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# The effect of food on the determination of sex ratio in *Calanus* spp.: evidence from experimental studies and field data

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The effect of food concentration on the sex ratio in *Calanus* spp. has been investigated in laboratory and mesocosm experiments. The results of the experiments are compared with time series in the field and with physiological rates. The food concentration and quality had an effect on the sex ratio of adult *Calanus*, with higher percentages of males obtained with increased food concentration. Laboratory experiments and field time series suggest that sex can still change at stage CIII–CIV, but is determined at stage CV. The energy budget of males was very unbalanced, suggesting that the shorter lifespan often reported could be due to exhaustion of lipid stores.

Key words: *Calanus* spp., copepods, sex ratio.

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## Introduction

“Of 137 adults produced in the laboratory, only one was a male” (Peterson, 1986). Such a skewed sex ratio is a common finding for planktologists culturing copepods of the genus *Calanus* (Conover, 1965; Mullin and Brooks, 1970; Hirche, 1980; Corkett *et al.*, 1984; Peterson, 1986). This is an extreme reflection of the situation in an environment where there are important fluctuations in the percentage of males, although females are generally more abundant (Marshall *et al.*, 1934; Mednikov, 1961; Tande and Hopkins 1981; Sameoto and Herman, 1990; Kouwenberg, 1993; Osgood and Frost, 1994; Svensen and Tande, 1999). For sexually reproducing animals, if the sex ratio is skewed, belonging to the minority sex would present such an advantage in terms of gene transmission that natural selection

would greatly favour mechanisms producing the less abundant sex. In fact, the pressure to produce offspring of the less abundant sex would start to act as soon as the sex ratio is unequal. Therefore, for sexually reproducing animals, a sex ratio of 1:1 is expected (Fisher, 1930). Deviation from that rule is unusual and requires explanation. Based on female dimorphism, Fleminger (1985) suggested a possible sex change from genotypic CV males to adult females. However no direct evidence of this has been found (Svensen and Tande, 1999).

In addition to a possible sex change, several authors have indicated that the environment may influence the sex ratio in copepods through such factors as nutrition, population density, and salinity (Takeda, 1950; Mednikov, 1961; Katona, 1970; Paffenhöfer, 1970; Alcaraz and Wagensberg, 1978; Grigg *et al.*, 1981; Hopkins, 1982).

In this work we combine the results of a series of experiments done as part of the Trans-Atlantic Study of *Calanus finmarchicus* programme with results from the literature to try to elucidate the factors influencing sex ratio in the genus *Calanus*.

## Materials and methods

### Experiments

Sex ratios were obtained from three types of experiments: mesocosms, 100-l tanks and 5-l beakers. The quantity and quality of the food were manipulated in each in different ways.

Mesocosm experiments were conducted in Bergen (western Norway) during spring 1997. Details of the mesocosm experiments can be found in Hygum *et al.* (2000). Briefly, 18.5 m<sup>3</sup> enclosures were filled with 50- $\mu$ m screened seawater enriched with different nutrient levels. Eggs were obtained from *Calanus* females in the fjord and allowed to hatch before being transferred to mesocosms. The development of the cohort was followed and the stages identified. Two mesocosms were used per treatment. The temperature during the study ranged from 6.3 to 8.3°C.

In four additional mesocosm experiments performed in Tromsø in spring 1998 (BWH, unpublished results), the four mesocosms were maintained at high food concentrations, but for a longer period with daily samples for the adult stages. The cohorts in two of the mesocosms originated from eggs produced by female *Calanus* from Bergen, but in the other two mesocosms the cohorts originated from eggs produced by females from Tromsø. The temperature during the study ranged from 3.7 to 10.3°C.

Two 100-l tank experiments were conducted, one tank per treatment, during spring 1998. In the first experiment, recently hatched *C. helgolandicus* nauplii were grown with three different algal diets at saturating concentrations (>200  $\mu$ g C l<sup>-1</sup>). The algae used represented the major groups in the ocean (flagellates, dinoflagellates, and diatoms), namely *Isochrysis galbana*, *Prorocentrum micans*, and *Thalassiosira weissflogii*. In the second experiment, *C. helgolandicus* was grown at two food concentrations, 50 (100  $\mu$ g C l<sup>-1</sup>) and 200 cells ml<sup>-1</sup> (500  $\mu$ g C l<sup>-1</sup>) of *P. micans*. Samples were collected daily and the sex ratio was recorded. All the tank experiments were conducted at 15°C.

Two types of experiment were also carried out in 5-l beakers during spring 1999. In the first, a cohort of *C. helgolandicus* was raised from egg to adult at different food concentrations (*P. micans*, 50, 100, 150, 200, 300 cells ml<sup>-1</sup>). The initial number of eggs in each beaker was about 100, and three replicates were performed per treatment. The mortality in those experiments was high (50%) and the sex ratios obtained are based on 40–50

