors, so one should always visually compare it with the images to determine what is correct.



DEMOGRAPHY AND SEX CHANGE IN PANDALID SHRIMPS

BO I. BERGSTRÖM



GÖTEBORGS UNIVERSITET 1992

Göteborg University
Faculty of Natural Sciences

Demography and sex change in pandalid shrimps

Bo I. Bergström

Dissertation

Department of Zoology
Section of Animal Ecology
Göteborg University
S-400 31 Göteborg
Sweden

Kristineberg Marine Biological Station
Pl. 2130
S-450 34 Fiskebäckskil
Sweden

Avhandling för filosofie doktors examen i ekologisk zoologi som enligt den biologiska sektionsstyrelsens beslut kommer att offentligt försvaras fredagen den 15:e maj kl 10.00 i zoologiska institutionens föreläsningssal. Disputationen sker på engelska.

To the memory of
Karin and Sven Bergström

Bergström, Bo I. 1992. Demography and sex change in pandalid shrimps.

Department of Zoology, Section of Animal Ecology, Göteborg University, S-400 31, Göteborg, Sweden.

Key words : Gullmarsfjorden, *Pandalus borealis* , sex allocation theory, demography, immigration, reproduction, growth, mortality, sex change.

Abstract: This thesis investigates whether year to year demographic variations are followed by corresponding changes in the age/size of sex change in populations of *Pandalus borealis* as suggested by sex allocation theory. Initially alternative life histories in sex changing shrimps are discussed as examples of phenotype limited evolutionary stable strategies (ESS). A sex allocation model for far-north *Pandalus* populations is proposed. In this model, the frequency of sex-changers among second breeding shrimp is predicted to be inversely related to the proportion of older breeders (all female) in the population.

The demographic study is based on data from a four year series (1984-1987) of trawl samples obtained at approximately monthly intervals in Gullmarsfjorden on the Swedish west coast. During deep water stagnation the fjord contained true, albeit short-lived (8-12 months) demes of *Pandalus borealis*. Differences in catch per unit effort, and length -frequency distributions after deep-water renewal in the fjord indicated that new demographic patterns were created by immigration of older shrimps and by varying recruitment. Immigration was facilitated by advective flows over the sill area during water renewal coinciding with the winter-spring onshore migration of shrimps in the Skagerrak.

A method of determining absolute densities of pandalid shrimp with the aid of a Remotely Operated Vehicle (ROV) is described.

The reproductive cycle in the demes of *P. borealis* was described by variations in the relative frequencies of adult females in different reproductive stages and the presence of larvae in the plankton. Spawning took place in September - October and hatching commenced in March-April. Mean durations of oogenesis and mean ambient temperatures from the deep water stagnation periods showed an inverse logarithmic relationship. This verifies laboratory findings concerning the temperature effect on the duration of oogenesis of *P. borealis* .

A revised growth model for pandalid shrimps incorporating seasonal variations in growth is presented and applied to size by age data from the fjord. The model is based on successive additions of sigmoid functions along a basic von Bertalanffy growth equation (VBG). The performance of this new model was compared with results obtained by the VBG equation and from a VBG model modified by the addition of a sine function. Growth of *P. borealis* from Gullmarsfjorden was best described by the seasonal models. Generally the new model gave slightly higher coefficients of determination. The seasonal variations in growth are discussed in relation to the reproductive cycle of *P. borealis* . Differences in growth pattern between sexes were also found. Male growth declined earlier in the year (late summer- autumn) than female growth which declined later and for a longer period (autumn-winter). Indications of differences in growth rate between sexes are discussed. The correlation between growth rate and mean ambient temperature was investigated in the temperature interval of 4-6°C based on the four temporally isolated demes. No correlation between these two factors were found. The recurring immigrations of adult shrimp during late winter- early spring from the Skagerrak population did not significantly affect growth rate estimates. Finally, sizes by age of *P. borealis* in the fjord were not found to be significantly different from reported sizes by age in other

boreal populations in the Atlantic ocean.

Age structure, relative frequency of sexual stages and mortality in each of the studied demes and age groups are described. In Gullmarsfjorden the majority of shrimps were females at an age of 3-4 years (transitionals at ca. 3 years, mean carapace length of ca 22 mm). Along with these, irrespective of variations in age/size structure, mortality, sex frequency or growth, there were always low proportions of younger shrimps that were females. Mean carapace lengths of sex changing shrimps which were found exclusively in spring- early summer were ca. 13.3 mm (age 12.4 months), 17.5 mm (age 23 months), 21.8 mm (age 35.4 months) and 23,3 mm (age 50 months).

No significant evidence, at the 95 % level of confidence, was found that mortality or frequency of older breeders in the breeding population affected the time of sex-change in this protandric species. An hypothetical explanation, based on these results, is presented and discussed as an alternative to the view that the protandric mode of reproduction in pandalid shrimps is combined with environmental sex determination. This alternative explanation suggests that cohorts in populations of *P. borealis* consist of mixtures of genotypes which develop into phenotypes predisposed to change sex at different sizes/ages and, in low frequencies, phenotypes that develop directly into primary females.

PREFACE

This thesis is based on the following papers, which are referred to by their Roman numbers (I to VI).

- I Charnov, E. L. and Bergström, B. I. 1987. Alternative life histories in sex change in shrimp: a phenotype limited ESS. *Evolutionary Ecology* 1: 107-111
- II Bergström, B. I. 1991. Yearly immigration of *Pandalus borealis* (Krøyer) into periodically isolated fjord populations. *Sarsia* 76:133-140.
- III Bergström, B. I., Larsson, J. and Pettersson J. O. 1987, Use of a Remotely Operated Vehicle (ROV) to study marine phenomena: I Pandalid shrimp densities. *Marine Ecology Progress Series* 37: 97-101.
- IV Bergström, B. I. 1991. Reproductive cycle and the effect of temperature on oogenesis of *Pandalus borealis* (Krøyer). *Journal of Shellfish Research*, 10(2), 327-331.
- V Bergström, B. I. Growth, growth modelling and age determination of *Pandalus borealis* (Krøyer). MS. (Accepted by *Marine Ecology Progress Series*)
- VI Bergström, B. I. Is there a relationship between demography and sex change in pandalid shrimp? MS.

Introduction

There are several reasons why the biology of the shrimp *Pandalus borealis* (Krøyer) has attracted scientific interest. Stocks of this species and its congeners represent a substantial economical value thus considerable interest has been directed towards fisheries-biology and stock assessment (e.g. Shumway et al. 1985). Additionally, *P. borealis*, as a protandric hermaphrodite, has been studied from histological and physiological viewpoints (Jägersten 1936; Carlisle 1959a, 1959b and 1959c) and more lately from evolutionary aspects.

This thesis focuses on the last aspect, namely *P. borealis* as a favoured model organism in sex allocation theory. Sex allocation theory in general seeks theoretical answers, in terms of the reproductive consequences, to the questions of when or under which environmental, social, or life history conditions, natural selection favours one or the other form of sexuality (Charnov 1982). Sex allocation theory also seeks to understand sexuality in terms of ultimate causes rather than the proximate mechanisms (sensu Popper, 1980). It generally predicts that protandric pandalid shrimps are able to control their age of sex change to match demographic variations in the surrounding population (Warner 1975; Charnov et al. 1978; Charnov 1979; Charnov 1982; Charnov and Bergström 1987 (I) and Charnov and Andersson 1989).

This account investigates the proposed link between demographic variation and sex reversal in pandalid shrimps, based on demographic results from a study of four temporally enclosed demes of *P. borealis* in Gullmarsfjorden on the Swedish west coast.

Evolution and protandric hermaphroditism

Basic to contemporary evolutionary ecology is the notion that natural selection operates in populations of organisms by differences in individual reproductive success (e.g. Pianka 1978). One important adaptation, with respect to maximising the life time reproductive success of an organism, is the way it reproduces. The overwhelming majority of Metazoa, especially those which have gained some degree of size and complexity of differentiation, reproduce sexually (Barrington 1967).

The evolution of sexual reproductive systems through natural selection has attracted much scientific interest (e.g. Darwin 1871; Fisher 1930; Parker et al. 1972; Maynard Smith 1978; Charnov 1982; Krebs and Davis 1982). Sexually reproducing organisms may either be gonochorists (separate sexes) or hermaphrodites (both sexes in the same individual). The latter may either be simultaneous (producing male and female gametes simultaneously) or sequential (producing male and female gametes at different times).

Ghiselin (1969) reviewed possible selective advantages for hermaphroditism and proposed that it evolves mainly under three conditions:

1. Where it is hard to find a mate, "Low density model".
2. Where one sex benefits from being larger or smaller than the other "Size advantage model".
3. Where there are small, genetically isolated populations "Gene dispersal model".

Of these three models the "Size advantage model", accounts for some of the known instances of sequential hermaphroditism. Protandry, according to this model, is favoured by natural selection if the male stage does not benefit in a reproductive sense from being large or old, while the fecundity of the female increases with age or size. Proterogyny, on the other hand, is favoured by selection if male fertility is promoted by large size or high age.

Sex allocation theory and pandalid shrimp.

Population data from pandalid shrimps were first used by Warner (1975) to discuss sequential hermaphroditism in terms of population genetics. This author developed models predicting the age of sex change maximizing the reproductive success of both protandric and proterogynic hermaphrodites. Warner's (1975) conclusions regarding protandric hermaphroditism agrees with the "Size advantage model". Protandric hermaphroditism is favoured by natural selection in randomly mating populations where female fecundity increases with age or size and where male fecundity does not depend on age or size. The theoretical results from Warner's (1975) models agreed with empirical data from a *P. borealis* population in the Gulf of Maine (Haynes and Wigley, 1969). The model used by Warner (1975) assumed that the age of sex change was genetically predetermined and under selective pressure. However, Warner (1975) suggested that if the individuals in the population had the ability to control the age of sex change in relation to the demographic situation the reproductive success would increase in a varying demographic environment.

The evolutionary advantages of such a trait, phenotypic or environmental sex determination (ESD), was further discussed by Charnov and Bull (1977) both for dioecious organisms and sequential hermaphrodites. These authors proposed that natural selection favours ESD when the reproductive success of the individual is dependant on the surrounding environment and when this cannot be controlled by the organism. Such conditions are enhanced when the off-spring is dispersed in a heterogenous or unpredictable environment. Examples of such unpredictability may be variations in sex ratio, differences in exploitation value for the sexual stages and sex differentiated mortality.

Charnov et al. (1978) proposed, based on sex allocation theory, that the individuals in a population of protandric hermaphrodites experiencing yearly variations in age structure will adapt the age of sex-change to the prevailing demographic situation. A testable hypothesis derived from the theory is that the frequency of early maturing females (EMF) will be negatively related to the frequency of older females in the population. Furthermore the proportion of older breeders functioning as males should be negatively related to the proportion of first breeders. Empirical data from two pacific populations of *Pandalus jordani* supported the theoretical predictions and this was taken as an indication that the shrimps were altering the age of sex change to match a variable demographic environment (Charnov et al. 1978 and Charnov 1982).

