

# Interannual variations in the population biology and productivity of *Thysanoessa spinifera* in Barkley Sound, Canada, with special reference to the 1992 and 1993 warm ocean years

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**ABSTRACT:** I monitored the population structure, abundance and growth, as well as the reproductive and production characteristics of *Thysanoessa spinifera* in Barkley Sound from March 1991 through March 1997. The years 1992 and 1993 were anomalously warm, 1992 due to an El Niño Southern Oscillation (ENSO). Summer upwelling was particularly strong in 1992 and downwelling in the winter of 1994–95. Mean annual larval (<10 mm) abundance was 2.4, 0.6, 0.4, 6.3 and 1.9 times greater in 1992 through 1996 respectively than in 1991. Adult abundance declined steadily since 1991 and in 1996 was about 0.14 of the pre-ENSO levels. Growth conditions, as indicated by the condition factor, varied seasonally but not interannually. There were no apparent interannual differences in length-at-maturity, sex ratio and spawning season length. I found no apparent relationship between parental and larval abundances. Indications are that the number of spawnings declined as of 1993. Mean annual larval biomass fluctuated. Biomass ranged between 0.19 (1994) and 6.9 (1996) times the 1991 value. Total production (growth + moult) was between 0.24 (1994) and 4.9 (1996) the 1991 value. Adult biomass and productivity fell continuously after 1991 and, in 1996, were about 0.13 of the pre-warm ocean years. Population *P:B* ratios fluctuated between 14.4 and 44.7, with the highest ratio in 1996.

**KEY WORDS:** *Thysanoessa spinifera* · Euphausiid · Population biology · Productivity · Ocean variability

## INTRODUCTION

Numerous studies describe the key role that euphausiids play in energy flow through marine systems. Pillar et al. (1992) describe a continuous presence of large quantities in the Benguela ecosystem and the importance of euphausiids to zooplanktivorous fish. They suggest that euphausiids possess several characteristics which contribute to their importance to the Benguela upwelling system. Euphausiids there are omnivorous and consequently can adapt to fluctuations in food availability. They are accessible to predators through the year because they are larger, live longer than mesoplankton and aggregate. Mauchline & Fisher (1969) state that euphausiids are amongst the

most abundant planktonic groups in the subarctic and boreal seas of the northeast Atlantic Ocean. Astthorsson (1990) comments on their importance as food for commercially exploited fish species in these waters. Kulka & Corey (1978) list studies which show that euphausiids are important prey for fish, bird and mammals in the northwest Atlantic and eastern Arctic. Euphausiids are also important to coastal marine ecosystems in the Pacific. Brodeur & Pearcy (1992) monitored fish diets in the coastal upwelling zone of Oregon and Washington, USA, over 4 summers. They found that euphausiids (*Euphausia pacifica*, *Thysanoessa spinifera*) dominated as prey in strong upwelling years. Ponomareva (1966) describes euphausiids as important prey for planktivorous fish and whales in the northwestern Pacific. Kock & Shimadzu (1994) state that within the 5 major groups of Antarctic high level consumers (seals, seabirds, cephalopods, fish and

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baleen whales), most species rely on krill (*E. superba*) as their diet at least in summer and during their breeding season. They warned that krill consumption estimates are biased because of uncertainty in estimates of predator abundance and consumption rates. Nevertheless, the integral importance of krill to the Southern Ocean is widely accepted.

Euphausiids are also an integral component of the coastal upwelling ecosystem along the southwest coast of Vancouver Island, Canada. This area has been studied by the Canadian Department of Fisheries and Oceans because it is highly productive for commercial fish species. The long-term study began in 1985. Its goal was to understand how interannual variations in ocean climate affect fish productivity, with special emphasis on Pacific herring *Clupea pallasii*. Results of diet analyses (Tanasichuk et al. 1991) indicate that euphausiids (*Thysanoessa spinifera*, *Euphausia pacifica*) account for 93 and 64 % of the daily ration for the dominant pelagic fish species, Pacific hake *Merluccius productus* and spiny dogfish *Squalus acanthias*, respectively. Adult Pacific herring feed exclusively on euphausiids. Mackas (1992) described the seasonal cycle of zooplankton in the study area over 1979 to 1989.

The goal of this study was to monitor the population biology and productivity of *Thysanoessa spinifera* through an anomalous change in ocean climate, to describe how this euphausiid responds to variations in ocean climate. The ultimate intent was to provide information, to the long-term study along Vancouver Island, for evaluating how changes in ocean climate, operating through effects on euphausiid productivity, affect fish production. The work began in 1991 and

fortunately there were 2 anomalously warm years, 1992 and 1993.

## MATERIALS AND METHODS

I present a summary of the materials and methods used. They are described in detail in Tanasichuk (1998, in this issue).

Euphausiids were collected at 4 sampling stations in Barkley Sound during 42 cruises beginning in March 1991 (Fig. 1). Cruises were made 9 times annually between March 1991 and 1994 to define accurately the seasonal growth, reproduction and abundance patterns. Thereafter, I collected samples 5 times a year (January, March, June, August and October) to monitor interannual variations. Samples were taken at night using obliquely towed bongo nets (60 cm mouth diameter, 330  $\mu$ m mesh nets) which traveled to within 10 m of the bottom. All samples were preserved in 5 % formalin. The sample from 1 cod-end was analysed completely. All adult-sized euphausiids were identified to species, counted and measured. Individuals from stratified random subsamples (a maximum of 5 individuals per millimeter length interval) were weighed, sexed and their maturity described (immature: no secondary sexual characters; male: petasma and with or without spermatophores; female: thelycum and unfertilized, fertilized or gravid). Samples of subadults were split using a Folsom splitter. Eggs and nauplii were counted and measured. Calyptopis and furcilia larva were identified to species, stage, and then counted and measured. Larvae were identified using a key we developed from the larval

descriptions for *Thysanoessa spinifera* that Summers (1993) presented. Abundance (no.  $m^{-2}$ ) was estimated from no.  $m^{-3} \times$  tow depth. Volume of water filtered was measured with a TSK flowmeter. Abundance is expressed as the mean over the 4 stations weighted by station-specific volume filtered. All mass measurements were multiplied by 0.20 because Parsons et al. (1984) reported a water content of 80 % for

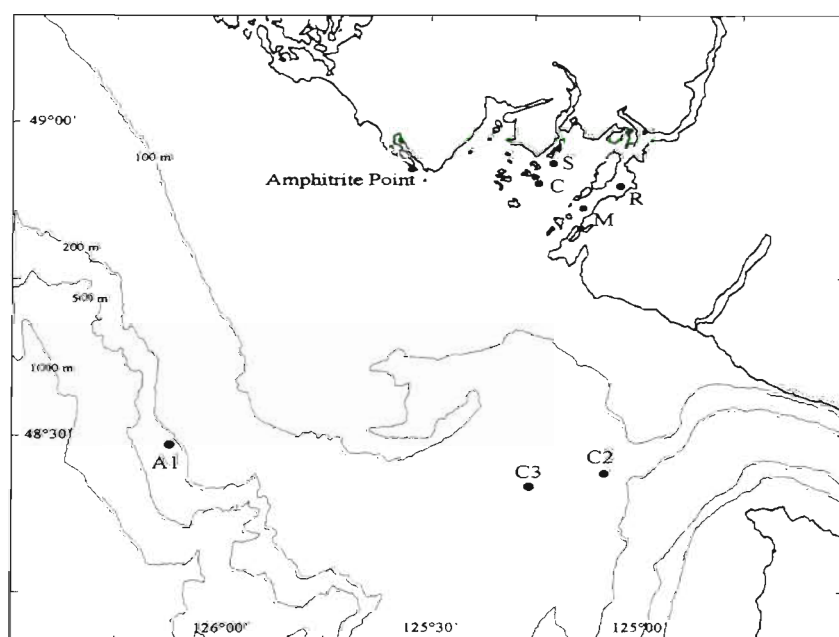


Fig. 1. Study area. C (Coaster Channel), S (Swale Rock), R (Robber's Passage) and M (Mackenzie Anchorage) are Barkley Sound sampling sites. Amphitrite Point shows the lighthouse location. C2, C3: offshore sampling stations. A1 the offshore mooring which provided data for current velocity indices

North Pacific euphausiids. Tanasichuk (1998) describes the procedure used to delineate spawnings. I assumed that larval stage durations were the same for *T. spinifera* as reported by Ross (1981) for *Euphausia pacifica* based on data presented by Summers (1993). However, *T. spinifera* has 5, not 7, furciliar stages; therefore I assumed that *T. spinifera* became juveniles when *E. pacifica* would reach F6. I estimated larval and adult growth production between successive sampling dates using the Petrovich method described by Ritz & Hosie (1982), and moult production using the equation developed by Sameoto (1976). I assumed that moults represent 11.6% of the dry body mass (Jerde & Lasker 1966). IP, the intermoult period, was estimated using the equation Iguchi & Ikeda (1995) developed for *E. pacifica*:

$$\log_{10}IP = 0.0321 \times L + 10^{0.0340 - 0.0435 T}$$

where  $L$  is length and  $T$  is the mean sea temperature at Amphitrite Point (see below) between sampling events.