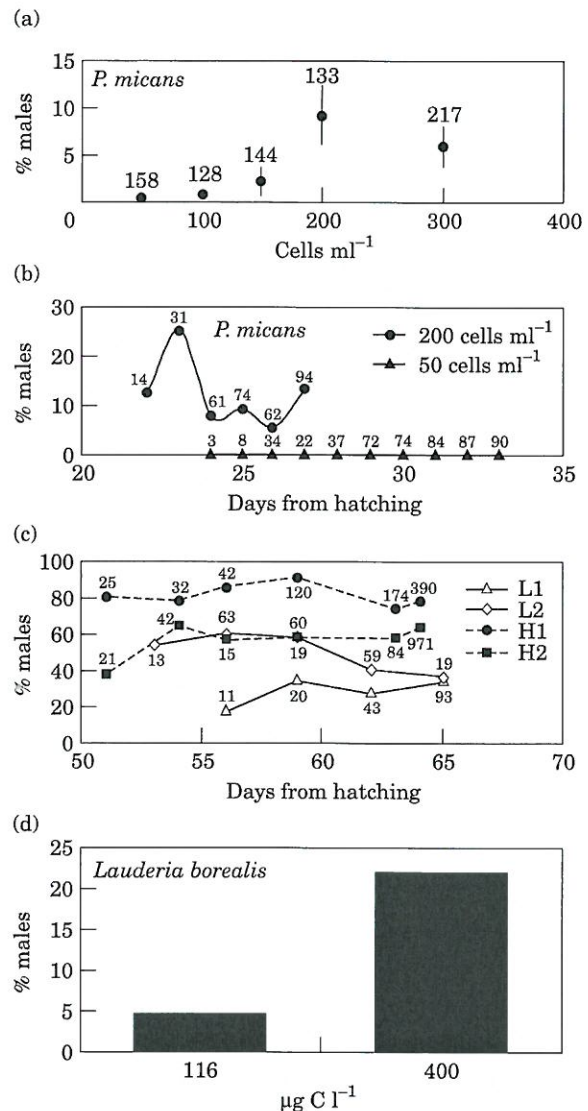


Figure 1. Influence of food concentration on the percentage of male *Calanus* for animals raised from egg to adult: (a) *C. helgolandicus* in 5-l beakers (error bars indicate the standard error of the average from the three replicates), (b) *C. helgolandicus* in 100-l tanks, (c) *C. finmarchicus* in mesocosms (Bergen, 27 April to 12 May 1997), (d) *C. pacificus* (modified from Paffenhöfer, 1970). The numbers in (a), (b), and (c) indicate the total number of animals counted to determine the sex ratio.

individuals per replicate or total counts of about 150 individuals (Figure 1). In the second experiment, different development stages (CIII, CIV, and CV) were collected from a station in the English Channel and grown at two different concentrations of *P. micans* (50 and 300 cells ml<sup>-1</sup>) in the laboratory until they reached the adult stage. Two replicates with 20 individuals per beaker were used in this experiment. The mortality being in the range of 1–4 individuals per beaker, the sex ratios

presented in Figure 3 are based on total counts of 70–80 individuals. All the 5-l beaker experiments were conducted at 15°C.

Some additional data on the effect of food concentration and quality on the sex ratio were obtained from Paffenhöfer (1970).

#### Time series

Data on seasonal variations in the sex ratio of *Calanus* sp., chlorophyll *a* and female abundance in different locations were collected from different sources:

- TASC database: time series in 1997 and occasionally 1998 for Murchison platform (North Sea), Iceland, Faroe, and Saltfjord (Norway).
- US GLOBEC Georges Bank program database: data on the sex ratio and female abundance 1995–1996 on the Georges Bank and in the Gulf of Maine.
- Station L4: data on sex ratio, chlorophyll *a* and female abundance were collected weekly from 1996 to 1997.
- Literature data: data from the literature were collected for the Norwegian Sea (Østvedt, 1955), the Clyde (Nicholls, 1933), and Loch Striven (Marshall *et al.*, 1934).

#### Physiological data

*Physiological data were collected from different sources:*

- Lipid storage: C:N ratios for CV, adult males, and adult females were measured in the mesocosm experiments. Details can be found in Hygum *et al.* (2000). Additional data were obtained from the literature (Marshall *et al.*, 1934).
- Respiration: respiration data for CV, adult males, and adult females were obtained from Marshall *et al.* (1935).
- Feeding: gut fluorescence for males and females was measured in the Norwegian Sea in March and April 1997. Details of the procedures can be found in Irigoien *et al.* (1998).

## Results

### Food concentration and quality

When the animals are grown from nauplius or egg to adult, the food concentration appears to affect the percentage of males at adulthood (Figure 1). When raised at low concentration of *P. micans* [Figure 1(a)] there were no males, whereas the highest percentages of males were found in the mesocosms with the greater food concentrations [Figure 1(c)]. However, the final sex ratios from the mesocosms have to be considered cautiously because the experiments were terminated when a high percentage of the population (72% in L1, 83% in L2, 74% in H1, and 39% in H2) was still at stage CV.

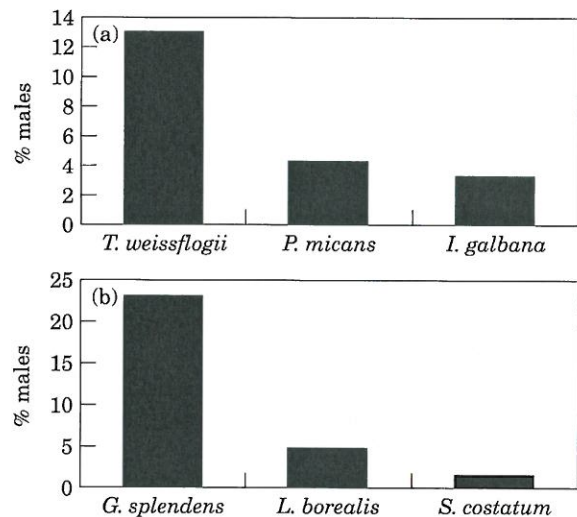


Figure 2. Influence of food type on the percentage of male *Calanus* in animals raised from egg to adults: (a) *C. helgolandicus* in 100-l tanks, (b) *C. helgolandicus* (modified from Paffenhöfer, 1970).

For animals grown from egg or nauplius to adult with different phytoplankton species, there also seem to be important differences in the percentage of males, depending on the food source (Figure 2).