Charnov (1979) further developed and tested sex allocation theory on pandalid shrimp data. In this study biogeographic variations in the length of time spent in the male stage were explained with the aid of data on growth, mortality and relative frequencies of males and females from 27 populations of pandalid shrimp extracted from the literature and from unpublished sources. On the basis of these tests, which corroborated the theoretical predictions, Charnov (l.c) concluded that the average time spent as a male increases in protandric pandalid shrimps with increasing life span (low grow rate/low mortality). Population with longer lifespans are found in the northern parts of the species' distributional area while shorter lifespans are found in the southern populations.

Charnov (1981) commented on Skagerrak shrimp investigations. In these studies the Danish/Swedish fishery on the Skagerrak stock of *P. borealis* were found to have changed the length-frequency distributions of shrimps from the eastern Skagerrak during the period 1949-1962. The mean size of the caught shrimps was decreasing and this was attributed to heavy exploitation by fisheries (fishing mortality). During approximately the same period the proportion of 1 year old females caught increased. These results were interpreted by Charnov (1981, 1982) as a mortality induced change of the age/size at which the shrimps changed sex.

In 1987 Charnov and Bergström (I) discussed alternative life histories in sex changing shrimp as an example of a phenotype limited evolutionary stable strategy (ESS). A sex allocation model for far-north *Pandalus* populations was proposed which predicts that the frequency of sex-changers among second breeding shrimps is negatively related to the proportion of older breeders (all female)

in the population. This prediction is compared with empirical results in paper (VI) and will be dealt with below.

Charnov and Andersson (1989) presented correlative evidence from a shrimp population off the Alaskan coast that the frequency of EMF increased when the mean size of the individuals in the breeding population decreased.

Common to all these studies are that they either propose or assume that pandalid shrimps, beside being protandric hermaphrodites, have environmental sex determination. Charnov 1982 discussing data from *Pandalus jordani* populations off the west coast of the US stated. "I find these data surprising since they support the idea that the shrimp are altering the time of sex reversal (here, the proportion of a cohort acting as male or female) in response to fluctuations in the population's age or size distribution. We can only wonder at what cues the animals may be using."

The Northern or Pink shrimp (Great Britain, Canada, U.S.A.), *Pandalus borealis* (Krøyer, 1838).

Populations of adult Northern shrimps are generally found at low temperatures (0-5° C) and fairly high salinities (34.1-35.7 ‰) at depths of 50-500 meters in the North Atlantic and North Pacific Ocean (Allen 1959; Shumway et al. 1985). The distribution of *Pandalus borealis* is mainly determined by temperature, salinity, bottom substratum and depth (Shumway et al., 1985). The species is stenohaline and has been recorded in salinities slightly less than 34 ‰ only in Oslofjorden (Hjort and Ruud 1938). In the deeper part of Skagerrak a well established stock of *P. borealis* exists at temperatures ranging between 4-6° C (Svansson 1975). The species prefers soft mud and sand-silt substrates and there is a direct correlation between abundance of shrimps and the organic content of the bottom sediments (Shumway et al. 1985).

General aspects of the reproductive cycle of *P. borealis* throughout its discontinuous circumboreal distribution have been reviewed by Shumway et al. (1985). Female shrimps spawn once a year. Eggs are extruded in late summer to early autumn and are carried on the pleopods until hatching commences in the spring. In the northern part of the shrimp's geographical range, however, deviations from this yearly pattern are common (Rasmussen, 1953).

After hatching, the larvae of *P. borealis* go through six pelagic stages (Berkely, 1930). The larvae tolerate lower salinities and higher temperatures than the adults. Wienberg (1982) found optimal growth and feeding of larvae at 31-32 ‰ and 9° C. The biology of the larval stage was also studied in detail by Stickney and Perkins (1977, 1981). Distribution and occurrence of the larvae of *P. borealis* have been studied in Kachemak Bay, Alaska, Sheepscot Bay, Maine, and in the Norwegian and Barents Sea (Shumway et al. 1985).

The protandric reproductive strategy of the Northern shrimp was first described by Berkely (1930) and further treated by Jägersten (1936). The latter described anatomical aspects of the protandric reproductive system on *P. borealis* material from Gullmarsfjorden, and gave brief information on the reproductive cycle. Carlisle (1959 a,b,c) examined the endocrinology of the sex change in *P. borealis*. This author described how the X-organ-sinus gland complex and the *vas deferens* interact in controlling the sexual biology of the Northern shrimp.

Berkely (1930) and Jägersten (1936) described *P. borealis* as an obligate protandric hermaphrodite although Jägersten (1936) reported incidences of females which never showed male characteristics in material from Gullmarsfjorden. Later studies have, however, reported variable life histories for the Northern shrimp. Life histories are reported to vary both within the species' discontinuous circum-boreal area of distribution and between different year classes at the same locality. Individuals may develop as females directly without going through a male stage (primary females, PF), they may change sex in time for their first breeding season (early maturing females, EMF) or change sex after having functioned as males once or twice (e.g. Allen 1959; Rasmussen 1953; Butler 1964 and Haynes and Wigley 1969). Rasmussen (l.c.) also found, especially in far north

populations with low growth rates, that shrimps did not change to the female stage before the age of 3-4 years. He also described year classes containing both males and females.

Growth in *P. borealis* was first studied by Berkely (1930) who demonstrated a general pattern of seasonal growth in this species. Such patterns have also been observed elsewhere (for a review see Shumway et al. 1985) but very few attempts to model seasonal growth in this species have been reported (V). According to the synopsis by Shumway et al (l.c.), growth rates vary between regions and between sexes and age classes. Arctic populations are reported to have slower growth and longer life spans than populations at the south of the range. Because of its relevance to stock management growth and age determination have also been the topic of the NAFO (North Atlantic Fisheries Organisation) "Working Group on Progress in Age Determination of Pandalus" (Frechétte and Parsons 1981 and Parsons 1989).

The *P. borealis* stock in Gullmarsfjorden: a well defined system for the study of pandalid population biology.

The earlier tests of sex-allocation models have all been performed on impressive sets of data from areas in the ocean where there are no clear population boundaries. This may in general cause difficulties in assessing population parameters because, as Brattegard (1980) stated "studies of population dynamics of oceanic species seldom give results of sufficiently high quality due to the difficulties of sampling from the same population over time.". Brattegaard (l.c.) further stated that "Deep fjords often contain oceanic species whose populations may be isolated from other populations for long periods of time. Such populations are close to the ideal populations for studies of growth, mortality, life span, and succession of generations". Against this conceptual background, stocks of *P. borealis* in shallow- silled fjords such as Gullmarsfjorden, seemed at the beginning of this study more likely to offer controlled circumstances for the estimation of population parameters than the oceanic stocks and provide opportunities to test predictions from sex allocation theory. In order to perform these tests, however, the shrimp populations under study have to be defined and the pertinent demographic parameters determined.

Paper II addresses questions about the geographical and temporal definition of the stock of *P. borealis* in Gullmarsfjorden. Furthermore, the effects of immigration and recruitment of new year classes on the demographic patterns observed at the beginning of the yearly deep water stagnation in the fjord are discussed. Utilizing the enclosed fjord demes, the effect of mean ambient temperature on the duration of oogenesis in *P. borealis* is investigated in paper IV. Information on the reproductive cycle of and the abundance of shrimp larvae in Gullmarsfjorden is also given. In paper V, growth and age determination in *P. borealis* is discussed in detail based on a comparison of three growth models, one of them developed for this study. Paper VI gives mortality rates and describes age structures and frequencies of sexual stages in four temporally enclosed fjord demes and compares these with predictions from sex allocation theory.

Material and methods (II, III, IV, V and VI).

In this section the study area and methods will be briefly reviewed, for more detailed information see papers II-VI.

Gullmarsfjorden, the habitat.

A stock of *Pandalus borealis* in the deep basin of Gullmarsfjorden has supported a minor commercial fishery since the beginning of the 20th century. Gullmarsfjorden with a maximum depth of 120 m was classified as a "shallow silled fjord" (sensu Gade and Edwards 1980) by Lindahl and

Hernroth (1988). The deep basin is separated from the deeper parts of the Skagerrak by a sill with an effective depth of approximately 50 m (Fig. 1). The hydrography of the fjord (Svanson 1984) as well as plankton community dynamics in relation to advective flows over the sill area were previously studied by Lindahl and Perisinotto (1987) and Lindahl and Hernroth (1988). According to these authors the water-body in the fjord is normally stratified in three layers (Fig. 1.). In the deep basin water with salinities of $> 34 \text{ }^{\circ}/\text{00}$ and with low stable temperatures ($4\text{-}6 \text{ }^{\circ}\text{C}$) is found at depths below 50 m. The residence time of this water mass is normally 8-12 months. Between these deep water stagnation periods the deep water is normally exchanged in January-April through the one or more intrusions of water from the Skagerrak (II). In a study on the effect of the yearly deep-water renewal on the fjord zooplankton community Lindahl and Hernroth (1988) found that both the structure of calanoid copepod populations and the biomass of the meso-zooplankton in the deep basin

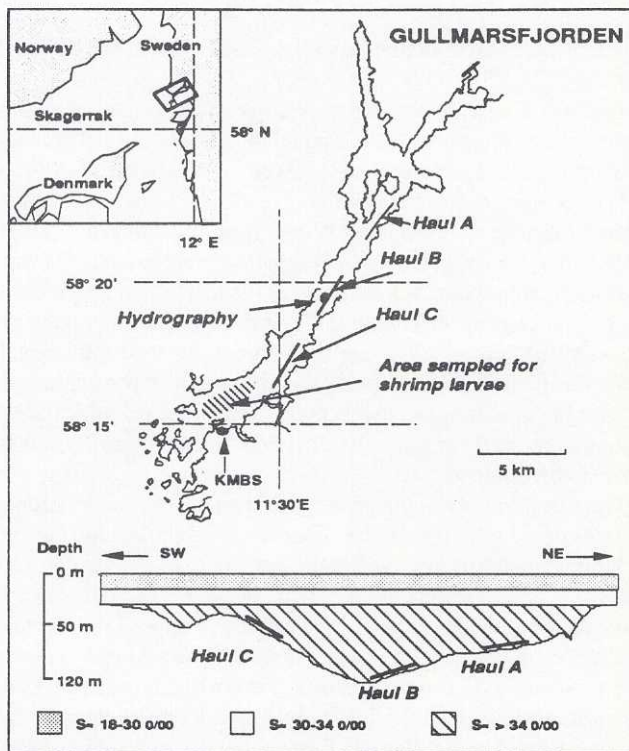


Fig. 1. Map and depth profile over Gullmarfjorden. The positions of the trawl hauls, the hydrographical station, and the area sampled for shrimp larvae are indicated in the figure.

of the fjord were dramatically influenced by intermittent water renewals. But during periods of deep water stagnation these plankton populations were effectively enclosed by the stratified water mass above sill depth. The bottom in the deep basin where the shrimps are found consists of very soft mud-like sediment. On the sill area a variety of coarser sediments are found.