I used log-transformed total length, total mass and ovarian mass estimates to develop cruise-specific length-mass and year-specific total mass-ovarian mass relationships. Ovarian mass was measured until 1995 only. Differences were tested using analysis of covariance (ANCOVA). I used the GT-2 method described by Sokal & Rohlf (1981) to test for the significance of slope and then intercept differences.

All annual estimates were made considering a year to begin in March and end in February. This was because major spawnings in a calendar year began in March, which I considered to signify the beginning of a new 'biological year'.

Sea surface temperature data came from Amphitrite Point. This is a lighthouse station located 20 nautical miles west of the study area (Fig. 1). I used the current velocity index developed by Thomson & Ware (1996) to describe the intensity of upwelling and downwelling over the study period.

## RESULTS

### Sea conditions

There were substantial interannual variations in sea conditions over the study period. Sea temperatures have been warmer on average between 1992 and 1996. They were anomalously high in 1992, because of an El Niño Southern Oscillation event (ENSO), and again in 1993 (Fig. 2). The winters of 1993-94, 1994-95 and 1996-97 showed some exceptionally low temperatures. The current velocity index suggested exceptionally strong upwelling in 1992 and strong downwelling in the winter of 1994-95 (Fig. 3).

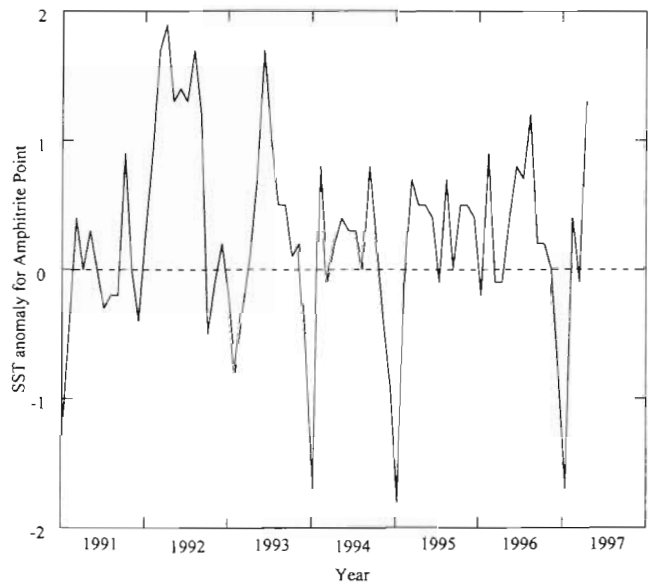


Fig. 2. Monthly sea surface temperature anomalies measured at Amphitrite Point lighthouse

### Sampling bias

I tested for bias in the sampling data before investigating variations in population biology and productivity. I considered 3 potential sources of bias. The first was between-station variability within a cruise. The second dealt with differences in euphausiid abundance and size composition between Barkley Sound and the La Perouse study area along the southwest

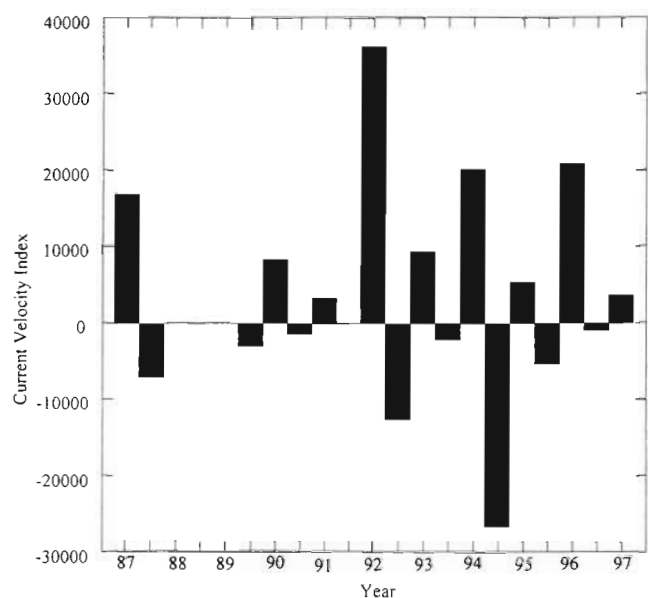


Fig. 3. Current velocity index. Positive values indicate upwelling. Bars show intensity

coast of Vancouver Island. Thomson (pers. comm.) felt that Barkley Sound and the coastal waters were continuous oceanographically. Therefore, if these locations supported different populations, then samples in Barkley Sound could be contaminated by euphausiids moving into the Sound. In addition, abundance estimates could be biased by euphausiids being advected out to coastal waters. Finally, there was a potential bias due to the reduced sampling intensity in the later years of the study. Important peaks or troughs in abundance or biomass could have been missing when sampling was reduced to 5 times a year.

I found no significant bias in the sampling. Fig. 4 shows the time series of station-specific abundance estimates. There were 3 sampling events where abundances appeared to vary substantially from other sampling stations. The abundance and biomass estimates for the aberrant stations were excluded. I compared samples collected in Barkley Sound with those collected at the same time in coastal waters as part of a zooplankton monitoring program (COPRA). Offshore sampling locations are shown in Fig. 1. These are occupied opportunistically; unfortunately there were only 3 instances where both coastal stations were sampled at night using obliquely-towed bongo nets. The abundances and size compositions of *Thysanoessa spinifera* are compared in Figs. 5 & 6. Results indicate that abundances agree well. I used log-linear models to compare size compositions and found that length-frequency distributions differed significantly between stations in 1991 only. Therefore, I concluded there was no difference in abun-

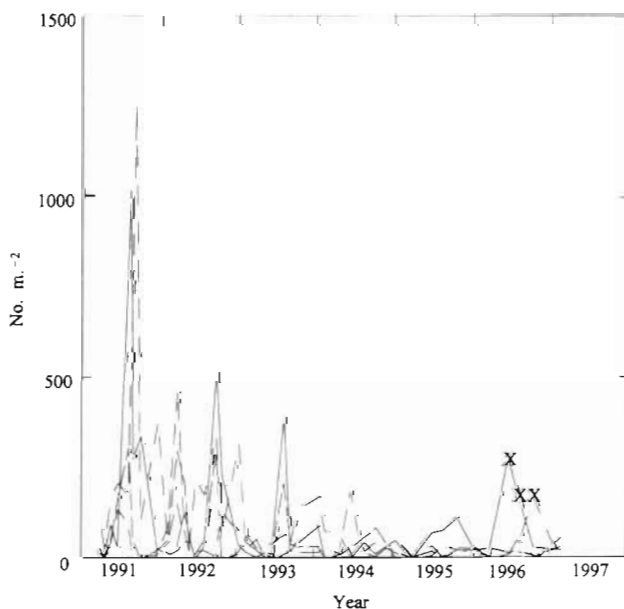


Fig. 4. *Thysanoessa spinifera*. Abundance of adults at each Barkley Sound sampling station. X: aberrant samples

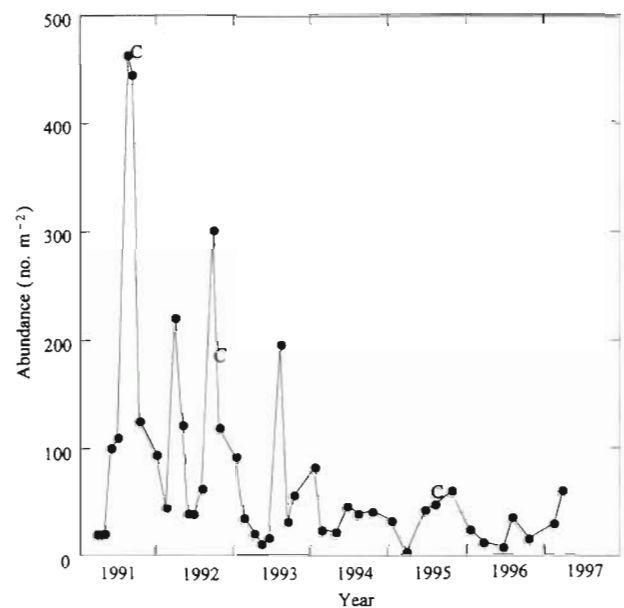


Fig. 5. *Thysanoessa spinifera*. Adult abundance for Barkley Sound (—) and offshore COPRA (C) sampling stations

dance and size composition between samples collected at the coastal stations and in Barkley Sound. I tested for bias due to changing sampling frequency by comparing mean annual larval and adult abundance estimates made using all data and then using data for those months sampled every year (January,