When animals collected from the field (Stn L4, English Channel) were raised at different food concentrations from CV copepodite stage to adult, there were no differences in the final percentage of males between the two food concentrations [Figure 3(a)]. The final sex ratio was similar to that found in the environment for the corresponding period. When raised from stage CIV to adult most of the animals obtained in both high and low food concentration were females [Figure 3(b)], and when raised from CII–CIII to adult, all animals in both treatments were female [Figure 3(c)]. In the field (Stn L4) for the corresponding period, adult males constituted some 20–30% of the adult population [Figure 5(c)].

In the four high-food-concentration mesocosm experiments in 1998, males were present for a period longer than 30 d. By the end of the experiment, stage CV represented on average 39% of the population for the cohort that originated in Bergen and 49% for the cohort that originated in Tromsø. The percentage of males (males/all adults) oscillated but consistently remained around 50%. The total percentage of males by the end of the experiment (total males sampled on the different days/total adults sampled on the different days) ranged from 51.6 to 59.7% (Figure 4).

#### Time series

With slight variation, most of the coastal time series show a general pattern: the percentage of males is at its

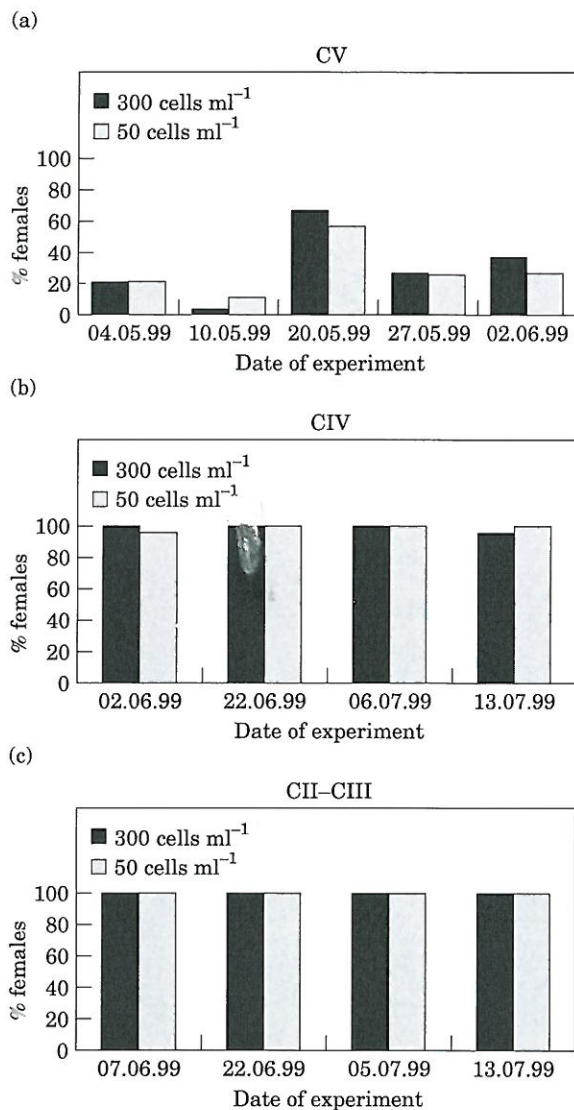


Figure 3. Influence of food concentration (*P. micans*) on the percentage of female *Calanus helgolandicus* for animals raised in 5-l beakers from (a) CV to adult, (b) CIV to adult, (c) CII-CIII to adult for animals collected from the field in the English Channel. Note that, for purposes of presentation, this figure represents the sex ratio as the percentage of females.

maximum before the maximum abundance of females, coinciding in general with the development of the spring phytoplankton bloom [e.g. Figures 5(a), (c), 8, 9(c)]. The oceanic stations, such as Weathership M, showed a slightly different picture, CV arriving at the surface and moulting to adults before the spring bloom (Figure 7). However, also in that case the highest percentage of males was earlier than the peak of females, both in the case of ascending animals and in the first cohort. It is noteworthy that, at the stations where *C. finmarchicus* and *C. helgolandicus*, or *C. finmarchicus* and

*C. hyperboreus* co-occurred, such as Murchison and Weathership M, the general trend in sex ratio seemed to be the same (Figures 7, 8).

### Physiology

In terms of lipid storage, both the C:N data from the mesocosm studies and the percentage of fat calculated by Marshall *et al.* (1934) show that males generally have a lipid storage level intermediate between CV and females [Figure 10(a), (b)].

Turning to respiration and the literature data, males appear to have the fastest rates of respiration, followed by females, and CV the lowest values [Figure 10(c)]. If it is assumed that 1 ml of oxygen is equivalent to 0.52 mg of carbon (Omori and Ikeda, 1984), the average carbon requirements would be 4650 ng C male<sup>-1</sup> d<sup>-1</sup>, 3785 ng C female<sup>-1</sup> d<sup>-1</sup> and 2740 ng C CV<sup>-1</sup> d<sup>-1</sup>.

On the subject of feeding, the gut fluorescence measured for male *C. finmarchicus* at Weathership M during spring 1997 is on average 15% of that of females [Figure 10(d)]. If we assume the same gut clearance rate and a C:chlorophyll ratio of 50, it implies an ingestion of 174 ng C male<sup>-1</sup> d<sup>-1</sup>. This represents only 3.7% of the respiration carbon requirements previously estimated.