Hydrography (II, IV and V)

Temperature, salinity, and oxygen concentration have been measured monthly at hydrographical standard depths in the central part (Fig. 1) of the fjord since 1978 by Dr O. Lindahl, Kristineberg

Marine Biological station. Temperature and salinity were measured with an accuracy of ± 0.05 °C and ± 0.05 ‰ respectively either with reversing thermometers and laboratory salinometer or with a CTD probe. Oxygen was measured by a modified Winkler method (Lindahl and Herroth, 1988). From this series, data from 10, 30, and 90 meters of depth were chosen to illustrate the conditions above and below sill depth for the purpose of paper II. Temperatures from the 70, 90, and 110 meter depths were chosen to represent the conditions in the deep basin of the fjord for the purpose of paper IV and V.

Trawling (II, IV, V and VI)

A total of 140 trawl hauls were made during 42 fishing days from December 1983 to the end of April 1988. Trawling was done at three fixed sites in the fjord during the same day (Fig. 1). Data from the three hauls made each fishing day were pooled in order to represent the demographic situation in the fjord basin. The used otter trawl had a maximal stretched foot rope length of 9 meters. Mesh size in the cod-end (measured as bar length) was 18 mm. Cruising speed was maintained at 2.5 knots and fishing time on the bottom was 30 minutes. The same trawl and procedure were used through out the study. The catch of shrimps in each haul was analyzed upon return to the laboratory.

ROV investigations (III)

In addition, parallel to the shrimp investigation, numerous dives with a Remotely Operated Vehicle (ROV) were carried out both in the deep basin and on the sill area. In paper III initial work to develop a method to estimate absolute densities of pandilid shrimps is reported as an alternative to the widely used method based on catch per unit of effort (CPUE). Basic to CPUE measures are assumptions that catch sizes are proportional to absolute population density and that the assumed proportionality factors remains constant between different sampling events. These assumptions are

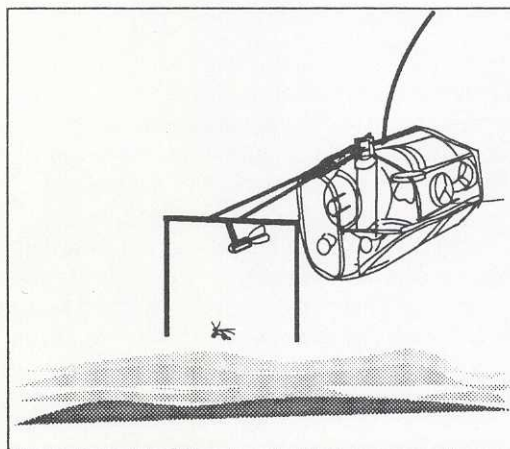


Fig. 2. Sea Owl Mk II equipped with flow meter and inverted U-frame.

largely untested. Against this background work aiming towards an alternative method of density estimation based on the use of an unmanned tethered Remotely Operated Vehicle (ROV) equipped with video camera ("Sea Owl MK II") was started in 1986.

By fixing two vertical rods (defining the width of the inspected area) and by attaching a calibrated flow meter (measuring the length of the inspected area) in front of the video camera of the

vehicle it was possible to determine numbers of shrimps per unit area along transects at ca. 90-110 m of depth (Fig. 2). The method has been further developed since publication. Instead of using the flow meter to determine the length of the surveyed transect a high frequency sonar and a sonar target is now being used (Bergström in prep). However, due to lack of funding, the planned comparisons between abundance estimates made by trawling (CPUE) and ROV transects at the same locality during the same day have not yet been conducted.

Catch per unit of effort (CPUE) and mortality (II and VI).

In paper (II) catch per unit effort (number of caught shrimp/trawled nautical mile) derived from samples obtained before and after the water renewal each year were compared in order to investigate to what extent migrations affected the demography of the fjord stock. Catch per unit effort was also used in paper VI to estimate total average mortality (Z) during each of the stagnation periods. This was done by the use of the expression, $N_t = N_0 e^{-Zt}$, commonly used in fisheries biology (Gulland 1985), where N_0 = CPUE at time 0 (1st of January each investigated year) and N_t = CPUE at time t (number of days since 1 st of January each investigated year) (VI).

Abundance of larvae (paper IV)

Information on abundance of shrimp larvae of different developmental stages was obtained by sampling with a bongo net (mesh size 300 and 500 μm) in the outer part of the fjord during late winter-early spring 1984-1987.

Determination of sexual and reproductive stage (paper IV, V and VI)

Specimens were sexed on the basis of the shape of the endopodite of the first pleopod according to Allen (1959). Females were further sorted into four different categories according to their reproductive status (Rasmussen 1953):

1. Females without reproductive characteristics
2. Females with ripe gonads visible through the carapace
3. Berried females (females carrying eggs on the pleopods)
4. Females in "breeding dress" (long setae on the pleopods)

Females in the latter stage occur just after the hatching period and during spawning. The relative frequencies of these categories were determined in pooled catches of females from the three hauls taken during each sampling day. These frequencies were used to estimate mean duration of oogenesis. The relationship between ambient mean temperature and the estimated durations of oogenesis in each of the study years was subsequently examined by correlation analyses, and linear, logarithmic, and exponential regressions, were fitted using the least square method (Sokal and Rohlf, 1969).

Length frequency distributions (III).

The carapace length (CL) of all shrimps divided by sexes was measured with callipers to within 0.1 mm. In the calculation of length-frequency distributions (LFD), measurements were pooled in 0.5 mm size classes. In order to investigate if the age distributions among older shrimp changed after the water renewals, LFD's in samples taken before and after the water renewal each of the studied years were compared after compensating for growth. For this comparison a Kolmogorov-Smirnoff test was used (Sokal and Rohlf, 1969).

Growth and growth models(V)

Growth is not easily studied in pandalid shrimps since easily identified structures indicating seasonal growth are absent in crustaceans. Hence the most used method of determining growth in pandalid shrimps, which have a well defined and relatively short reproductive period (IV), involves the identification and tracing in time of modes (cohorts) in length frequency distributions. This praxis builds on the generally accepted assumption that size and age are positively correlated in shrimps. Another assumption is that the asynchrony in moulting between individual shrimps generates cohorts where carapace length at age is normally distributed.

Separation of cohorts representing year classes in the LFD's as well as estimation of mean size by age were made using the computer program MIX 2.3 (Macdonald and Pitcher 1979, Macdonald 1987). This program enables the user to analyze length frequency histograms by finding sets of best fitting normal distributions defined by means and variance.

Three different equations describing growth in length were fitted to mean CPL at age. The von Bertalanffy growth (VBG) equation was used in its original form and in a form modified to describe seasonal variations in growth by the addition of a sine function (VBG_{sine}) (Pauly and Gaschutz 1978).

The third model (VBG_{sigma}), which was developed for paper V, is also a modification of the VBG, but in this seasonal variations in growth are represented by the use of periodically recurring sigmoid functions:

$$L(t) = L_{\infty} \{ 1 - e^{-Kt} + A(1 + e^{-bP/2} / 1 + e^{-b(t-t_n - P/2)} - 1) \}; \quad t_n \leq t \leq t_{n+1}$$

where

$$A = e^{-Kt_n} (1 - e^{-KP}) (1 + e^{-bP/2} / e^{bP/2} - e^{-bP/2})$$

L_{∞} = Asymptotic carapace length;

K = Growth coefficient;

t = Age;

P = Period. In the case of *P. borealis* in Gullmarsfjorden P was assumed to be 1 year;

n = Period number;

b = Constant determining shape of sigmoid;

$t_n = WP_{\sigma} + (n-1)P$; where WP_{σ} is the seasonal phase constant (i.e. the time of year when growth rate is 0).

Fitting of the growth models to the estimated average cohort carapace lengths, weighted by number of shrimp in the different cohorts, were in all cases done with the least square method implemented in the PC program "Statgraphics®".

Comparison of growth "year class wise" and "stagnation wise" (V).

Data were analyzed in two different ways, "year class wise" and "stagnation wise", in both cases data were treated both separated by sexual stage and pooled. When data were analysed "year class wise" year classes were followed for as long as possible through the entire study period including both samples taken during water renewal and deep water stagnation periods. Growth was also analyzed for each of the studied stagnation periods ("stagnation wise"), excluding samples taken during the water renewals.

Comparison of growth patterns (V)

Since L_{∞} and K are negatively related to each other, comparisons of estimated growth rates were made by reparameterizing the three different von Bertalanffy growth models, and tests were performed on a new, single parameter, $\Omega = K \cdot L_{\infty}$ (Gallucci and Quinn 1979). The parameter Ω corresponds to the growth rate near t_0 and is suitable for comparisons because of its statistical robustness (i.c.). Using Ω and the differences in mean ambient temperature between the studied deep water stagnation periods (Table 1) it was also possible to investigate the effect of temperature on growth rate in the range of 4-6° C by correlation analysis. Both comparisons between growth rates and between seasonal patterns in growth the sexual stages were performed by unpaired t-tests (Sokal and Rohlf 1969).

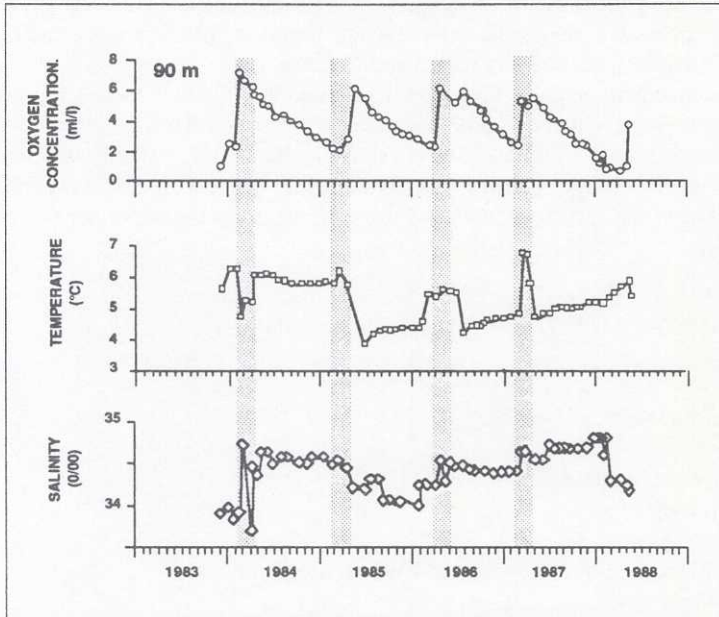


Fig. 3. Oxygen concentration, temperature, and salinity at 90 meters of depth in Gullmarsfjorden 1984-1988. Stippled bars indicate the water renewal periods.

Growth of *P. borealis* in Gullmarsfjorden compared with other populations (V).