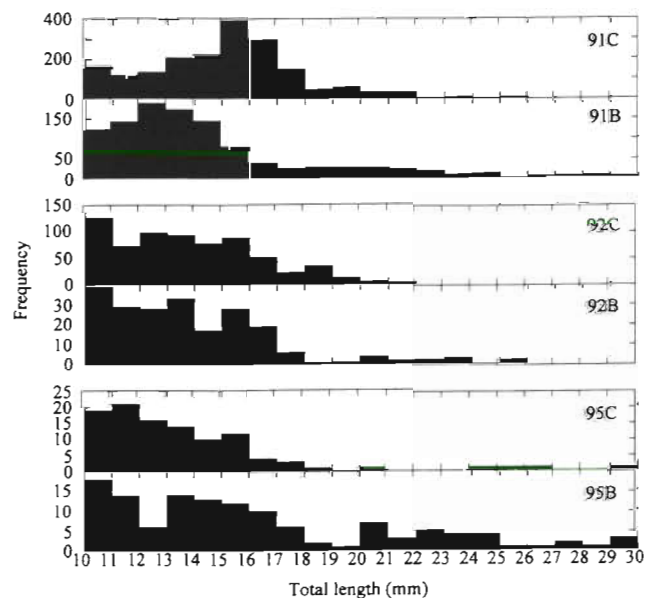


Fig. 6. *Thysanoessa spinifera*. Adult length-frequency distributions for Barkley Sound and offshore COPRA sampling stations. Labels indicate year and sampling location (B: Barkley Sound; C: COPRA stations)

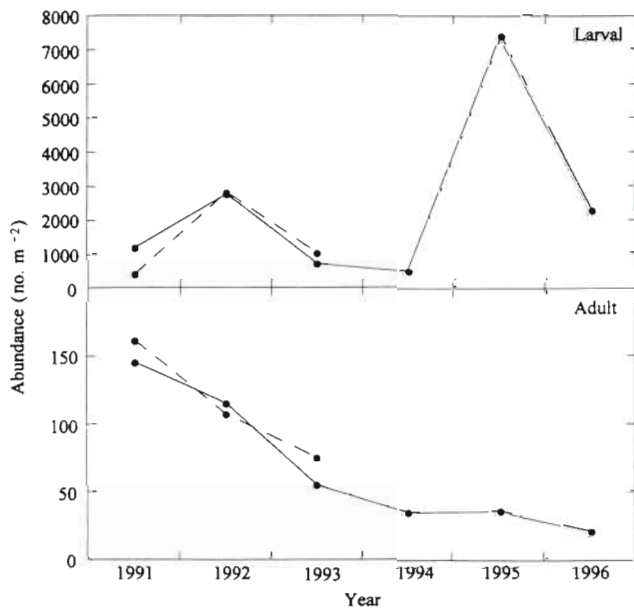


Fig. 7. *Thysanoessa spinifera*. Mean annual larval and adult abundance based on data for all samples within the March-February sampling year (---) and data for March, June, August, October and January samples (—)

March, June, August, October). Fig. 7 shows that larval and adult abundance estimates did not appear to be affected by sampling intensity. In summary, excluding the instance when 3 sampling events had unusually high abundances of *T. spinifera*, there was no sampling bias with respect to between-station and Sound-coastal waters differences. In addition, sampling frequency did not influence abundance estimates.

#### Size composition and abundance

There was considerable variation in larval abundance and a reduction in adult abundance over the study period (Fig. 8, Table 1). Larval abundance increased 2.4 times from 1991 to 1992 but then decreased to below pre-ENSO levels in 1993 and 1994. There was a 16-fold increase in 1995, due to a high concentration of young larvae in August. Adult abundance decreased continuously and was 0.14 of the 1991 value in 1996.

Length-frequency histograms for all cruises are presented in Fig. 9. Larvae were present in all months except January 1994 to 1997; only larger larvae were present in February. Changes in size composition of adults over time are shown in Fig. 10. The peak at 10–14 mm in 1991 progressed through the larger size categories over time. The peak in 1992 did not progress beyond the next category. It appears that changes in

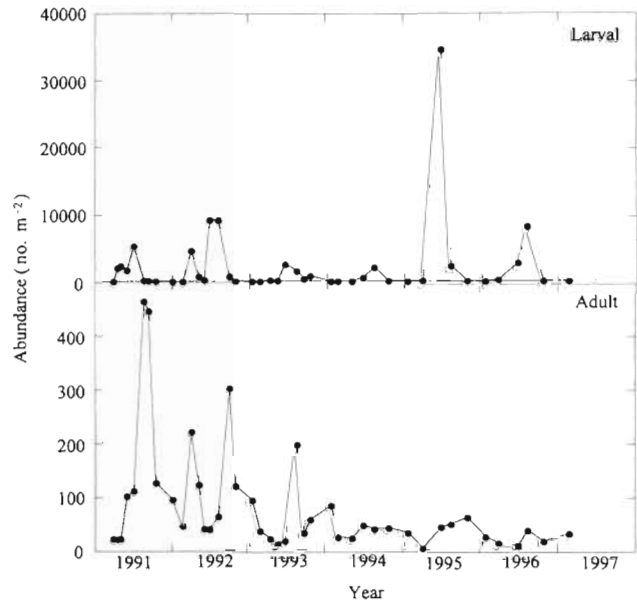


Fig. 8. *Thysanoessa spinifera*. Larval and adult abundance for Barkley Sound sampling stations

abundance were essentially due to changes in abundance of all size categories of adults.

#### Growth

I developed a growth trajectory (Fig. 11) for the progression of a distinct mode from April to October 1991 (Fig. 9). I accepted this as a realistic growth trajectory because the accompanying abundance trend approximated an exponential decrease in numbers over time. I used the non-linear parameter estimation procedure in SYSTAT (1994) and fit length-at-time ( $L_t$ , where  $t$  is days since the mode appeared) data to a von Bertalanffy growth function. The equation was:

$$L_t = 34.72(1 - e^{-0.9076t}), R^2 = 0.96, p < 0.0001$$

I used an ANCOVA of the total length-total mass regressions to evaluate interannual variations in

Table 1. *Thysanoessa spinifera*. Mean annual abundances (no. m<sup>-2</sup>) for larvae and adults

Year	Larvae	Adults
1991-92	1168	145
1992-93	2742	115
1993-94	669	55
1994-95	450	34
1995-96	7372	35
1996-97	2222	20