### Discussion

The results presented here support the hypothesis suggested previously, that the quality and concentration of food during growth affects the sex ratio of adult *Calanus* (Mednikov, 1961; Paffenhöfer, 1970). Other environmental factors, such as turbulence (Alcaraz *et al.*, 1988), pressure (Vaquier and Belser, 1965), salinity (Katona, 1970), temperature (Monakov, 1965), population density (Alcaraz and Wagensberg, 1978), and parasitism (Cattley, 1948) may also correlate with variations of the sex ratio in copepods. All these factors present the common characteristic of being able to modify the development rate directly or indirectly. Takeda (1950), using different chemicals at different stages of *Tigriopus japonicus*, showed that a "substance or conditions which accelerate development in the latter part of the Nauplius VI stage induce masculinization, while those which decrease it induce feminization". Here we suggest that this is a common factor for all copepods, individuals developing rapidly through certain key stages will tend to become males, whereas those developing slowly would be females. This would explain not only the effect of factors such as food concentration, food quality, or physical parameters that could affect the growth with respect to an optimum, but also the effect of factors having an indirect influence, such as population density, by increasing competition for resources, or turbulence, which is known to decrease the gross growth efficiency (Saiz *et al.*, 1992; Alcaraz, 1997).

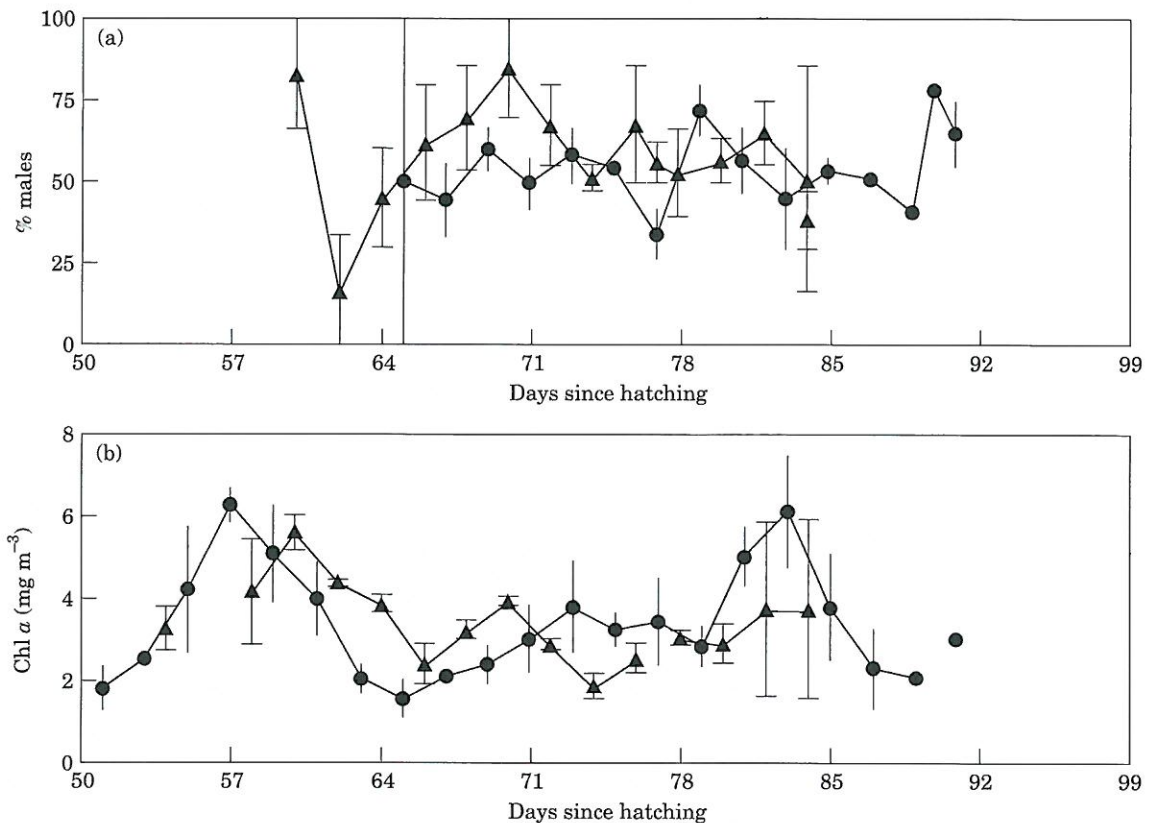


Figure 4. Percentage of males in *Calanus* raised from egg to adult in mesocosms with a high concentration of food (Tromsø 15 May to 30 June 1998): (a) sex ratio, (b) chlorophyll *a* concentration. Dots indicate the average of the cohorts originating in Bergen and triangles the average of the cohorts originating in Tromsø. Vertical bars indicate s.e. of the average.

The field data concur with other published series for *Calanus* species (Tande and Hopkins, 1981; Sameoto and Herman., 1990; Osgood and Frost, 1994; Svensen and Tande, 1999). They seem to support the same hypothesis, with the highest percentages of males appearing during the periods of fast growth of the cohort, usually coinciding with phytoplankton blooms.

However, at oceanic stations such as Weathership M and south of Iceland, the CV copepodites coming to the surface after overwintering produce adults with a large percentage of males, during a period when the food resources are scarce (Irigoiien *et al.*, 1998). Also, Grigg and Bardwell (1982) observed CV copepodites moulting to adult males in the absence of food. Usually CV have large lipid stores that can explain why they develop into males in the absence of food, but those results can also be interpreted in the sense that the sex may change at an earlier stage than CV, in the previous spring/summer (Svensen and Tande, 1999). This hypothesis is supported by the experimental results, in which the sex ratio of adults was similar to that in the field, raising *Calanus* in the laboratory from CV to adult, though most animals are females when raised from CII to CIV.