Sizes at age predicted by the mean male and female VBG_{sigma} functions derived from the investigation in Gullmarsfjorden were compared, with sizes by age reported from other boreal populations using a one group X^2 test (Sokal and Rohlf 1969).

Frequency of sexual stages in age groups (VI)

Relative frequencies of males, females and transexuals were calculated in each sample and the average frequency of females was calculated for each stagnation period together with proportions of females in each year class. In addition, in order to estimate the proportion of EMF present in each deme during the breeding period, the proportion of females among the 1-2 year old shrimp were calculated in the pooled samples from August-October. In order to test whether low mortality rates in the population gave an increase in male average age, the proportions of males among shrimp older than 2 years were also calculated and correlated with total mortality each of the studied years.

Results and conclusions.

The shrimp stock in Gullmarsfjorden: a succession of periodically enclosed demes (III).

The recurring water exchanges in the deep basin of the fjord during the study period are illustrated by the variations in oxygen concentration at 90 m depth (Fig. 3). When the exchanges occurred oxygen concentrations generally increased by a factor 3-4. Temperature and salinity variations at the same depth during both water exchange periods and stagnation periods are also presented (Fig. 3). Catch per unit effort (CPUE) generally increased in the fjord after the water renewals and then decreased during the stagnation periods (Fig.4). Mean number of shrimp per trawled nautical mile, caught immediately before water renewal for the studied years was 82.9 ± 19.0

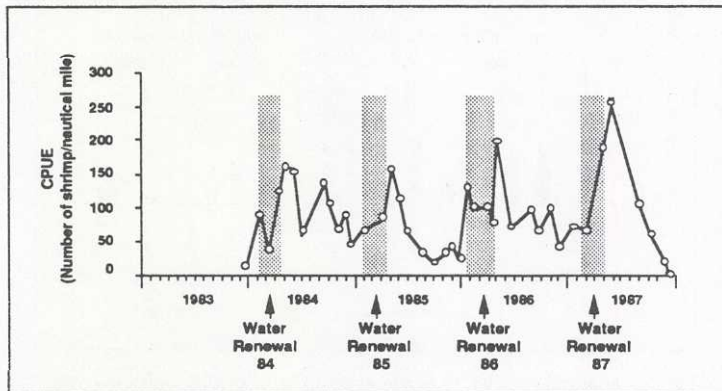


Fig. 4. Variations in CPUE (Number/Nautical mile) calculated on total catches of *Pandalus borealis* in the Gullmarfjord, 1984-1987. Stippled bars indicate the water renewal periods.

(99 % level of confidence) while immediately after the water renewal it was 178.1 ± 26.0 (99 % level of confidence).

Increases in CPUE after the water exchange were evident both among recruits and older shrimp. In 1984, 1985, and 1987 the increases in abundance after the water renewal were mostly due to increases in the catch of older shrimp while in 1986 the increase was mostly made up by the new year class (Fig. 5). These results are corroborated by the results from comparisons between transformed length-frequency distributions of older shrimps from before (LFD_{PRE}) and after (LFD_{POST}) the water renewals which indicate significant differences ($P(H_0; LFD_{PRE} = LFD_{POST}) < 0.05$) all years except in 1986.

The results indicate that immigration of older shrimps took place in 1984, 1985 and 1987. Immigration was probably facilitated by strong advective flows over the sill area during water renewal coinciding with the winter-spring on-shore migration in the Skagerrak. In 1986, the demographic pattern after the water renewal was dominated by the recruiting year class (shrimps hatched in the spring 1985) and negligible immigration of older shrimps. Generally in populations recruitment (nativity) and immigration, together with mortality and emigration, are crucial in producing variations in population structure. In the case of shrimps in Gullmarsfjorden the population can be defined as those shrimps enclosed in the fjord deep basin beneath sill depth during

the stagnation period. In between water renewals, the water layers above sill depth do not provide the combination of salinity and temperature at which *Pandalus borealis* normally is found in the Skagerrak proper. This conclusion is corroborated by the fact that during a period of 33 years of epibenthic collecting on the sill area of the fjord, *P. borealis* were never caught during the deep water stagnation periods (Dredgemaster S. Robertsson, Kristineberg Marine Biological Station, pers. comm.).

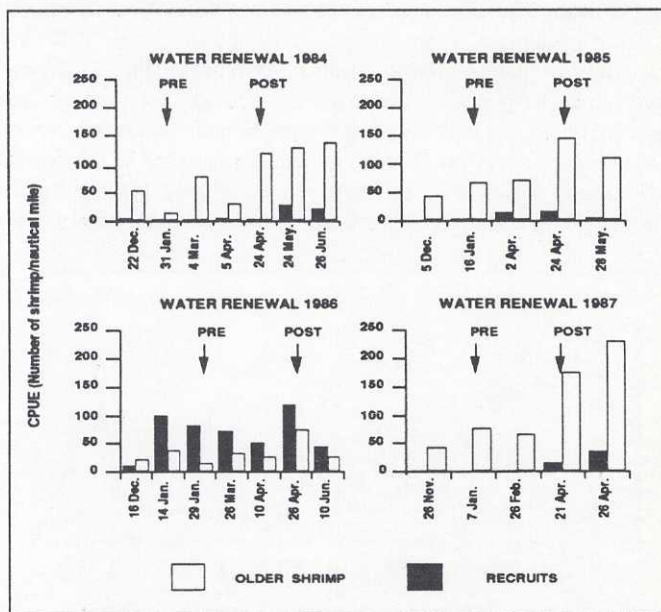


Fig. 5. Variations in CPUE of *Pandalus borealis* belonging to the new year class (recruits) and older shrimp (> one years of age) during the water renewal periods 1984-1987.

The short lived (8-12 months) stagnation populations found in Gullmarsfjorden meet the definition for distinct populations given by Pianka (1978), since mating takes place in September-October in the fjord (Jägersten 1936 and paper IV), but they should perhaps more appropriately be considered as demes or periodical isolates of the Skagerrak stock.

The recurrent additions of adult shrimps to the fjord seem to be important in maintaining a stock of *P. borealis* in Gullmarsfjorden. This immigration during the water renewals, also creates different demographic patterns in the fjord stock at the beginning of each stagnation period. Depending on the structure of the Skagerrak shrimp stock available just outside the fjord sill area at the time of water renewal, different size/age and sex categories might dominate the immigration, and hence the population structure during the following stagnation period.

Reproduction, larvae and the effect of temperature on oogenesis (IV)

The general reproductive cycle of *P. borealis* in the fjord is illustrated by frequencies of female reproductive categories (Fig. 6). These as well as the occurrence of larvae indicate that the period from spawning to hatching of *Pandalus borealis* in Gullmarfjorden spans from late September/early October to March. This duration of 6-7 months agrees with general information about the stock in Gullmarsfjorden given by Jägersten (1936) and with durations reported from southern Norway (Rasmussen 1953), the Gulf of Maine (Haynes and Wigley 1969) and the Gulf of Alaska and Kodiak area (Shumway et al. 1985). Mean temperatures and estimated durations of oogenesis for the four

deep water stagnation periods showed a significant negative correlation ($P > 0.05$, $R = -0.98$, $r^2 = 0.95$), i.e. the duration of oogenesis increases with decreasing temperature. Fitting of logarithmic, $Y = 339.61 - 245.99 \text{LOG}_{10} X$ ($r^2 = 0.960$), ($Y =$ duration in days, $X =$ average temp in $^{\circ}\text{C}$), exponential and linear functions, revealed that the logarithmic model gave the best fit to the empirical data.

Larvae occurred during the hatching time (March- April) in the fjord and seemed to be most abundant in the 25-60 meters depth interval. The observed peak densities in Gullmarsfjorden were generally lower than densities reported from the Gulf of Maine (800-300 larvae/1000 m^3) by Stickney and Perkins (1981). Only in April 1985 did the abundance of larvae reach a peak in Gullmarsfjorden (306 larvae/1000 m^3) comparable with that of the year with lowest reported abundance in the Gulf

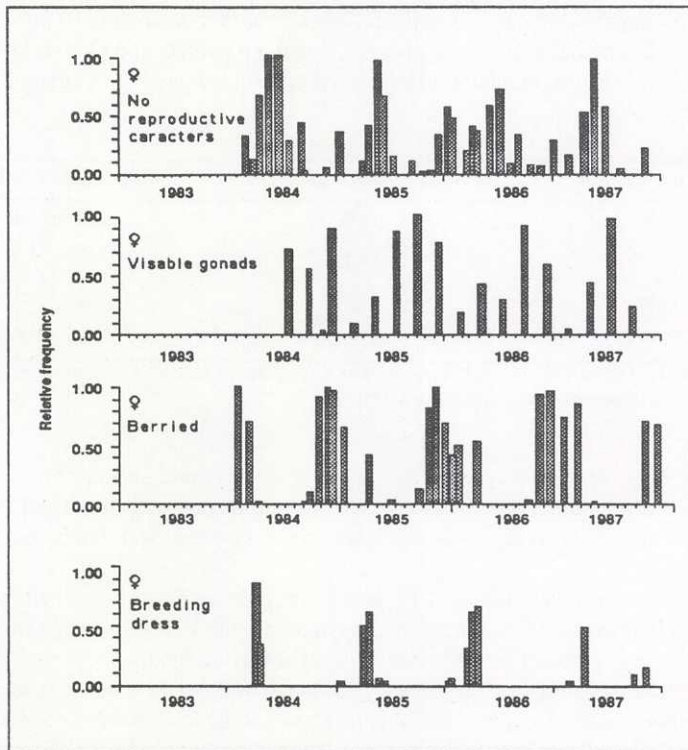


Fig. 6. Relative frequencies of different female reproductive stages of northern shrimp, *Pandalus borealis*, in samples taken in Gullmarsfjorden the years 1984-1987.

of Maine; in the other years, abundances were 10-20 times lower in Gullmarsfjorden than in the Gulf of Maine (Stickney and Perkins l.c.). The observed variations in larval abundance between samples in Gullmarsfjorden were probably caused by the highly dynamic hydrographical pattern of the water layers above sill depth in the fjord.

Despite the observed low densities of larvae, *P. borealis* is well established in the fjord, a fact that is illustrated by the presence of a small commercial shrimp fishery established in the beginning of the 20:th century. Hence it seems possible that the immigration of adult shrimps during the water renewal period, which may occur most years (II) plays the most important role in maintaining a stock of *P. borealis* in Gullmarsfjorden.

In paper (IV) the usefulness of the temporally enclosed demes as "natural experiments" was illustrated by the verification of laboratory results regarding the temperature effect on the duration of oogenesis of *P. borealis* (Stickney and Perkins, 1980).

Growth, growth modelling, and age determination (V and VI).