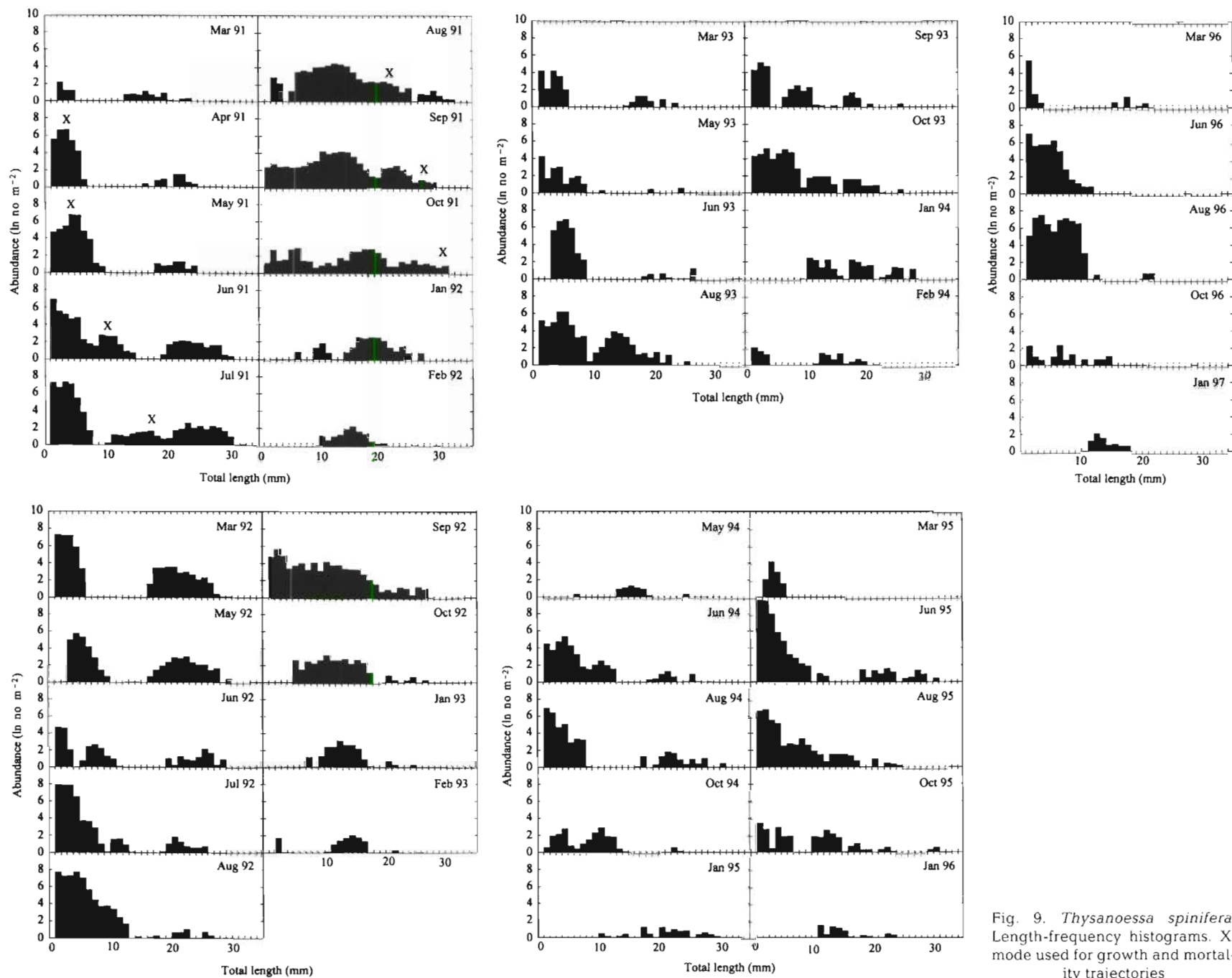


Fig. 9. *Thysanoessa spinifera*. Length-frequency histograms. X: mode used for growth and mortality trajectories

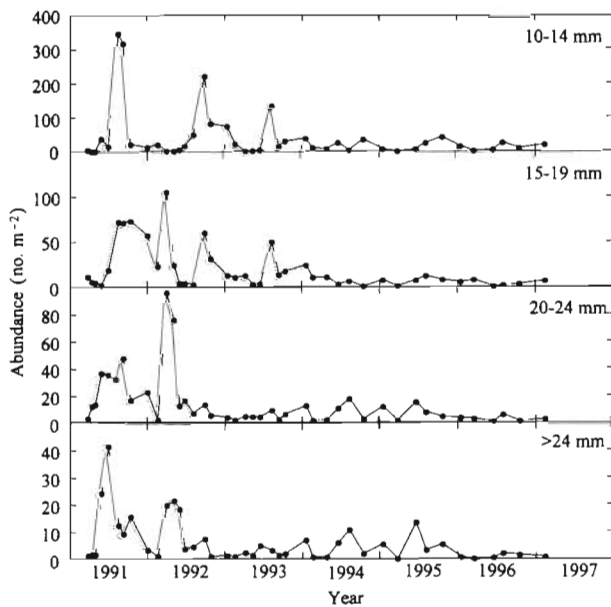


Fig. 10. *Thysanoessa spinifera*. Abundance in arbitrary size categories

growth conditions. Results of the GT-2 comparison test showed that regression slopes did not differ significantly ( $p > 0.05$ ). Therefore, I compared the intercepts by using the mean mass adjusted for the grand mean length (18 mm). Length-specific mass declined every winter (Fig. 12). Results of a 1-way analysis of variance (ANOVA) showed that adjusted mean mass differed between years ( $p < 0.01$ ). A subsequent com-

parison of means using Tukey's test (Wilkinson et al. 1996) indicated that this was because the adjusted group mean mass in 1996 (9.2 mg) was significantly greater than in 1992 (8.2 mg) and 1991 (8.0 mg). These small differences are not likely to be significant biologically.

### Reproduction

I examined the biological characteristics of the parents, spawning itself, the relationship between larval and adult abundance, and larval size.

#### Adult reproductive characteristics

I found seasonal but no interannual variations. Sex ratios, expressed as the proportion of adults which were male, are presented in Fig. 13. Results of a 1-way ANOVA detected no difference ( $p = 0.80$ ) in sex ratio between years. The grand mean sex ratio over the study period was 0.51. In all years, there was a progressive increase in length-at-maturity, defined as the median length of mature euphausiids, over a year (Fig. 14). I tested the effect of the apparent change in length-at-maturity by comparing observed adult abundances with those estimated using the month-specific length-at-maturity data for 1991 (Fig. 15). It appears that variations in length-at-maturity were too small to have any effect on adult abundance.

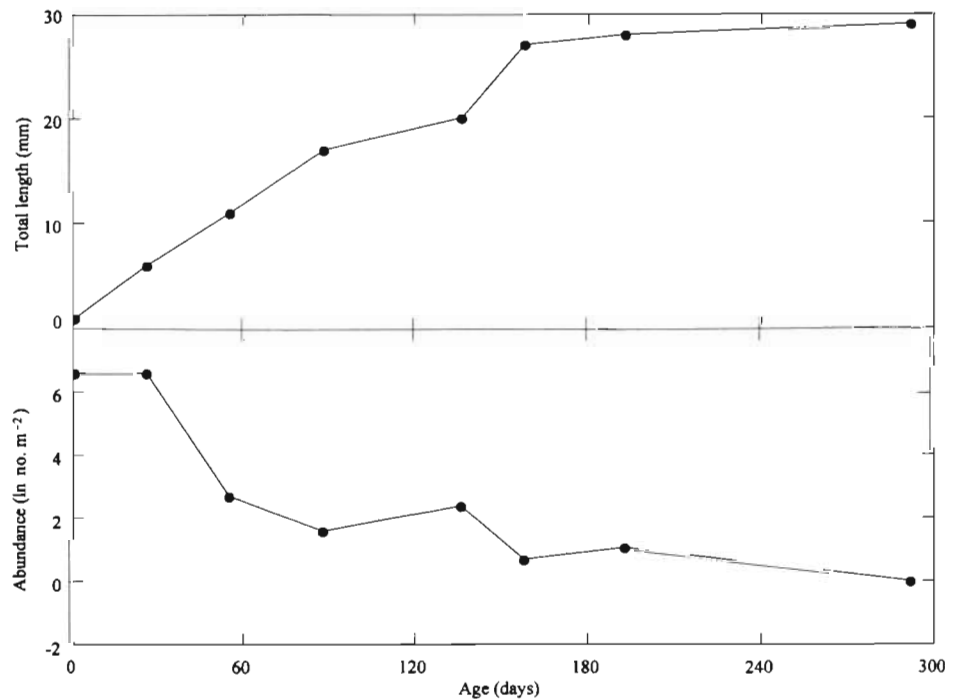


Fig. 11. *Thysanoessa spinifera*. Growth and mortality trajectories

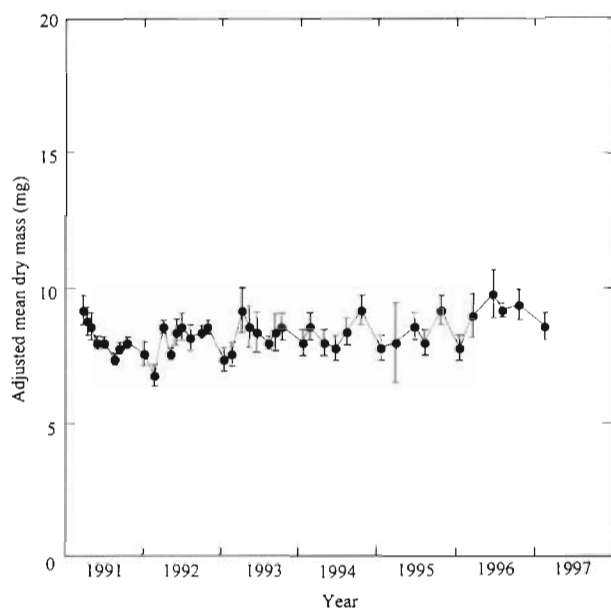


Fig. 12. *Thysanoessa spinifera*. Total dry mass adjusted for the grand mean adult length (18 mm). Error bars are 95% comparison limits

Year-specific ovarian mass - total mass data are plotted in Fig. 16. There was no tendency for unfertilised, fertilised or gravid females to have low or high mass-specific ovarian mass. I assumed that the upper limit of the data distribution defined maximum size-specific ovarian mass, in other words, ripe ovarian mass before any broods were released. I estimated ovarian mass at