The objective of our experiments was to increase the male/female ratio in the copepodites raised with greater food concentration from the younger stages. However, because the experiment was carried out in spring, when food resources in the field are abundant, it is possible that the young copepodites collected from the field and raised in the laboratory slowed their growth rate as a result of stress of capture and/or being grown in a small volume, or because the quality of a mono-specific diet may be poorer. The fact that most individuals raised from CIV become females suggests that the sex can still change at stage IV and not be completely determined until CV. That the sex ratio could already be biased towards females at CV (Tande and Hopkins, 1981) supports this idea. Woodhead and Riley (1959) suggested that males develop faster than females in the fourth and fifth stages. In view of the hypothesis posed above, this could be interpreted as showing that the individuals developing faster through CIV and CV become males. However, further research is necessary to confirm this, especially taking into account the fact that the gonads are undifferentiated until stage CV (Tande and Hopkins, 1981).

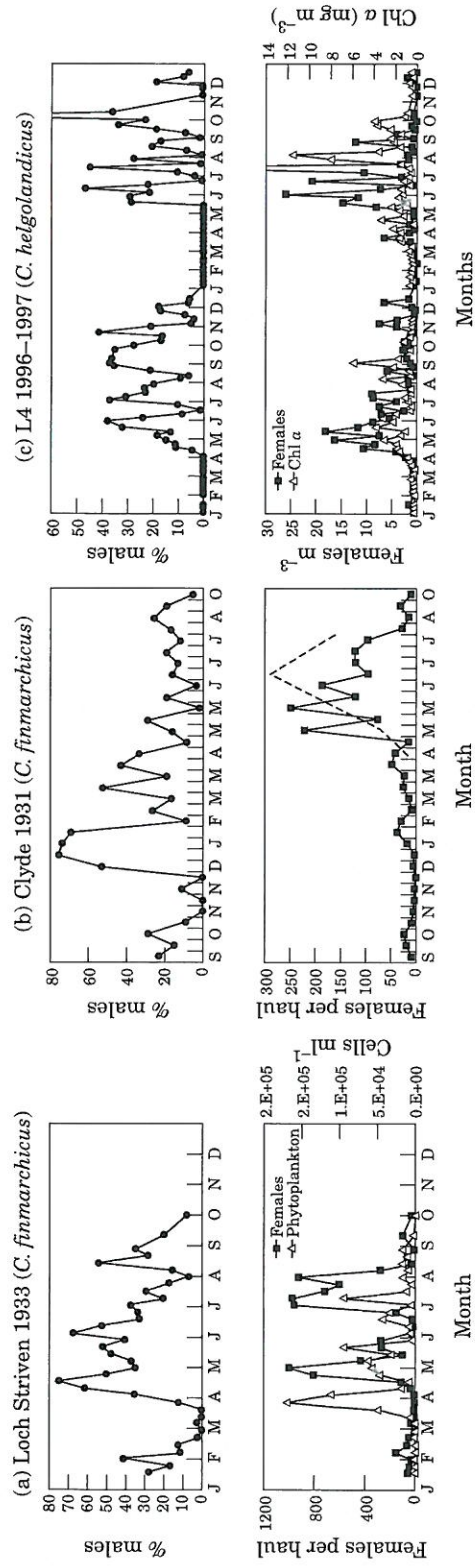


Figure 5. Annual variation in sex ratio at different stations and for different species of *Calanus*: (a) Loch Striven, Scotland (after Marshall *et al.*, 1934), (b) Clyde sea area, Scotland (after Nicholls, 1933), (c) Station L4, English Channel. The dashed line in (b) represents the approximate time of the bloom.



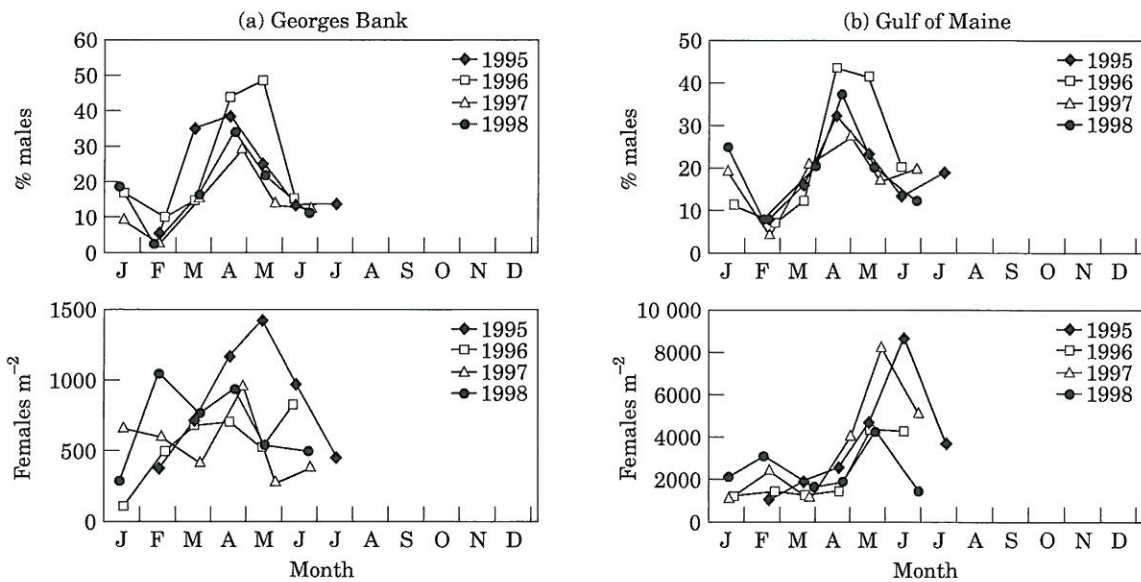


Figure 6. Annual variation in *Calanus finmarchicus* sex ratio (a) over the Georges Bank, (b) in the Gulf of Maine (both from the US GLOBEC database).