Sizes by age of shrimps in Gullmarsfjorden were very similar to those of *Pandalus borealis* in other boreal populations and the yearly immigrations of shrimps from the Skagerrak stock did not significantly disrupt the growth curves. The comparison of growth models showed that for detailed growth descriptions the models which incorporate seasonal growth gave the highest coefficients of determination. Seasonal variations in growth are apparent in earlier studies (e.g. Berkeley 1930; Rasmussen 1953; Haynes and Wigley 1969 and Shumway et al. 1985), but not until recently have there been attempts to use models incorporating seasonal variations in growth (Hopkins and Nielssen 1990). In many of the cases the VBG_{sigma} model gave slightly better results (V). This model combines sigmoid growth patterns with the von Bertalanffy growth equation, which in its unmodified form is unable to represent sigmoidal growth in a linear dimension (Gallucci and Quinn, 1979). Growth of macrobenthos is frequently sigmoidal with an inflection point early in life (Yamaguchi 1975). Thus

Stagnation year	Max. growth rate (Ω)	Meantemp. \pm s.d. ($^{\circ}$ C)
1984	15.00	5,88 \pm 0.11
1985	15.14	4.33 \pm 0.12
1986	14.66	4,56 \pm 0.21
1987	12.37	5,04 \pm 0.09

Table 1. Estimated maximal average growth rate for *Pandalus borealis* and mean temperatures during four deep water stagnation periods in Gullmarsfjorden

variants of the VBG_{sigma} model may be useful not only for pandalid shrimps but also to describe growth in other invertebrates. Theisen (1973) for example, studying growth of lamellibranchs, suggested that growth of all bivalves is sigmoidal and recommends a combined Gompertz-von Bertalanffy model.

In paper V the seasonal variations in CPL growth are proposed to be explained by physiological switches between investment in reproductive tissue and growth in length, rather than variations in external factors such as ambient temperature and availability of food.

Present results also indicate differences in growth patterns between sexual stages. Differences in growth rate between sexual stages could only be shown at the 75% level of confidence, probably due to the relatively small number of observations. There was however a significant (95 % level of confidence) difference in growth seasonality between sexual stages. The estimates of winter points from both seasonal growth models indicated that growth in length generally stagnated earlier for males (autumn-early winter) than for females (winter). Indications of differences in growth between male and female *P. borealis* have previously been mentioned by Rasmussen, (1953), Allen, (1959) and observed in a preliminary study by Bergström (1989), but no quantitative evaluation has been attempted before..

Growth rate in this study did not correlate with mean ambient temperature in the interval of 4-6 $^{\circ}$ C (Table 1). A similar observation was made by Parsons et al. (1989) in the temperature interval of 2-4 $^{\circ}$ C based on data from four regions of the Northwest Atlantic. Hopkins and Nilssen (1990) also stated that "although on a broad latitudinal scale, age at first spawning can be correlated with ambient temperature, there might be more important overriding factors than temperature at any one locality". My conclusions agree with this statement.

Figure 7 gives mean sizes at sampling dates for 1980-1986 year classes as observed during the studied period. Cohorts of hatched in the spring 1980 could still be identified with MIX during the summer of 1985. These had at the age of approximately 5.3 years reached a CPL of 28.1 \pm 1.2 mm

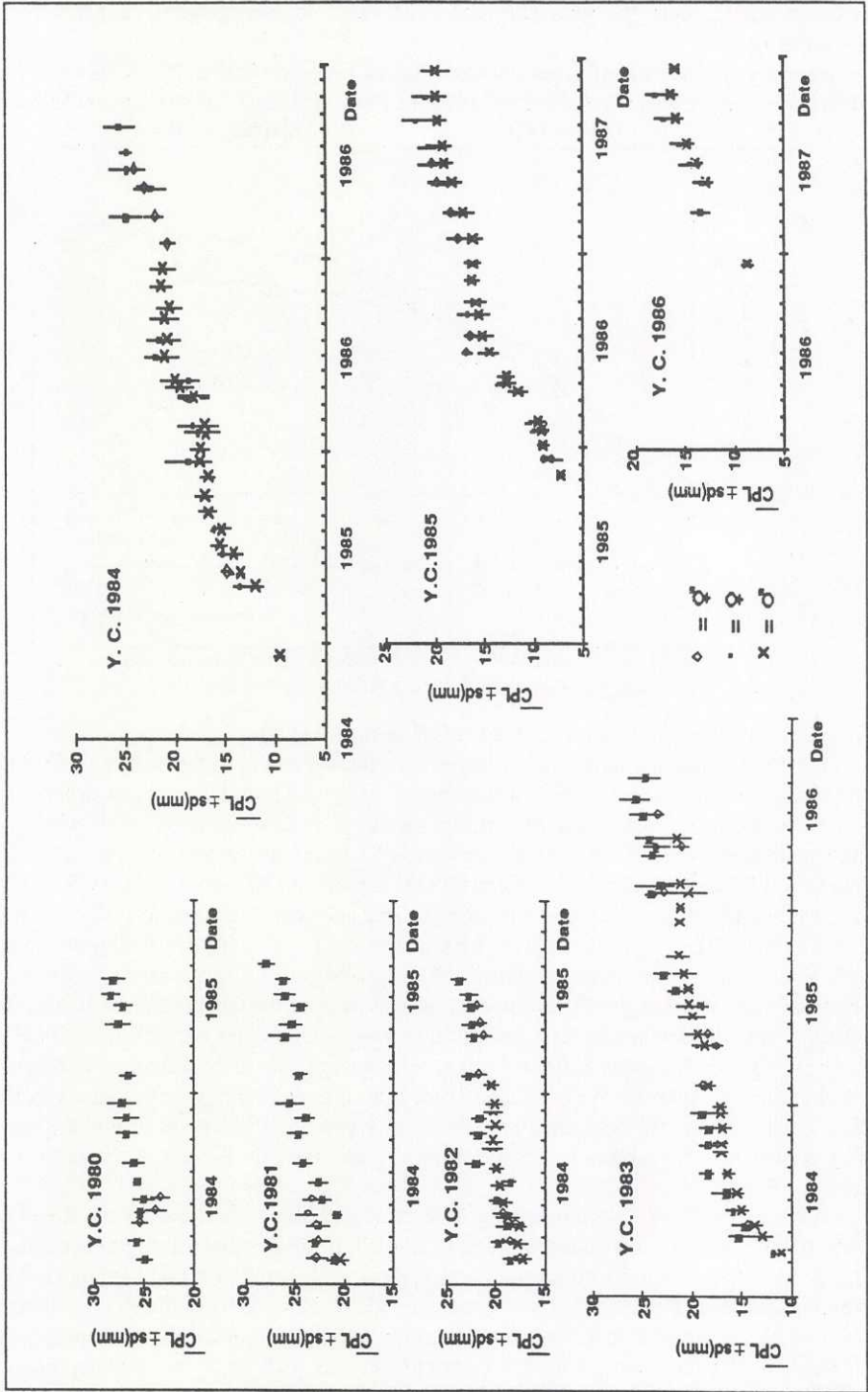


Fig. 7. Mean carapace length (CPL) and standard deviation at sampling date of male, transitional, and female *Pandanus borealis* in year-classes

and were all females. Also larger shrimps with a CPL of 30-32 mm occurred regularly in the samples from Gullmarsfjorden. It is likely that these shrimps were 6 years or older. Females of all sizes / ages were found in the samples, but young females (< 1.5 years old) were generally much rarer than males of the same age.

Generally the male stage did not last more than ca 2.8 years (CPL of 20.1-22.2 mm). Exceptions are 4 larger male specimens found in 1987 (CPL of 25.0- 28.0 mm). These shrimps (belonging to the

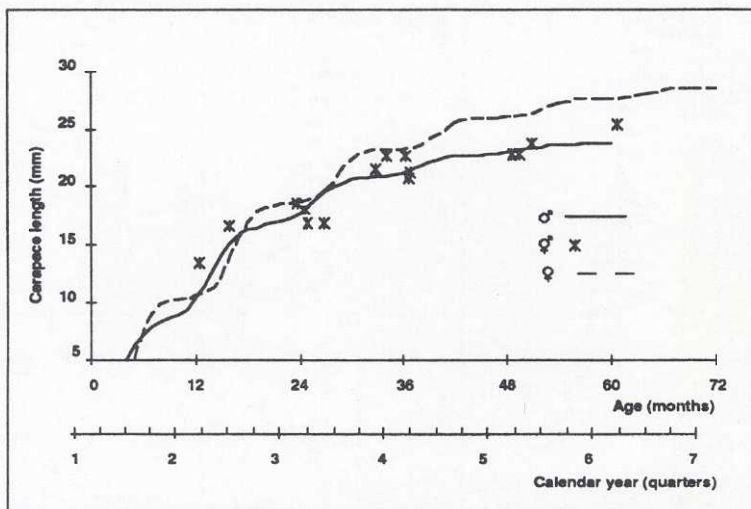


Fig 8. Average growth curve (VBG_{σ}) for *Pandalus borealis* in boreal waters based on data from year-classes 1980-1986 in Gullmarsfjorden 1984-1987.

1983 year class) were still males at an age of more than 4 years.

Transitional shrimps were slightly larger than average males of the same age. These occurred in the spring samples except in 1987 when transitionals were found in very low proportions also in the summer samples. Sex changing shrimps occurred in low numbers in all age groups. The approximate mean ages of the sex changers were 12.4 months (mean CPL 13.3 mm), 23 months (mean CPL 17.5 mm), 35.4 months (mean CPL 21.8 mm) and 50 months (mean CPL 23,3 mm,) Of these transitional shrimps the group with an estimated age of ca 3 years were always most abundant. In Fig. 8 average VBG_{σ} growth curves for the male and female stages of *P. borealis* are presented to give a basis for age estimation of shrimps in Gullmarsfjorden. Comparisons between size by age predictions made with the aid of these models and size by age from the literature indicated that growth of shrimps in Gullmarsfjorden were very similar to growth in other boreal populations.

Growth modelling in pandalid shrimps is pertinent not only to stock assessment, but also to sex allocation theory. Apart from giving a basis for descriptions of age structure, the von Bertalanffy growth equation has also been used to estimate size/age specific female fecundity, together with results showing that fecundity in marine shrimps increases with the thirde power of body length (Charnov 1979).

Charnov (1979 and 1982) indexed growth rates with the growth coefficient K and stated that growth decreased with increasing latitude in north European waters and that the age of female maturity and life span increased proportionately. It is well established that life span increases with increasing latitude in *P. borealis* (e.g. Rasmussen 1953 and Shumway et al. 1985) but there is a major problem with the use of K to index growth rates for comparative or correlational purposes. Growth rates are difficult to compare, or for that matter to correlate with, since two essential factors, growth coefficient K and the asymptotic length L_{∞} in the von Bertalanffy growth equation are inversely related (Galluci and Quinn 1979). Charnov (l.c.) illustrated declining growth rates with increasing

latitude in Rasmussens 1953 and 1969 data using the growth coefficient K without the accompanying L_{∞} and length at age 0 (t_0). This practise may lead to erroneous results since the variation in K may not only show variations in the rate at which CPL approaches L_{∞} , but may also show an unspecified variation in the estimate of the asymptote. Due to these difficulties Galluci and Quinn (1979) reparameterized the VBG equation and proposed that the parameter $\Omega = K \cdot L_{\infty}$ should be used instead. In paper V and VI this parameter was used to investigate the correlation between growth rate and mean ambient temperature and between growth rate and frequency of EMF in Gullmarsfjorden.