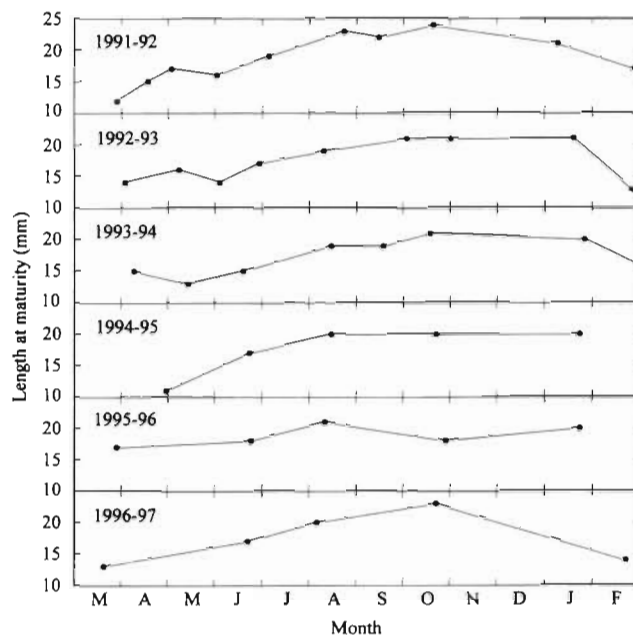


Fig. 14. *Thysanoessa spinifera*. Seasonal variation in length-at-maturity

specific total mass values along the upper limit of the distribution to generate the dataset for calculating year-specific maximum ovarian mass - total mass regressions. Results of an ANCOVA showed that regression slopes differed significantly ( $p < 0.0001$ ) between years. Parameter estimates for the year-specific ovarian mass - total mass regressions are presented in Table 2.

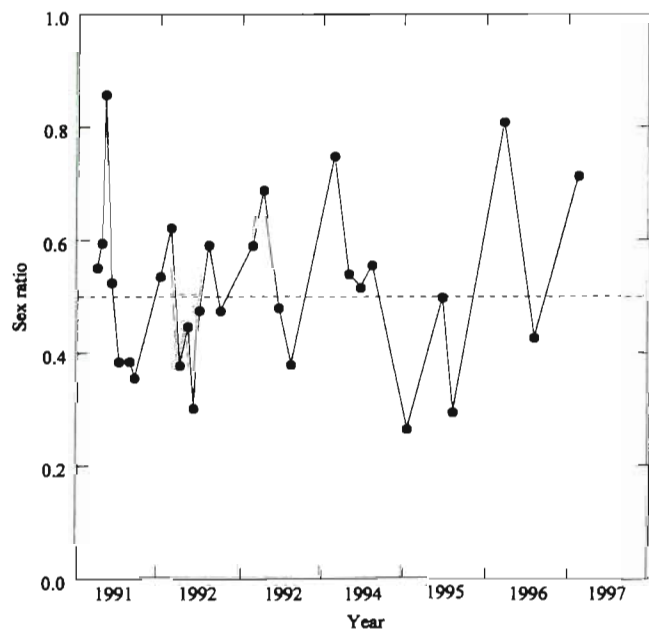


Fig. 13. *Thysanoessa spinifera*. Sex ratios (prop. male)

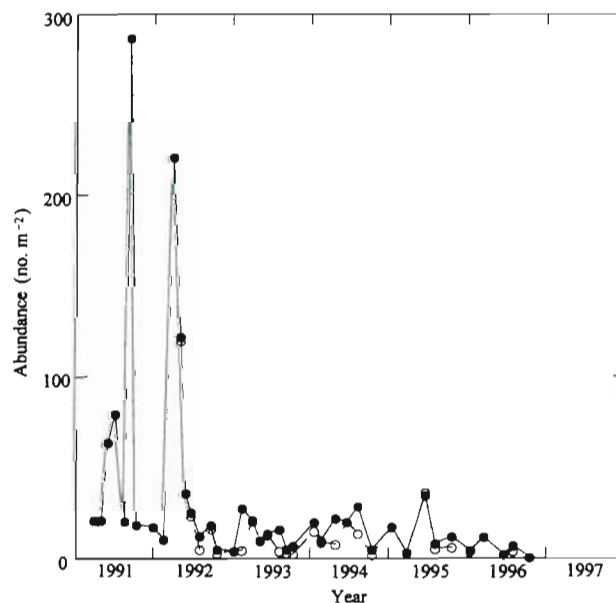


Fig. 15. *Thysanoessa spinifera*. Abundance of adults using observed length-at-maturity (○) and that for the 1991-92 sampling year (●)



### Spawning

The overall spawning season, as defined by the period when females bore spermatophores, varied among years (Fig. 17). No fertilized females were captured after September in 1991. In subsequent years, females bearing spermatophores were collected until at least October. Results of 1-way ANOVAs, using arcsine-transformed proportions, indicated no significant effect of year on the proportion of males ( $p = 0.66$ , mean = 0.92) or females ( $p = 0.76$ , mean = 0.44) with spermatophores over the spawning season.

Fig. 18 shows the discrete spawning as defined by the back-calculated birth-dates of larvae. In 1991 and 1992, there were 4 protracted spawnings over the March–October period and some very restricted spawnings in November and December. There were 3 protracted spawnings in 1993. Unfortunately, the reduced intensity of sampling confounds defining spawnings after 1993. I determined, retrospectively, that the interval between sampling events was longer than the entire pre-adult phase for *Thysanoessa spinifera*.

### Stock-recruit relationship

I used the estimates of adult abundance, sex ratio and maturity ogives to estimate the abundance of female parents over the study period (Fig. 19). Mean annual female parent abundances were 16, 29, 5, 8, 7 and 4  $m^{-2}$  for 1991 through 1996 respectively. Larval abundance is plotted against parental abundance in Fig. 20. Neither the Ricker (Ricker 1975) nor Beverton-Holt (Beverton & Holt 1957) stock-recruit models described the relationship between larval and parental abundances.

Table 2. *Thysanoessa spinifera*. Parameter estimates for ovarian mass - total mass regressions where  $\ln$  ovarian mass =  $a \times \ln$  total mass +  $b$

Year	$a$	$b$
1991-92	0.92	-1.07
1992-93	1.09	-1.59
1993-94	1.08	-1.60
1994-95	1.08	-1.80
1995-96	1.25	-2.02

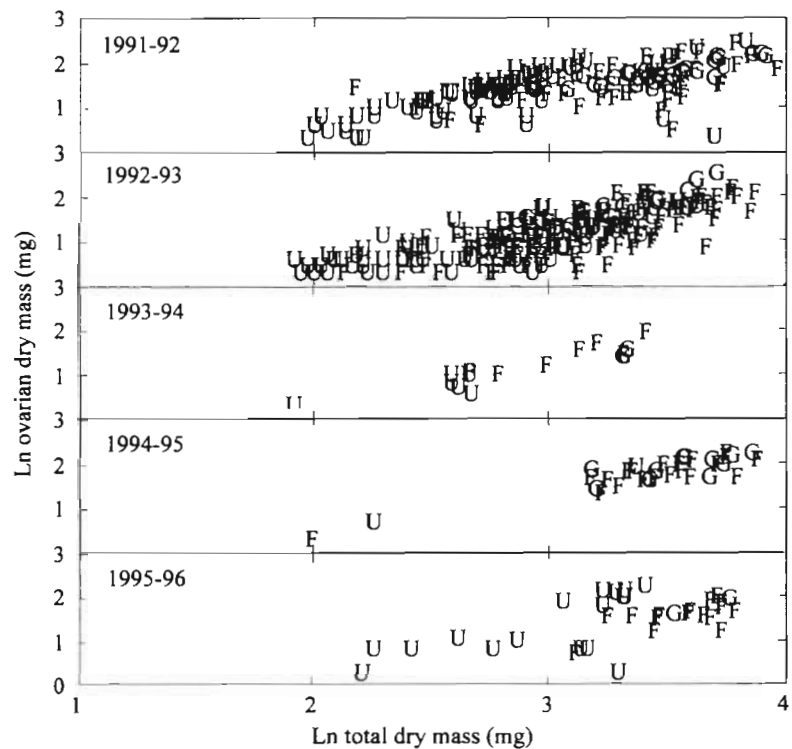


Fig. 16. *Thysanoessa spinifera*. Scatterplots of ovarian dry mass versus total dry mass. U: unfertilized. F: fertilized. G: gravid