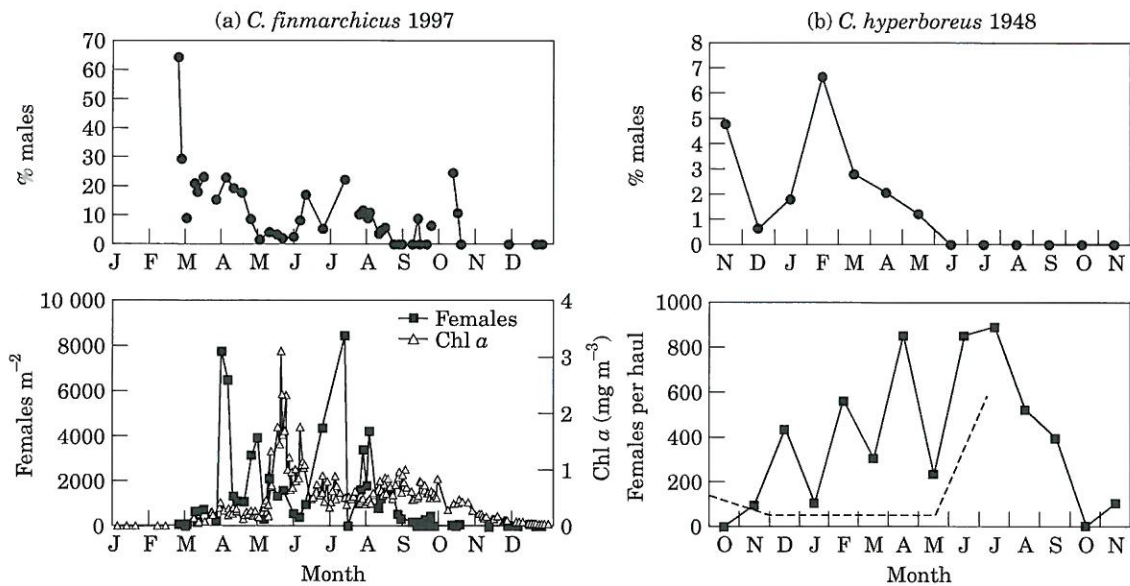


Figure 7. Annual variation in sex ratio at Weathership M in the Norwegian Sea in different years and for different species of *Calanus*: (a) *C. finmarchicus* in 1997 (from the TASC database), (b) *C. hyperboreus* in 1948 (after Østvedt, 1955). The dashed line in (b) represents the approximate time of the bloom.

Our survey of field data also confirms a general observation that males usually appear earlier than females and that they tend to disappear after the peak of abundance (Marshall *et al.*, 1934; Woodhead and Riley, 1959; Tande and Hopkins, 1981). However, this is not the case for *C. helgolandicus* in the English Channel (L4), where overwintering is not possible and all copepodite stages are present during the whole year (Green *et al.*, 1993).

In that case, the percentage of males only increases when phytoplankton is abundant, confirming a possible relationship between rates of development and sex.

In respect of overwintering, where moulting to adult is fuelled by lipids, the fact that male maturation precedes female maturation agrees with the hypothesis that individuals developing faster will become males. Nevertheless, the cause is likely to be differences in gonad