Charnov (1979) also fitted von Bertalanffy growth equations to growth data from 27 populations of pandalid shrimp from the literature and from unpublished sources. The growth coefficients (K) obtained were subsequently used to estimate total average mortality (Z) by using an empirically established (for fish) relationship $Z=6.4/T_{\max}$ (Beverton and Holt 1957), where T_{\max} is the oldest breeding age, and results by Fox (1972) (cited by Charnov 1979) that indicate that K in the VBG is inversely proportional to T_{\max} in pandalid shrimps. Combining these two findings, Charnov, (see Charnov 1979 for details) formulated the expression $Z=2.7 \cdot K$ where Z is total average mortality and K is the growth coefficient from the VBG. I have compared these results with K 's (V) and Z 's (VI) directly estimated from the four different temporally enclosed demes in Gullmarsfjorden. These K 's and Z 's do not show a positive relationship as reported by Charnov (l.c.). Instead a non significant (95 %) negative correlation ($r=-0.704$, $r^2=0.495$, $n=4$) was found.

Demography and sex change in *P. borealis* (VI)

As indicated above, Gullmarsfjorden contained four different temporally enclosed demes during the study period, which may be viewed as "natural demographic experiments". Paper VI describes for each of these demes, the age structure, mortality, and relative frequency of the different sexual stages within each age group is described. These descriptions form the basis for the test of predictions from sex allocation theory concerning pandalids.

To recapitulate, variations in proportion of primary females (PF), early maturing females (EMF) and males that breed more than once as males during the breeding period in populations of protandric pandalid shrimps have been interpreted as the indicator of a special kind of phenotypic or environmental sex determination (ESD). This trait would allow the shrimps to alter the age/size at which they change sex to match a variable demographic environment in order to maximise individual reproductive success.

Charnov et al (1978) predicted that the proportion of first breeders acting as females during the breeding period should be negatively related to the frequency of older females in the population and that the proportion of older breeders functioning as males during the breeding period should be negatively related to the proportion of first breeders.

Charnov (1981 and 1982) suggested that the age/size of sex change should decrease when mortality increases i.e the frequency of early maturing females should be positively related to mortality.

In paper I the frequency of sex-changers among second breeding shrimp is suggested to be negatively related to the proportion of older breeders (all female) in the population.

Charnov and Andersson (1989) proposed that the frequency of EMF increased when the mean size of the individuals in the breeding population decreased based on correlative evidence from a shrimp population off the Alaskan coast .

These are results and proposals, in which theory predicts relationships between variations in the frequency of EMF and long or short term demographic variations in populations found at a given locality. But based on biogeographic patterns in the length of time spent in the male stage, Charnov (1979, 1982) also suggested that the average time spent as a male increases in protandric pandalid shrimp with increasing life span (decreasing growth rate/decreasing mortality).

As shown by the age structures (Fig. 9), mortality rates (Fig. 10) and growth rates (V) the demographic patterns varied substantially between the four studied temporally enclosed demes in

In 1984 four breeding age classes were present in the fjord. The deme was characterised by a high presence of females; on average $42.3 \pm 4.4\%$ (95 % level of confidence) of the caught shrimps were females. Shrimps older than 2 years clearly dominated the samples. Of these the 3-5 year old shrimps were all females. By contrast, only about 5 % of the 2-3 year olds were females, the great majority being males. A similar situation could be seen among the 1-2 year old shrimps, but the average frequency of females (EMF) was slightly higher (7%). Non-breeding shrimps less than one year old (hatched in the spring 1984) and all showing male external morphology, appeared in very low abundance in the late autumn samples (Fig. 9). No transitional shrimps were caught during the stagnation period, these were confined to the samples obtained during the water renewal period. The estimated mortality (Fig. 4 a) was the lowest during the four studied years ($Z=1.46$ shrimp/trawled km/year) (Fig. 10). In conclusion the average age was high this period and so was the proportion of

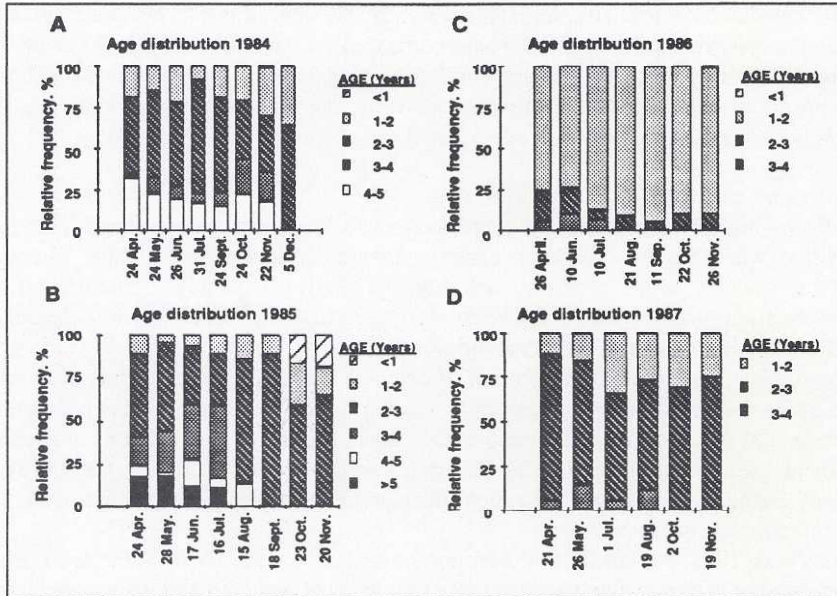


Fig. 7 Age structure in the four temporally enclosed demes of *Pandalus borealis*.

older females. This situation should according to sex allocation theory, favour a very low incidence of EMF and thus a postponed sex change among the males. The findings indicated a low incidence of sex change among the 2-3 year old shrimps which is in agreement with theory, but simultaneously 4 % of the 1-2 year old shrimps were females during the breeding period.

At the beginning of 1985 there were at least 5 breeding age classes in the population, but by late summer shrimps older than 3 years had largely disappeared from the population (Fig. 9). The deme this year was also characterised by a high average abundance of females ($47.2 \pm 8.1\%$ (95 % level) as calculated on an annual basis, but this was largely due to the dominance of older females at the beginning of the year. The 3-4 year olds changed sex during the spring, as indicated by the high frequency of transitional shrimps in the early samples but this year class was absent in samples from the breeding period. The samples from the later part of 1985 were dominated by shrimps younger than 3 years. Of these, the 2-3 year olds were most abundant, these being mostly males (on average 93%), although females were found in the July and August samples. The first breeders (1-2 years old) were dominated by males (average 94%) (Table 3) with a small proportion of early maturing females (EMF-average 6%). Relatively high numbers of non-breeding shrimps, less than one year

old, occurred in the autumn samples. An average of 9 % of these showed female external morphology, and were thus primary females (PF). Transitional shrimps were only found in the spring. The mortality was the second highest ($Z=3.65$ specimens/trawled km/year) experienced in the study (Fig. 10). In 1985 the deme was also dominated by older females especially during the first half of the year, but the mortality more than doubled as compared with 1984. According to theory, this increase in mortality ought to have induced some increase in proportion of EMF during breeding, but the found proportion was the lowest observed in the study.

In 1986 the demographic pattern in the fjord was dramatically altered. At the beginning of the year there were three classes of breeding age represented in the samples, but shrimps over 3 years old (Fig. 9), mostly females and sex-changers, were only present in low proportions in the spring

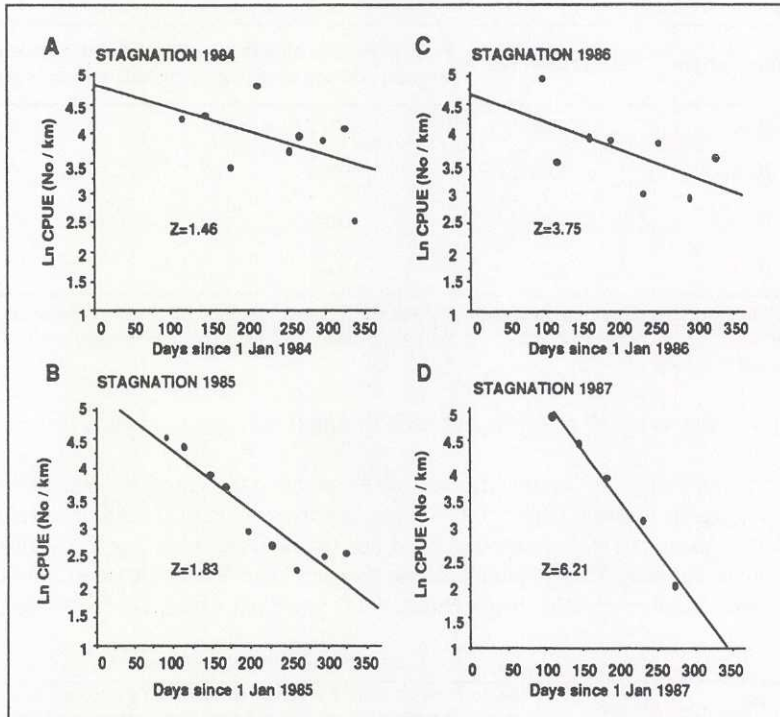


Fig. 10 Mortality in four temporally isolated demes of *Pandalus borealis* in Gullmarsfjorden

and summer samples. The average annual proportion of females was 20.9 ± 5.4 % (95 % level). Instead, the samples were dominated by 1-2 year old shrimps belonging to the 1985 year class. Of these on average 4 % were females (EMF). These females, and some sex-changers, were however only found in the spring and summer samples and not during the breeding period. Shrimps 2-3 years old were also present but in low proportions. Non-breeding shrimps less than 1 year of age started to appear in the late autumn in very low proportions. These shrimps were mainly males towards the end of the period, while females were present during spring and summer. Generally transitional shrimps were present among all shrimps older than one year, but only in the spring-early summer samples. The highest frequencies of transitional shrimp were found among 3 year old shrimp. In 1986 the mortality was second lowest ($Z=1.83$ specimens/trawled km/year) in the study (Fig. 10). In 1986 the mortality decreased again. The mean proportion of females was less than half of those found in the previous years. The deme was this year dominated (on average 74 %) by the very strong 1985

year class. According to theory, a substantial proportion of these should have developed as females in time for the breeding period, but only 2 % did.