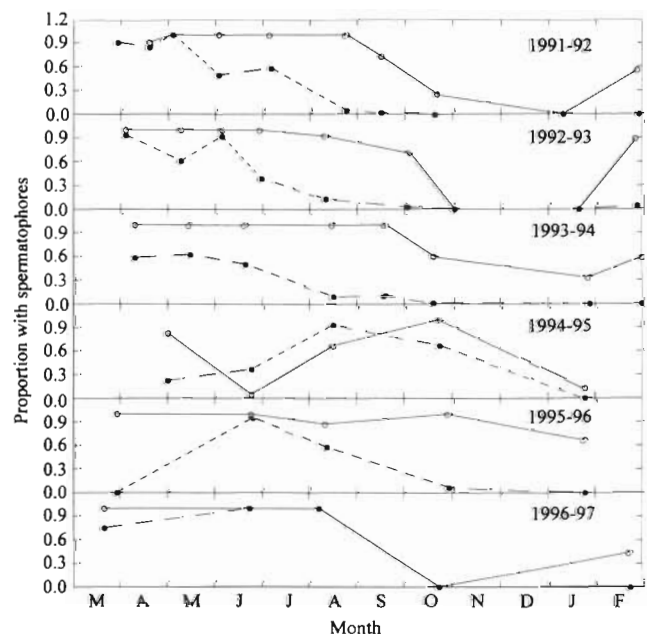


Fig. 17. *Thysanoessa spinifera*. Proportion of males (○) and females (●) with spermatophores

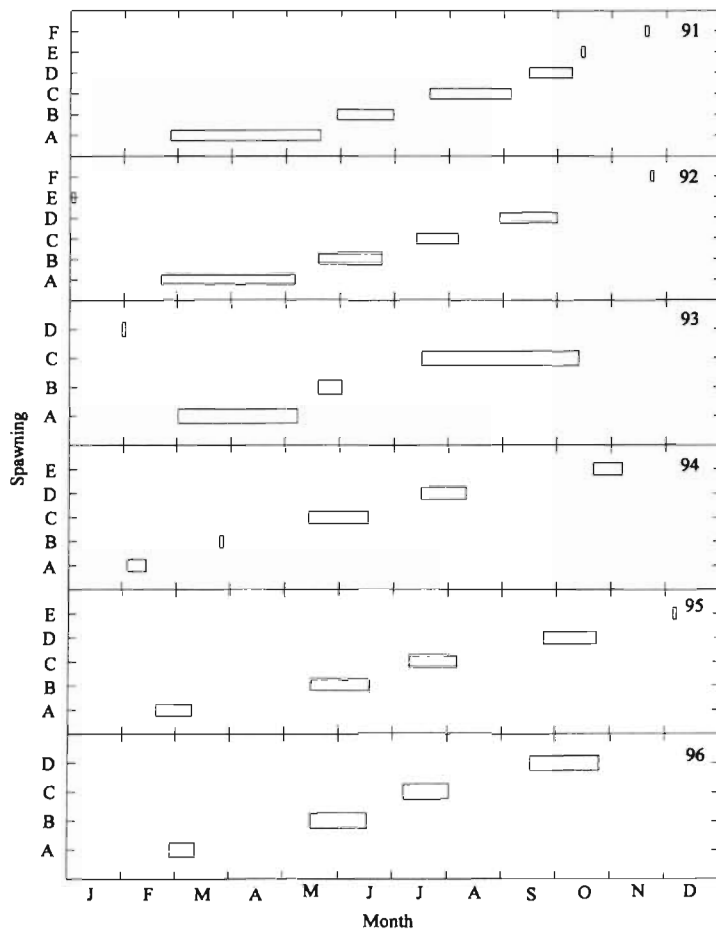


Fig. 18. *Thysanoessa spinifera*. Timing and duration of spawns

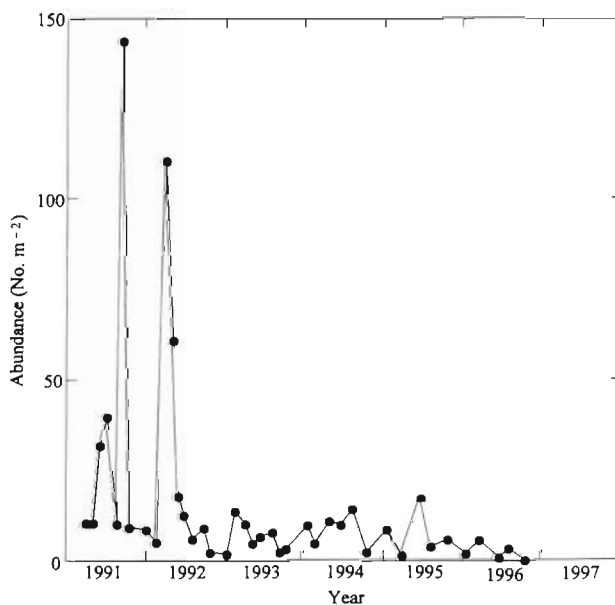


Fig. 19. *Thysanoessa spinifera*. Abundance of females

### Larval size

Mean total lengths of each larval stage are presented in Fig. 21. There appeared to be no seasonality in mean larval size for any stage. Results of 1-way ANOVAs showed no significant ( $p > 0.25$  at least) interannual variations in length for any larval stage except F5 ( $p = 0.02$ ). However, Tukey's means comparison test showed no years which differed significantly ( $p > 0.05$ ).

### Biomass and productivity

Larval biomass fluctuated over the study period (Fig. 22, Table 3). It increased by 1.6 times in 1992 and then declined to 0.2 of the 1991 level in 1994. It increased to 1991 levels in 1995 and was 6.9 times higher in 1996 than in 1991. In contrast, adult biomass essentially declined from 1991 through 1996, when it was about 0.12 of the 1991 level.

Production trends (Fig. 23, Table 3) were similar to those for biomass. Larval productivity peaked in 1996. Adult production declined continuously to 0.14 of the 1991 level in 1996. Moults production accounted for 0.09 (1995) to 0.21 (1996) of total larval production. For adults, moults production accounted for 0.33 (1996) to 0.37 (1995) of the total. Population  $P:B$  ratios fluctuated between 14.4 and 44.7, with variations following the proportion of the biomass accounted for by larvae. For example, the lowest  $P:B$  ratio was in 1994 when larvae accounted for 0.05 of mean annual biomass and the highest was in 1996 when larvae represented 0.80 of the biomass.

### DISCUSSION

The biomass and productivity of *Thysanoessa spinifera* adults has decreased dramatically coincident with the 1992 ENSO. It appears that this decline is due simply to a reduction in abundance. As Tanasichuk (1998) reported for *Euphausia pacifica*, it appears that changes in adult productivity are not influenced by changes in the growth or reproductive characteristics of the population. Fig. 10 suggests that there has not been a substantial change in the relative size composition of adults either. *T. spinifera* larval and adult production appear not to be as closely linked to upwelling as for *E. pacifica* (Tanasichuk 1998). Variation in *E. pacifica* productivity appeared to be a consequence of an un-

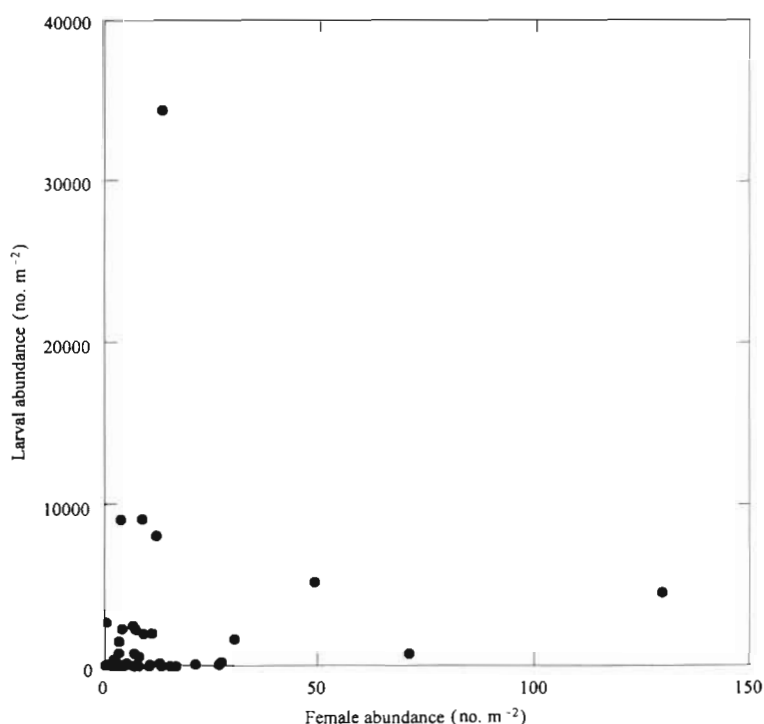


Fig. 20. *Thysanoessa spinifera*. Scatter plot of female and larval abundances

usually successful recruitment in the summer of 1992 and the movement of these individuals through the population. (Brodeur & Pearcy [1992] recently queried if responses in growth rate or survival of young euphausiids are rapid enough to increase available biomass [presumably for fish as prey] in a matter of months during strong upwelling years. The results presented in Tanasichuk [1998] suggest that *E. pacifica* from the southwest coast of Vancouver Island are capable of this.) In contrast, *T. spinifera* larval production peaked in 1996, a year of significant but not exceptional upwelling, and adult production declined since 1991.