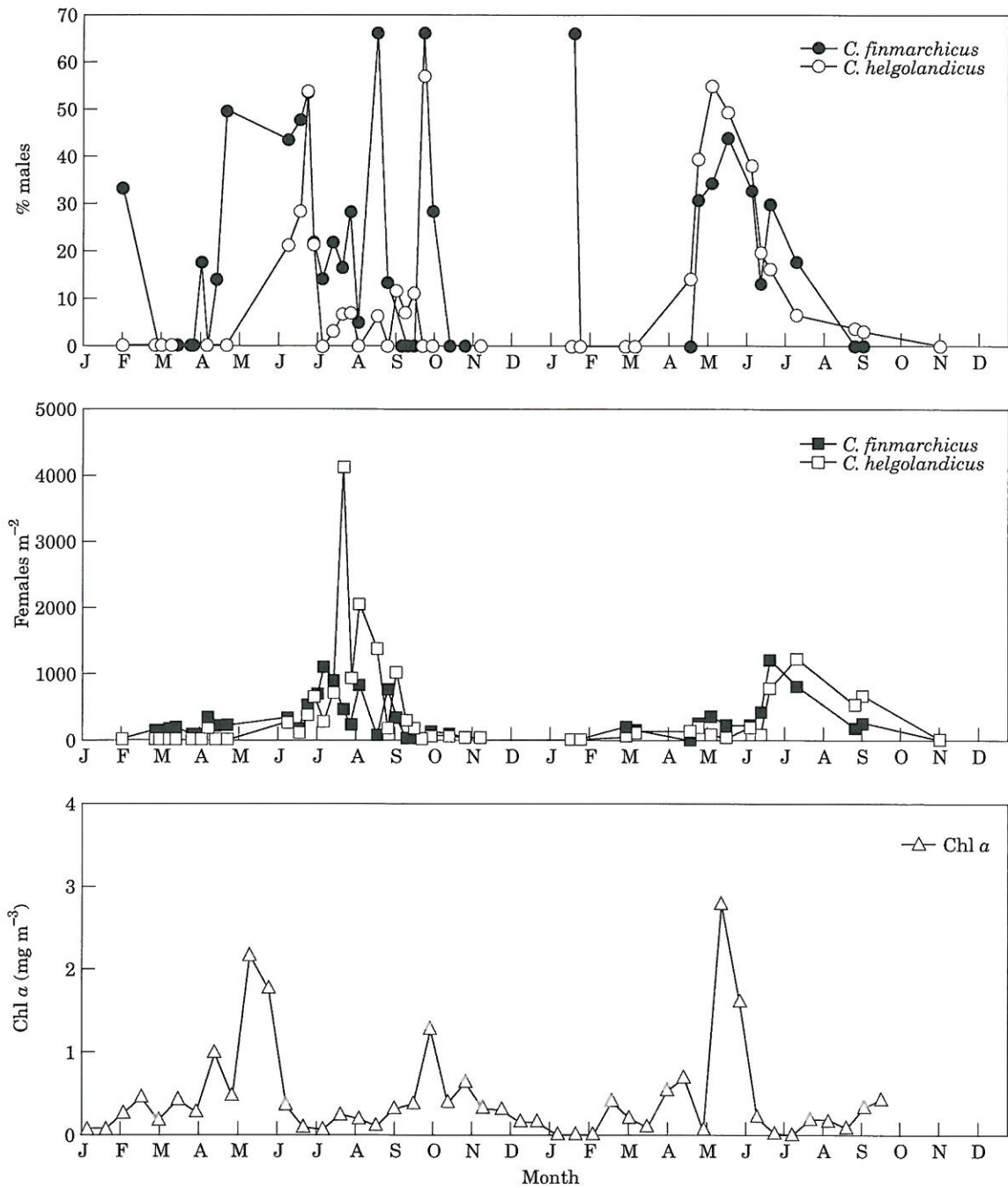


Figure 8. Annual variation in sex ratio and chlorophyll concentration at the Murchison Platform in the North Sea in 1997 and 1998 (from the TASC database).

development at stage CV (Tande and Hopkins, 1981). Niehoff and Hirche (1996) showed that early gonad maturation in female *C. finmarchicus* was fuelled by internal reserves. Considering that the extent of lipid storage in males is closer to that of CVs (Gatten *et al.*, 1980; this paper), it is likely that the passage

from CV to adult male is less energy-consuming and faster than for females (Tande and Hopkins, 1981).

A shorter lifespan of male *C. finmarchicus* has also been reported under laboratory conditions (Raymont and Gross, 1942), but Peterson (1986) reports male

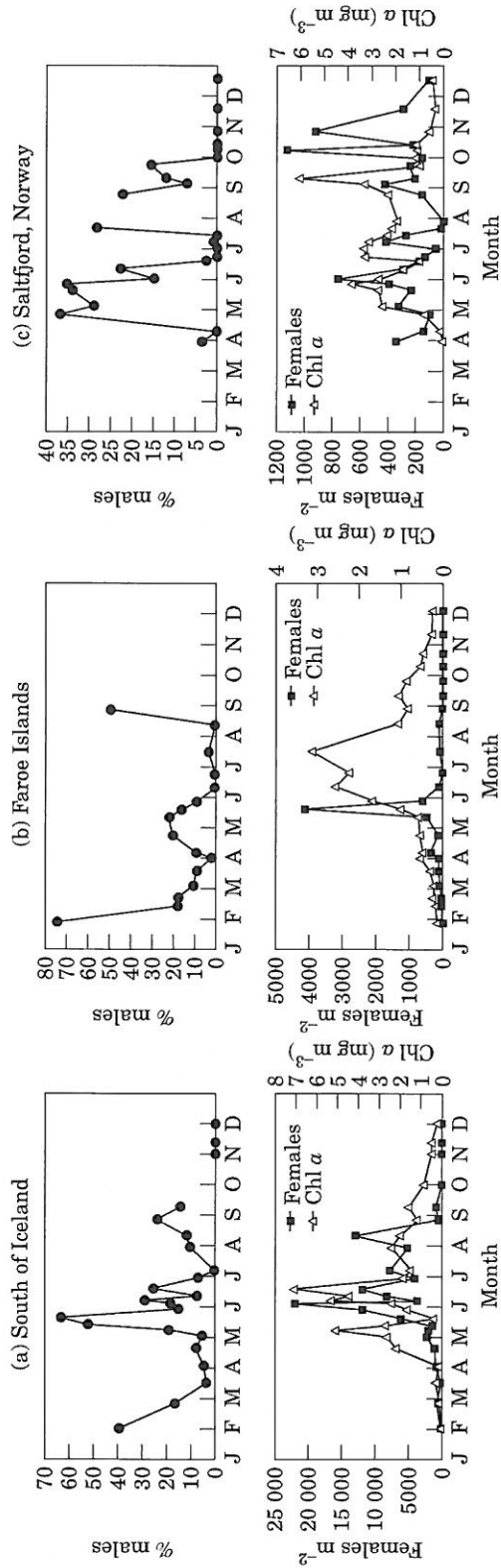


Figure 9. Annual variation in *Calanus finmarchicus* sex ratio and chlorophyll concentration in 1997: (a) south of Iceland, (b) off the Faroe Islands, (c) in Saltford, Norway (all from the TASC database).