The 1987 stagnation population held 3 age groups of breeding shrimps (Fig 9). The average frequency of females was 27.3 ± 5.5 % (95% level). Two-three year olds were most abundant throughout the period (Table 1). These were mostly males (88 %) but a relatively high proportion were females(12 %). Transitionals in this age group were found in the spring. One-two year olds, of which a relatively high proportion changed sex in the spring, were more common than 3-4 year olds. The latter generally changed sex in the spring and summer, and were absent from the autumn samples. This year showed the highest mortality of the four years, with an average of $Z=6.21$ specimens/trawled km/year (Fig. 10), while the growth rate was the lowest. The very high mortality

Stagnation period	Mortality (Z)	Prop. of females among 1st breeders during breeding	Prop. of males among >2 year olds during breeding
1984	1.46	0.042	0.82
1985	3.65	0.000	0.29
1986	1.83	0.02	0.48
1987	6.21	0.065	0.78

Table 2. Total mortality, proportion of females (PF and EMF) among 1st breeders during the breeding period and proportion of males among >2 year old shrimps in each of the studied temporally enclosed fjord demes of *Pandalus borealis*

should have given rise to a high proportion of EMF during breeding according to theory, but only 2 % were found.

The majority of shrimps in Gullmarsfjorden were females at the age of 3-4 years (transitionals at an approximate age of 3 years). Together with these, low proportions of shrimps that were females during their 3rd (transitionals at ca. 2 years) and 2nd year (transitionals at ca. 1 year, and PF) of living were always found. The proportion of females being between 2 and 3 years old varied between 5 and 12 % and the proportion of females being between 1-2 years old varied between 4 and 7 %. In

Stagnation period	Prop. of females among 2nd breeders	Prop. of 3rd and older breeders
1984	0.063	0.240
1985	0.125	0.099
1986	0.000	0.032
1987	0.115	0.079

Table 3 Proportion of females among second breeding shrimps and older breeding shrimps during the breeding period in four demes of *Pandalus borealis*.

addition, in two of the demes, female shrimps younger than 1 year were present in the populations. In 1985 on average 9 % of these were found and in 1987 on average 5 %. These results indicate a lack of relationship between demographic patterns and age of sex change in *P. borealis* in the four temporally enclosed demes.

This conclusion is corroborated by the results from the correlation analyzes performed between different demographic parameters. No significant correlation (95% level of confidence), ($n=4$, $R=0.461$, $R^2=0.212$) was found between total mortality in each of the enclosed fjord population and

the relative frequency of females among 1:st breeders (1-2 years of age) during the breeding period (Table 2). No significant ($R=0.113$, $R^2=0.013$) correlation between total mortality and proportion of males among > 2 years old shrimp were found (Table 2). Furthermore no correlation ($R=0.162$, $R^2=0.026$) between the frequency of females among second breeding shrimps and the frequency of 3 d and older breeding shrimps during the breeding period in four periodically isolated demes of *P. borealis* (Table 3) could be shown.

To conclude the results from this study on four temporally enclosed demes of *P. borealis* in Gullmarsfjorden show no significant evidence, at the 95 % level of confidence, that mortality, or frequency of older breeders in the breeding population affects the time of sex-change in this protandric species as suggested by Charnov et al. 1978, Charnov 1981, 1982 and Charnov and Bergström 1987. Moreover since age is related to size in this species (V) there seems to be no correlation between the average size of the breeding individuals and the average size at sex change as reported by Charnov and Andersson (1989) working with a shrimp stock in Pavlov Bay (Alaska).

Concluding discussion.

A common feature of the earlier studies on sex allocation and pandalids is the surprising suggestion that pandalid shrimps have environmental sex determination (ESD) and that the male shrimps, via some environmental clue, are able to estimate the frequency of older females in the population. While this suggestion awaits experimental verification I would like to propose a tentative alternative explanation to the observed variations in age/size of sex change in protandric pandalid shrimps.

The overwhelming majority of post larval shrimps in boreal populations of *Pandalus borealis* show male external morphology during their first year of life. Some may however, develop directly into females, (primary females, PF) without passing through the male stage. Most 1-2 year olds breed as males, but a low proportion of individuals change sex during their first year and reproduce as females at ca. 1.5 years of age, (early maturing females, EMF). During the following reproductive periods, varying proportions of the males change sex. (Jägersten, 1936; Rasmussen, 1953; Allen, 1959; Butler, 1964; Haynes and Wigley, 1969; V; VI). Thus 2-3 year olds can be either males or females or a mixture of both, whilst those older than 3 years (larger than ca 22 mm CPL) are generally females (e.g. Rasmussen, 1953).

In Gullmarsfjorden, the majority of shrimps were females at an age of 3-4 years (transitionals at an approximate age of 3 years). There were however always low proportions of younger shrimps that were females irrespective of variations in age/size structure, mortality or sex frequency . The 1-2 year old females were largely composed both of shrimps that went through the transitional stage at ca. 1 year of age, as well as primary females, while the 2-3 year olds had been transitionals at ca. 2 years. The mean carapace lengths of sex changers in Gullmarsfjorden were 13.3 mm (age 12.4 months), 17.5 mm (age 23 months), 21.8 mm (age 35.4 months) and 23,3 mm (age 50 months) (V; VI). It is also noteworthy that some transitional shrimp older/larger than the majority of the sex changers were occasionally found in the demes (V; VI).

This situation suggests that populations of *P. borealis* may be regarded as assemblages of cohorts composed by a mixtures of genotypes predetermining the phenotypes either to develop directly into females (PF) or to protandric shrimp changing sex at different sizes/ages. Hypothetically the occurrence of the protandric genotypes in each age group (cohort) may show a modal distribution with a dominance of individuals changing sex at an age when a total length of 110-120 mm (CPL. 20-22 mm) has been reached (Rasmussen 1953; V; VI). This size was in Gullmarsfjorden reached at the aproximative age of three years. In Gullmarsfjorden, along with the majority of shrimps which were females at an age of 3-4 years (transitionals at an approximate age of 3 years), were always low proportions of younger shrimp that were females irrespective of variations in age/size structure,

mortality, sex frequency or growth. The 1-2 year females were most likely composed of shrimp that went through the transitional stage at ca. 1 year of age plus primary females (PF), while the 2-3 year old shrimp had been transitionals at ca. 2 years of age.

In shrimp populations, combinations of different age/size groups make up the observed age/size structure. In populations dominated by genotypes predisposing for protandric hermaphroditism, sex ratio is a function of mortality. In such populations females always occur in lower proportion than males (Shumway et al. 1985).

How would natural selection work to maintain the suggested hypothetical mixture of genotypes? Generally in populations with a biased sex ratios, individuals of the scarcer sex have the higher probability of getting mated and thus propagating its genotype (e.g. Fisher 1930). Thus in the case of *P. borealis* all females, irrespective if they younger/smaller (PF and EMF) or older/larger are likely to get mated. However females of different sizes are not equally fecund. Fecundity in shrimps is proportional to the cube of the body length in female shrimp (Shumway et al. 1985). Thus the larger female shrimps give rise to more off-spring than the smaller ones because they are capable of carrying more eggs attached to their pleopods. It seems possible that this fecundity difference between females contribute to maintain sex change at larger size/higher age. Moreover these larger females may have already propagated their genome during previous breeding seasons as males, thus further increasing the frequency of their genome. This hypothesis would, however, not exclude the existence of low proportions of genotypes predisposing the phenotypes to be either PF or EMF in the population, because they belong to the favoured sexual stage. If, for example, mortality dramatically increased, PF and EMF would be favoured disproportionately because mortality would lower the frequency of protandric shrimp changing sex at the average larger size/higher age. If on the other hand mortality decreased PF and EMF would still be selected for because of the biased sex-ratio, but to a much lower extent.

How would variations in life span affect this mixture of genotypes? Charnov (1979 and 1982) using biogeographic patterns in the length of time spent as a male, showed that with increasing latitude the length of time spent as male increased. In shrimp populations at the northern end of its distribution, life span is typically longer and growth slower than in the southern part of the species' distribution (e.g. Shumway et al 1985). Charnov (1979 and 1982) explained this cline in time spent in the male phase with sex allocation theory by suggesting that individual shrimps alter the age of sex change in response to the length of life span (mortality and growth rate) which varies with latitude.

Alternatively, the observed gradient in time spent in the male phase may be explained by natural selection working on mixtures of genotypes predisposing for sex change at different sizes/ages. It seems possible that different combinations of mortality, recruitment, and growth in different parts of the shrimps distributional area may favour the genotypes differently. In Arctic shrimp populations where growth rates are reported to be low and life spans long, smaller female shrimps are rarely or never found (e.g. Shumway et al. 1985). In southern populations, however, e.g. North Sea (Allen, 1953) and British Columbia (Butler, 1964), where life spans are shorter and mortality and growth rates higher, primary and early maturing females are often found. In populations in between, such as in Gullmarsfjorden (this paper), along the coast of southern Norway (Rasmussen 1953) or in the Gulf of Maine (Haynes and Wigley 1965) all types occur intermittently.

Against this background it seems possible that natural selection at higher latitudes may select against PF and EMF with longer time spent in the male phase. In lower latitudes, by contrast, natural selection seems to work in the opposite direction. However, because the Northern shrimp and its protandric congeners are oceanic organisms with planktonic larvae and because post larval shrimps are reported to perform substantial migrations (Shumway et al. 1985), genetic exchange between different populations through larval drift and adult migration may be substantial. Such movements may replenish genotypes which are suboptimal in a given locality but might have been better adapted to conditions in their locality of origin.

Although it seems that some of the variations in age at sex change and the occurrence of primary females in populations of pandalid shrimps may be explained by the above mentioned reasoning, this hypothesis should of course be stated in quantitative terms to facilitate tests before any conclusions regarding ultimate mechanisms behind sex change in protandric pandalid shrimp can be drawn. Besides such work there is also a great need for experimental, behavioural and genetical studies in order to better understand the mating behaviour and cytological mechanisms behind sex determination in protandric pandalid shrimp.

ACKNOWLEDGEMENTS

First of all I would like to thank my family, Barbro, Petter and Maja for putting up with the hardships of thesis writing; without their understanding, tolerance and affection this thesis would not have seen the light of day.

The *Pandalus* project has since 1984 been supported by Kristineberg Marine Biological station, The Royal Swedish Academy of Sciences. In 1988 some funding from the Swedish Natural Science Research Council as well as from the County Board of Nature Conservancy in Gothenburg was received. Since 1990 financial support has been received from the Faculty for Mathematics and Natural sciences and the Marine Research Centre, University of Göteborg.

My supervisor J. -O. Strömberg has put the practical means and opportunities for this study at my disposal and in addition, trusted in my ability to navigate on my own in the perilous waters of population ecology. For this I am deeply grateful.

I'm also indebted to Malte Andersson, Ric Charnov, Bengt Sjöstrand and J. -O. Strömberg for constructive advice. I may not always have agreed but I always learned in the process.