*Thysanoessa spinifera* and *Euphausia pacifica* adults responded very differently to changes in ocean conditions, possibly due to the effect of differential

predation pressure. I (unpubl. results) have been monitoring the size and species composition of euphausiids consumed by Pacific hake over the summer feeding periods. I am finding that *T. spinifera* has persisted as the preferred euphausiid prey even though they have declined from representing 60 to 16% of adult euphausiids. Brinton & Reid (1986) and Drobysheva (1987) have commented on how euphausiid species respond differently to changes in sea temperature. Both studies describe warmer water species flourishing during periods of warmer sea conditions and a converse situation when temperatures are cool. These differences could possibly be due to differences in tolerance to changes in environmental conditions, similar to that Gillfillan (1972) described for coastal and oceanic populations of *E. pacifica*. However, the changes in temperature that the *T. spinifera* and *E. pacifica* populations I studied were exposed to are well within the temperature range that adults move through during diel vertical migrations.

The species differences in predation pressure appear to be a more reasonable explanation.

I cannot explain why *Thysanoessa spinifera* and *Euphausia pacifica* recruitment should be so different. Both species showed greater larval abundance in 1992, when upwelling was particularly strong. However, recruitment was much more successful for *E. pacifica*.

The *P:B* ratios I estimated for *Thysanoessa spinifera* are the highest reported for any euphausiid species to date. There are 4 main reasons for this. First, there are few studies (Hosie & Ritz 1983, Stuart & Pillar 1988, Lavaniegos 1995) which consider more than just growth production. Second, it appears that *T. spinifera* grow much more rapidly than any other euphausiid for which production has been estimated. Fig. 24 shows the

Table 3. *Thysanoessa spinifera*. Mean annual biomass (mg dry mass  $m^{-2}$ ), production (mg dry mass  $m^{-2} yr^{-1}$ ) and *P:B* ratios. Population *P:B* values are calculated using the sums of biomass and productivity for larvae and adults

Year	- Larvae -						- Adults -						Population <i>P:B</i>
	Biomass	Production			<i>P:B</i>		Biomass	Production			<i>P:B</i>		
		Growth	Moult	Total	Growth	Moult		Growth	Moult	Total	Growth	Moult	
1991-92	88	5656	911	6567	64.2	10.3	1185	8481	4800	13282	7.2	4.0	15.6
1992-93	138	12258	1971	14228	88.9	14.3	1046	6658	3479	10136	6.4	3.3	20.6
1993-94	86	6492	1220	7712	75.7	14.2	382	3112	1569	4680	8.1	4.1	26.5
1994-95	17	1369	210	1578	80.7	12.4	326	2156	1202	3358	6.6	3.7	14.4
1995-96	83	9293	867	10161	112.6	10.5	394	2147	1240	3386	5.4	3.1	28.1
1996-97	607	25161	6783	31943	41.4	11.2	148	1228	594	1822	8.3	4.0	44.7

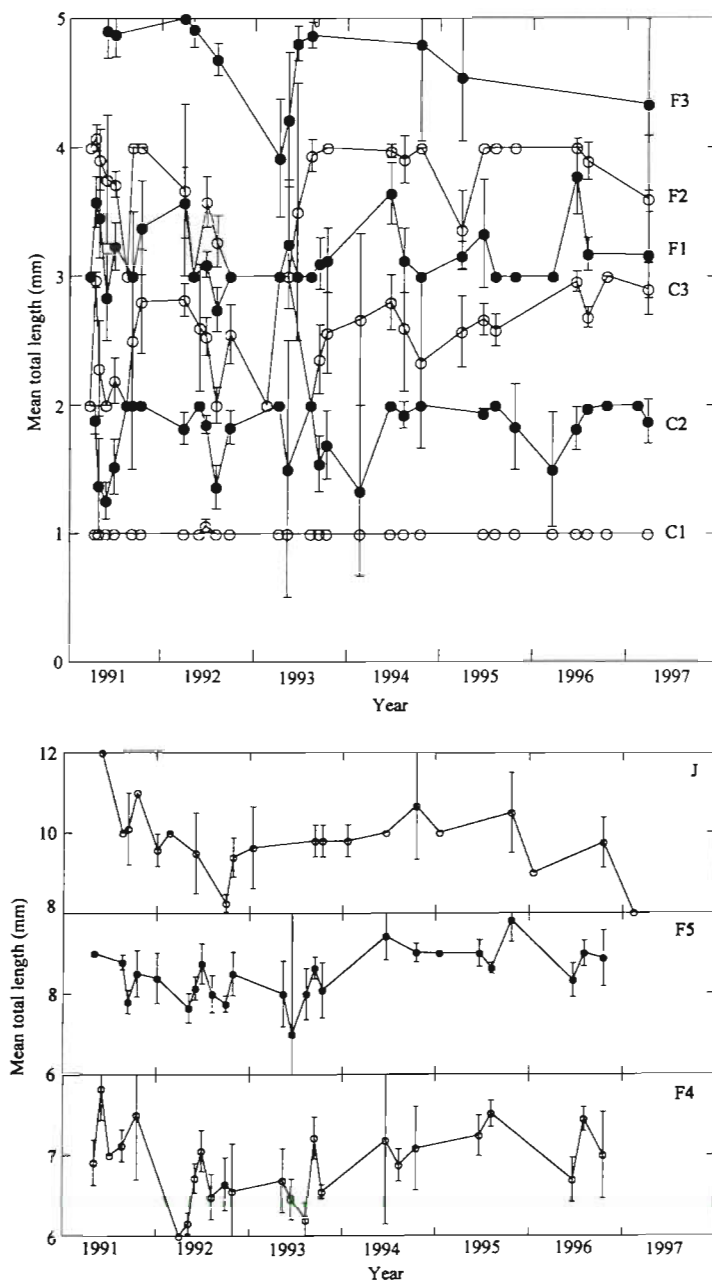


Fig. 21. *Thysanoessa spinifera*. Variations in larval size (mean  $\pm$  2 SE)

growth trajectories I estimated for *T. spinifera*, *Euphausia pacifica*, *E. lucens* and *Nyctiphanes australis*. The growth trajectory for *E. pacifica* is from Tanasichuk (1998). Those for the latter 2 species were von Bertalanffy growth function fits to growth data presented in figures in Stuart & Pillar (1988) and Ritz & Hosie (1982) respectively; these are the only other studies of euphausiid production which presented growth trajectories. Growth is much more rapid in *E. pacifica* and especially *T. spinifera*. Therefore, the production of bio-

Table 4. Mean larval and adult abundance (no.  $m^{-2}$ ) and biomass (mg dry mass  $m^{-2}$ ) for *Thysanoessa spinifera* and *Euphausia pacifica* combined

Year	Larval		Adult	
	Abundance	Biomass	Abundance	Biomass
1991-92	1647	110	246	1862
1992-93	5465	327	318	1870
1993-94	2337	237	244	1722
1994-95	986	37	148	1070
1995-96	8675	121	123	1070
1996-97	3509	803	150	669

Table 5. Larval and adult moult and total production (mg dry mass  $m^{-2} yr^{-1}$ ) for *Thysanoessa spinifera* and *Euphausia pacifica* combined

Year	Larval		Adult	
	Moult	Total	Moult	Total
1991-92	1154	8226	7511	19083
1992-93	4175	27202	8259	20564
1993-94	2829	17215	9308	17989
1994-95	446	3329	4441	11118
1995-96	1247	12983	4210	10746
1996-97	8959	42743	3191	7748

mass per unit time would be substantially greater. I also compared mass-length relationships between *E. pacifica* and *T. spinifera* to test if differences in growth in mass with respect to length accounted for the differences in *P:B* ratios for *T. spinifera* and *E. pacifica*. Results of an ANCOVA showed that the slopes of these regressions were different. Therefore, adjusted group means were incomparable. A plot of estimated mass at specific lengths suggested a small difference (Fig. 25). The third reason for differences in *P:B* ratios is that, according to Jerde & Lasker (1966), the mass of the exuviae of *T. spinifera* relative to total mass is higher (11.7%) than for *E. pacifica* (10.6%) and much higher than for *N. australis* (5.75%; Hosie & Ritz 1983) and *E. lucens* (6.75%; Stuart & Pillar 1988). Therefore, the more rapid growth in length by *T. spinifera* over time, and hence mass, enhances the differences in total production even more because the moults are about twice the percentage of total mass for *T. spinifera* than they are for *N. australis* and *E. lucens*. Finally, the highest *P:B* ratio occurred in the year when larvae accounted for about 0.80 of the mean annual biomass. Tanasichuk (1998) discussed how size structure of a euphausiid population can affect the *P:B* ratio essentially because of the decline in growth rate with age (size).