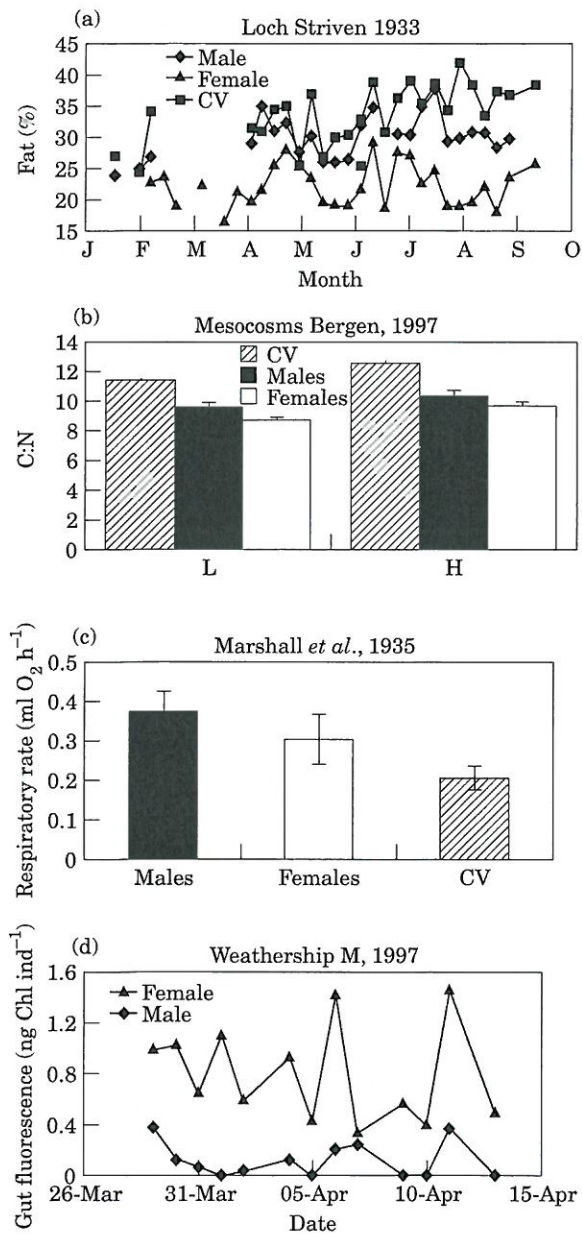


Figure 10. (a) Percentage of fat in stages CV, male and female *Calanus finmarchicus* in Loch Striven in 1933 (modified after Marshall *et al.*, 1934). (b) Average C:N for CV, male and female *C. finmarchicus* in mesocosm experiments (error bars indicate SE of the average). (c) Average respiration rates for CV, male, and female *C. finmarchicus* (modified after Marshall *et al.*, 1935). (d) Gut fluorescence of male and female *C. finmarchicus* at Weathership M, March/April 1997.

*C. marshallae* living as long as females. We are aware that the energy budget we have estimated here is only an approximation, with respiration and ingestion rates not derived from the same study, as well as the lack of accuracy of the gut fluorescence method in estimating

total ingestion. However, even if it is only an approximation, the male budget appears to be extremely unbalanced, with the male respiration rate being 20% higher than that of females and the male ingestion rate only 15% of that of females. Paffenhöfer (1971), in laboratory experiments, found the ingestion rate of *C. helgolandicus* males to be 20% of that of females. The same has also been reported for other copepods, such as *Temora longicornis* (Harris and Paffenhöfer, 1976), to the extent that, in some copepod species, the male loses its feeding appendages (Boxhall *et al.*, 1997). The strategy of the males seems to be to invest maximum energy looking for females to the detriment of time spent feeding. This concurs with the exclusively male behaviour of search, dance, and chase swimming described by Tsuda and Miller (1998) for *Calanus marshallae*, and with the observations of Doall *et al.* (1998) that male *Temora longicornis* swim faster and along more sinuous paths than females.

During the same study at Weathership M [Figure 10(d)], Irigoien *et al.* (1998) estimated that ingestion satisfies some 23% of a female's carbon requirements and also found that females were using stored lipids to sustain metabolism and egg production. Even if the males' lipid storage is initially higher, it is likely that, with such an unbalanced budget, males would die earlier because of faster exhaustion of the lipid stores during periods when food concentration is low. This statement is supported by the results of the mesocosm experiments performed at high concentration of food, without predation, and where (Figure 4) males consistently constituted around 50% of the adult population for periods longer than a month.

In addition to the energetic aspect of spending more time searching for females and less time eating, the increased activity and area covered will probably increase the risk of encountering predators (Tiselius and Jonsson, 1997) and contribute to greater mortality of males.

Copepods in general and *Calanus* in particular fulfil some of the conditions in which environmentally influenced sex determination can be expected (Charnov and Bull, 1977): the individual has little control over which environment it will experience, it lives in a patchy environment, and there is possible sex-specific mortality. Our results show that there is an environmental factor involved in sex determination of *Calanus*, and in some experiments males outnumbered females, suggesting complete environmental control over the sex ratio [Figure 1(c)]. However, in those experiments, a large percentage of the population did not moult to adult, so the sex ratios obtained cannot be considered as the final ratio for the population. In that sense the information obtained from the mesocosm experiments performed in Tromsø is more valuable, because a larger percentage of the population moulted to adult. The fact that, when

*Calanus* was raised in mesocosms at non-limiting food concentration and without predators, females constituted about 50% of the adult population suggests a genetic component in the sex determination (Figure 4). A certain capacity for environmental sexual determination has been observed in several genetically determined systems (Bull, 1983).

Grigg *et al.* (1985, 1987) showed that the frequency distribution of prosome length of CV and adult female *C. finmarchicus* and *C. helgolandicus* was bimodal, small CVs always moulting to females and larger ones to both males and females. In their data [Figure 2 of Grigg *et al.*, 1985; Figure 2(c) of Grigg *et al.*, 1987], the sex ratio for large individuals seems to be close to 1:1. A relatively similar mechanism has been described for the parasitic copepod *Pachypygus gibber*, which, in rich trophic environments, develops into typical males and typical females (no swimming), whereas development under poor trophic conditions results in an atypical male able to swim and to leave the host (Michaud *et al.*, 1999). We suggest, as an hypothesis for further research, that individual *Calanus* suffering growth-rate limitation will tend to mature as small females, whereas those developing at maximum growth rates will become males and large females, with a genetically determined sex ratio of 1:1.

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