Mikael Andersson, Ziad Thaib and Bernt Wennberg, the Gothenburg Center for Applied Mathematics, Chalmers University of Technology not only gave invaluable help with the growth model and general statistical advice throughout the study but also enthusiastically participated in discussions about shrimp ecology.

My colleagues at the Kristineberg Marine Biological Station has provided an interesting work atmosphere throughout the study period. Odd Lindahl generously provided me with hydrographical data and Ib Svane gave constructive criticism on some of the manuscripts.

Krister Green, Berne Pettersson and Sylve Robertsson, gave expert help with the trawling irrespective of weather or season.

The Institute of Marine Research in Lysekil gave technical assistance through A. -M. Bratt, Y. Ericsson and J.-O. Pettersson.

Finally many thanks are due to Robert A. Brown for giving linguistic advice.

REFERENCES

- Allen, J. A. 1959. On the biology of *Pandalus borealis* (Krøyer), with reference to a population of the Northumberland coast. J. Mar. Biol. Assoc. U. K. 38:189-220.
- Barrington, E. J. W. 1967. Invertebrate structure and function. Thomas Nelson and Sons LTD. London. Pp. 549.
- Bergström, B. I. 1989. Preliminary results on growth and age determination of *Pandalus borealis* (Krøyer) in periodically enclosed fjord populations. Nafo SCR Doc. 89/ Serial No N1690.
- Bergström, B. I. 1991 a. Yearly immigration of Northern shrimp *Pandalus borealis* (Krøyer) into periodically isolated fjord populations. Sarsia 76: 133-140

- Bergström, B. I. 1991 b. Reproductive cycle and the effect of temperature on oogenesis of *Pandalus borealis* (Krøyer). J. Shellfish. Res., Vol. 10, (2) 327-331.
- Berkely, A. A. 1930. The post-embryonic development of the common pandalids of British Columbia. Contrib. Can. Biol. N.S. 6:79-163.
- Bertalanffy, L. von (1938). A quantitative theory of organic growth. Hum. Biol., 10(2): 181-213.
- Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food.U. K. (Series 2), No. 19: 533 pp.
- Brattegard, T. 1980. Why biologists are interested in fjords. In: Freeland, H J, D.M Farmerand C D Leving, (eds.) Fjord oceanography pp. 53-67. Plenum Press, New York and London.
- Butler, T. H. 1964. Growth, reproduction, and distribution of pandalid in British Columbia. J. Fish. Res. Board Can. 21: 1403-1452.
- Carlisle. D. M. 1959a. On the sexual biology of *Pandalus borealis* (Crustacea Decapoda). I. Histology of incretory elements. J. Mar. Biol. Assoc. U. K. 38: 381-394.
- Carlisle. D. M. 1959b. On the sexual biology of *Pandalus borealis* (Crustacea Decapoda). II. The termination of the male phase. J. Mar. Assoc. U.K. 38: 481-489.
- Carlisle. D. M. 1959c. On the sexual biology of *Pandalus borealis* (Crustacea Decapoda). III. The initiation of the female phase.J. Mar. Assoc. U.K. 38: 493-506.
- Charnov, E. L. 1979. Natural selection and sex change in pandalid shrimp: Test of a life history theory. Amer. Natur. 113:515-734.
- Charnov, E. L. 1981. Sex reversal in *Pandalus borealis* : effect of a shrimp fishery? Mar. Biol. Letters 2: 53-57.
- Charnov, E. L. 1982. The theory of Sex Allocation -Princeton University Press, Princeton, New Jersey. 355 pp.
- Charnov, E. L. and B. I. Bergström. 1987. Alternative life histories in sex changing shrimp: a phenotype limited ESS. Evol. Ecol. 1: 107-111.
- Charnov, E. L. and P. J. Andersson. 1989. Sex change and population fluctuations in pandalid shrimp. Amer. Natur 134, 824-827.
- Charnov, E. L. and J. J. Bull. 1977. When is sex environmentally determined? Nature 266: 828-830.
- Charnov, E. L., D. Gotschall. and J. Robinson. 1978. Sex ratio: adaptive response to population fluctuations in Pandalid shrimp. Science 200: 204-206.
- Darwin, C. 1871. The descent of man , and selection in relation to sex. John Murray, London
- Fisher, R. A. 1930. The Genetical Theory of Natural Selection. Oxford Universty Press. 291pp.

- Frechette, J., and D. G. Parsons. 1983. Report of shrimp ageing workshop held at Ste.Foy, Quebec, in May and at Dartmouth, Nova Scotia, in November 1981. NAFO Sci. Counc. Stud. 6: 79-100.
- Gade, M. G. and A. Edwards. 1980. Deep-water renewal in fjords.-Pp.453-489 in: Freeland, H J, D.M Farmerand C D Leving, (eds) Fjord oceanography . Plenum Press, New York and London.
- Gallucci, V. F. and T. J. Quinn. 1979. Reparameterizing, fitting, and testing a simple growth model. Trans. Am. Fish Soc., 108:14-25.
- Ghiselin, M. T. 1969. The evolution of hermaphroditism among animals. Q. Rev. Biol. 44: 189-208.
- Gulland, J. A. 1985. Fish stock Assessment: A Manual of Basic Methods - FAO/Wiley series on Food and Agriculture 1. John Wiley and Sons. 223 pp.
- Haynes, E. B. and R. L. Wigley. 1969. Biology of the northern shrimp, *Pandalus borealis*, in the Gulf of Maine. Trans. Am. Fish. Soc. 98:60-76.
- Hjort, J., and J. T. Ruud. 1938. Deep-sea prawn fisheries and their problems. Hvalr. skr. 17:1-144.
- Hopkins, C. C. E and E. M. Nilssen. 1990. Population biology of the deep water prawn (*Pandalus borealis*) in Balsfjord, northern Norway: I. Abundance, mortality and growth, 1979-1983. J. Cons. int. Explor. Mer 47: 148-166.
- Jägersten, G. 1936. Über die Geschlechtsverhältnisse und das Wachstum bei *Pandalus*. - Ark. Zool. 28A (20): 1-27.
- Krebs, J. R. and N. B. Davies. 1982. Behavioural Ecology an evolutionary approach Blackwell, London. 494 pp.
- Lindahl, O. and L.Hemroth. 1988. Large scale and long-term variations in the zooplankton community of the Gullmarfjord, Sweden, in relation to advective processes. Mar. Ecol.Prog. Ser. 43: 161-171.
- Lindahl, O. and R. Perissinotto. 1987. Short-term variations in the zooplankton community of the Gullmarfjord, Sweden related to water exchange processes. J. Plankt. Res. 9:1113-1132.
- Macdonald, P. D. M. 1987. Analysis of length- frequency distributions. In R.C. Summerfelt and G.E. Hall (eds), Age and Growth of Fish, Iowa State University Press, Ames, Iowa. 371-384.
- Macdonald, P. D. M. and T. J. Pitcher. 1979. Age-groups from size-frequency data: a versatile and efficient method of analysing distribution mixtures. J. Fish. Res. Board Can. 36: 987-1001.
- Maynard Smith, J. 1978. The evolution of Sex. Cambridge University Press.
- Nilssen, E. M. and C. C. E. Hopkins. 1986. Biological variation between and within populations of the deep-water prawn *Pandalus borealis* in two north Norwegian fjords. International

Council for the Exploration of the Sea. Shellfish Committee, CM 1986/K:15.

Nilssen, E. M., R. B. Larsen and C. C. E. Hopkins. 1986. Catch and size -selection of *Pandalus borealis* in a bottom trawl and implications for population dynamics analyses. International Council for the Exploration of the Sea. Shellfish Committee, CM 1986/K:4.

Parker, G.A., R.R. Baker and V.G.F. Smith. 1972. The origin and evolution of gamete dimorphism and the male female phenomenon. J.Theor. Biol. Biol. 36: 529-553.

Parsons, D. G. 1989. Report of the Working Group on Progress in Age Determination of *Pandalus* . Northwest Atlantic Fisheries Organisation (NAFO), SCS Doc. 89/22. Serial No. N 1700.

Parsons, D. G., V. L. Mercer and P. J. Veitch. 1989. Comparison of the growth of Northern shrimp (*Pandalus borealis*) from four regions of the Northwest Atlantic. J. Northw. Atl. Fish. Sci., Vol. 9: 123-131.

Pauly, D and G. Gaschutz. 1978. A simple method of fitting oscillating length growth data with a programme for pocket calculations. ICES Doc. C. M. 1979/G. 24 (mimeo.).

Pianka, E. R. 1978. Evolutionary Ecology. Harper and Row, New York. 397 pp.

Popper, K. R. 1980. The Logic of scientific discovery. Hutchinson. 479 pp.

Rasmussen, B. 1953. On the geographical variation in growth and sexual development of the deep sea prawn (*Pandalus borealis* Kr). Report on Norw. Fish. and .Mar. Invest. 10 (3):1-160.

Sokal, R. R. and F. J. Rohlf 1969. Biometri. W. H. Freeman and Co., San Fransisco, California, 776 pp

Shumway, S.E., H. C. Perkins, D. F. Schick, and A. P. Stickney. 1985. Synopsis of Biological Data of the Pink Shrimp *Pandalus borealis* (Krøyer, 1838). NOAA Technical Report NMFS 30 (FAO Fisheries Synopsis No. 144), 57 pp.

Stickney, A. P. and H. C. Perkins. 1977. Environmental physiology of commercial shrimp, *Pandalus borealis*. Project 3-202-R Completion Report, February 1, 1974 to January 31, 1977, Dep. Mar. Resour., W. Boothbay Harbor, Maine, 78 p.

Stickney, A. P. and H. C. Perkins. 1980. Environmental physiology of northern shrimp (*Pandalus borealis*). Completion report (revised), Project #3-324-R, Dept. Mar. Resour., W. Boothbay Harbour, Maine, 47 p.

Stickney, A. P. and H. C. Perkins. 1981. Observations on the food of the larvae of the northern shrimp, *Pandalus borealis* Krøyer (Decapoda, Caridea). Crustaceana 40: 36-49.

Svanson, A . 1975. Physical and chemical oceanography of the Skagerrak and the Kattegat. Fisheries Board of Sweden, Institute of Marine Research rep. No. 1.

Theisen, B. 1973. The growth of *Mytilus edulis* L.(Bivalvia) from Disco and Thule district, Greenland. Ophelia 12: 59-77.

Warner, R. R. 1975. The adaptive significance of sequential hermaphroditism in animals. Amer. Natur. 109: 61-82.

Wienberg, R. 1981. On the food and feeding habits of *Pandalus borealis* Krøyer 1838. Arch. Fischerei wiss. 31: 123-137.

Yamaguchi, M. 1975. Estimating growth parameters from growth rate data. Oecologia (Berlin) 20: 321-332.

På grund av upphovsrättsliga skäl kan vissa ingående delarbeten ej publiceras här.
För en fullständig lista av ingående delarbeten, se avhandlingens början.

Due to copyright law limitations, certain papers may not be published here.
For a complete list of papers, see the beginning of the dissertation.