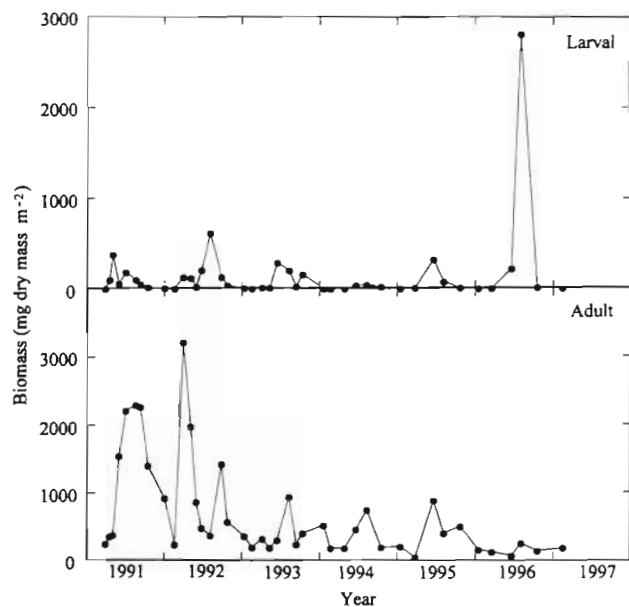


Fig. 22. *Thysanoessa spinifera*. Larval and adult biomass

In an ecosystem sense, the results I present here must be considered in terms of *Euphausia pacifica* as well as *Thysanoessa spinifera*, because they collectively account for well over 90 % of the euphausiid biomass in the study area. Table 4 presents the abundance and biomass and Table 5 productivity estimates for *T. spinifera* and *E. pacifica* combined; data for *E. pacifica* are from Tanasichuk (1998). Larval abundance, biomass and productivity again seem to vary

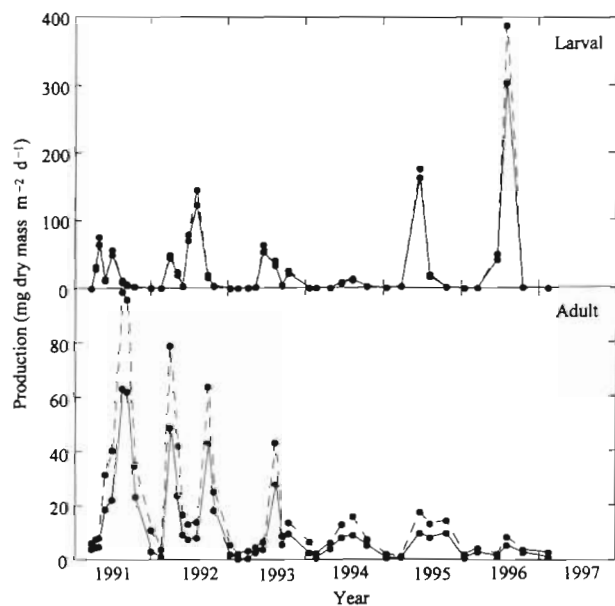


Fig. 23. *Thysanoessa spinifera*. Larval and adult production. Dotted line indicates contribution of moults to total production

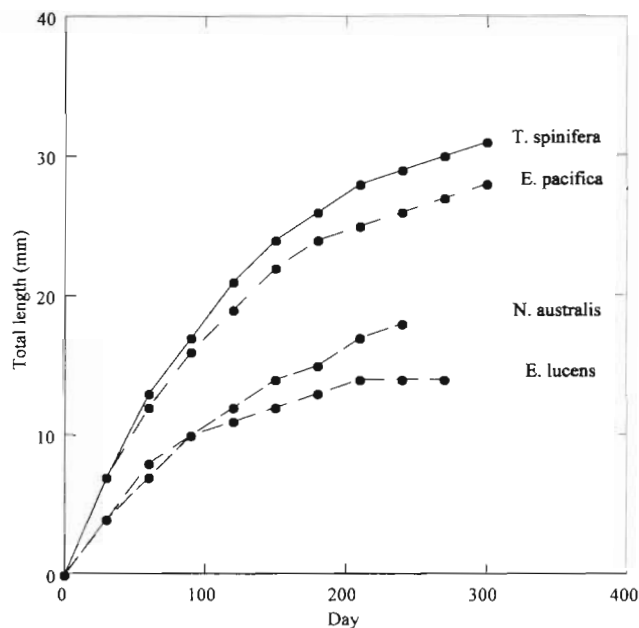


Fig. 24. Growth trajectories for *Thysanoessa spinifera*, *Euphausia pacifica*, *Euphausia lucens* and *Nyctiphanes australis*. Data are from this study, Tanasichuk (1998), Stuart & Pillar (1988) and Ritz & Hosie (1982) respectively

randomly. On the other hand, adult abundance, biomass, moult and total production have declined since 1993. Biomass in 1996 was 0.36 of that in 1991 and moult and total production were about 0.4 of the 1991

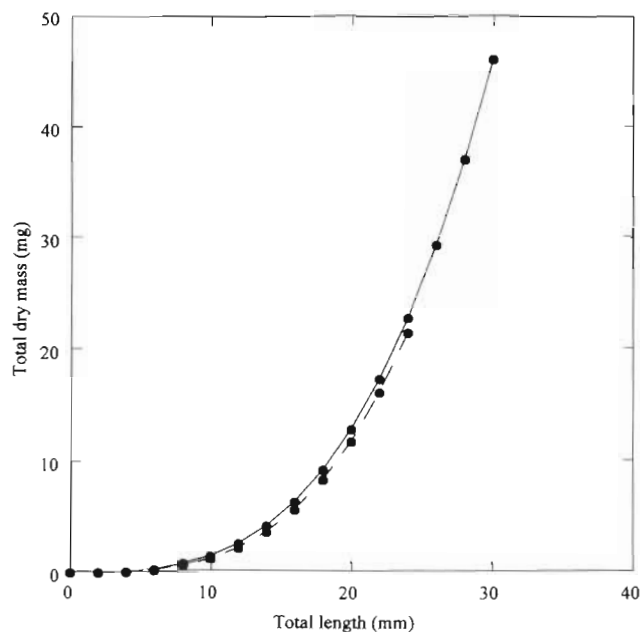


Fig. 25. Dry mass - total length relationships for *Thysanoessa spinifera* (—) and *Euphausia pacifica* (---). Data are from this study and Tanasichuk (1998) and are pooled over the entire study period



amounts. Total euphausiid biomass was 1972, 2197, 1959, 1107, 1191 and 1472 mg dry mass  $m^{-2}$  for 1991 through 1996 respectively. Total euphausiid production was 27309, 47766, 35204, 14447, 23729 and 50491 mg dry mass  $m^{-2} yr^{-1}$  for 1991 through 1996 respectively. Therefore, it appears that euphausiid biomass and productivity reached a minimum in 1994. Production in 1996 was the highest of all years, due to the growth production by *T. spinifera* larvae.

Changes in overall euphausiid productivity may not result in parallel changes in food availability for planktivorous fish. As stated earlier, Tanasichuk et al. (1991) reported that euphausiids represent over 90% of the diet of Pacific hake, the dominant planktivore. Preliminary results of the monitoring of the hake diet indicate that about 75% of the euphausiids consumed by hake are longer than 17 mm and about 75% of those are *Thysanoessa spinifera*. I applied these estimates to those for length-specific biomass of *Euphausia pacifica* and *T. spinifera* to calculate prey biomass availability for hake. I find that prey availability for hake has declined since 1991. In 1996, it was 0.13 of the 1991 value.

In summary, *Thysanoessa spinifera* adult biomass and productivity have been adversely affected by the 1992 and 1993 warm water years. It appears to be due to a series of recruitment failures in terms of poor survival from larvae to adult. Larval productivity was not affected. Total euphausiid biomass and productivity peaked in 1992 and reached a minimum in 1994. However, these changes in euphausiid productivity do not result in parallel changes in prey availability, at least for Pacific hake.

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