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Predator-limited population growth of the copepod *Pseudocalanus* sp.

M.D.Ohman[1]

Oceanography WB-10, University of Washington, Seattle, WA 98195, USA

[1]*Present address: Marine Life Research Group A-027, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, USA*

Abstract. The impact of predators on population growth of *Pseudocalanus* sp. was investigated in Dabob Bay, Washington. Mortality of *Pseudocalanus* sp. was determined from stage-specific survivorship, from seasonal changes in mortality rates of adult males and females and from incidence of injuries to adult copepods. The principal predators of adult *Pseudocalanus* were identified as the predatory copepod *Euchaeta elongata*, the omnivorous euphausiid *Euphausia pacifica* and the chaetognath *Sagitta elegans*. Predator attack rates — and prey mortality rates — are highly density-dependent and thus sensitive to prey dispersion in the water column, particularly to layering in the vertical plane. Predation rates by the three principal predators exceeded 100% of the recruitment rate to adult *Pseudocalanus* sp. beginning in early summer, thus restricting population growth. Planktivorous fish predation (by adult three-spine stickleback, *Gasterosteus aculeatus*, and juvenile chum salmon, *Oncorhynchus keta*) on *Pseudocalanus* sp. adults was estimated to be two orders of magnitude lower than consumption rates by predatory zooplankton, at a deep water station in July. Analysis of seasonal changes in prey ingested by *Sagitta elegans* revealed that *Pseudocalanus* sp. was the major prey item of *S. elegans* in April (61.0% of prey) and in June (67.0% of prey), thereafter declining seasonally in importance. Predation by *S. elegans* varied seasonally with changes in chaetognath stage structure, vertical distribution and diapause, not size structure alone. Although chaetognath recruitment and population growth appear to be directly coupled to the abundance of *Pseudocalanus* sp., predation by *S. elegans* has little reciprocal impact on *Pseudocalanus* sp. population growth; hence asymmetries may occur in the interaction of planktonic prey and predators.

Introduction

Dramatic consequences of planktivory have been demonstrated in closed aquatic systems such as microcosms (Neill, 1975), small lakes (Hrbácek, 1962; Brooks and Dodson, 1965), ponds (Hall *et al.*, 1970; Hebert and Loaring, 1980; Luecke and O'Brien, 1983), and field enclosures (Neill and Peacock, 1980), but the evidence for major effects of predation on zooplankton populations in open marine ecosystems is less clear. In open marine ecosystems the consequences of predation are more difficult to detect for several reasons, including the generally lower population density of predators, mixing by advection and diffusion of populations of different predation histories, e.g. during larval or juvenile stages of some fish species and the refuges achieved by many zooplankton species by large amplitude vertical migration.

Approaches that have been taken to estimate the impact of predators on marine zooplankton populations include field sampling in the wake of predators (Koslow, 1981), simulation modeling (e.g. Landry, 1976; Steele and Frost, 1977; Kremer and Kremer, 1982; Koslow, 1983; Davis, 1984a), extrapolation from laboratory feeding experiments (e.g. Reeve and Walter, 1978) and analysis of gut contents of field-caught predators (e.g. Hirota, 1974; Purcell and Kremer, 1983; Feigenbaum and Maris, 1984). Marine field enclosures have also been used (see Grice and Reeve, 1982), but they have more

successfully reproduced phytoplankton — grazer interactions than grazer — carnivore interactions. Surface-dwelling predatory zooplankton may develop in enclosures (e.g. ctenophores and cyclopoid copepods in CEPEX experiments), but large deeper-dwelling vertically migrating zooplankton such as euphausiids, predatory copepods and mature chaetognaths are generally excluded at the onset of an enclosure experiment. Exclusion of these organisms may fundamentally alter predation pressure on the enclosed assemblage.

Here the impact of predators on the calanoid copepod *Pseudocalanus* sp. was investigated in Dabob Bay, Washington. In combination with previous results (Ohman, 1983, 1985), this study tested the hypothesis that predation rather than resource limitation was the principal mechanism controlling *Pseudocalanus* sp. population growth. Previous laboratory studies suggested that species of *Pseudocalanus* have low food requirements for maximal rates of ingestion (Frost, 1974, 1980; Paffenhöfer and Harris, 1976), development (Vidal, 1980b; Klein-Breteler *et al.*, 1982) and for maximum body size (Vidal, 1980b; Klein-Breteler and Gonzalez, 1982). A field study in Dabob Bay further suggested that population growth occurs at resource-satiated rates nearly all year round; five lines of evidence indicated that fluctuations in phytoplankton abundance were of little significance in altering *Pseudocalanus* growth rates (Ohman, 1985). Arguments have been made that species of *Pseudocalanus* are food-satiated in other regions as well (McLaren, 1978; Davis, 1984b). In light of evidence that food supply is not a major factor limiting population growth in Dabob Bay, predation pressure was evaluated as an alternative.

The approach taken here was to obtain independent estimates of mortality rates of *Pseudocalanus* sp. and of predation rates upon *Pseudocalanus* sp. by its principal predators, to determine whether predation rates balanced observed mortality. Mortality in the prey population was estimated from the stage-specific survivorship function, from seasonal changes in mortality rates of adults and from seasonal changes in the frequency of injured individuals. Predators on adult *Pseudocalanus* sp. were identified by survey predation experiments in the laboratory and by analysis of gut contents of those predators which ingest their prey whole (the chaetognath *Sagitta elegans* and two species of planktivorous fish). Seasonally changing predation pressure on *Pseudocalanus* sp. was quantified by combining information concerning predator feeding behavior with predator abundance, stage composition and *in situ* vertical distribution. Interannual variability in abundance of *Pseudocalanus* sp. and predators was also determined in a 4-year time series. Adult female *Pseudocalanus* sp. were the principal focus of this analysis because brooding of egg sacs confers particular demographic importance upon their survivorship.

The study site, Dabob Bay, Puget Sound, was selected because of faunistic affinity of the zooplankton with open ocean waters of the northeastern Pacific and containment of planktonic populations in a semi-enclosed fjord where deep waters remain oxygenated all year round. Previous studies treating circulation in Dabob Bay indicate that advection is reduced within the fjord (Kollmeyer, 1965; Ebbesmeyer *et al.*, 1975; Christensen and Packard, 1976; Smethie, 1981), thus permitting the analysis of temporal changes within a planktonic population.

Methods

Sampling

Four cruises were made to Dabob Bay during 1978 and 57 cruises during 1979 – 1980 from surface vessels or a pontoon aircraft. Sampling was performed at or near Station D (47° 45′ N, 122° 49′ W), the deepest location in Dabob Bay (mean depth = 185 m), although all parameters could not be measured on all cruises. Temperature profiles were determined with a conductivity – temperature – pressure unit, or occasionally with reversing thermometers or a calibrated bathythermograph. The methods agreed to ~ ±0.5°C. For contouring, temperatures at the following depths were averaged at 5-day intervals: 0 – 16 m at 2 m intervals; 20, 30, 50, 75, 100 m. Chlorophyll samples were taken with 2.5 – 5.0 l Niskin bottles, usually at 8 depths (0, 3, 6, 9, 12, 15, 25, 50 m). Chl a retained on Gelman A/E glass-fiber filters was extracted in 90% acetone and analyzed fluorometrically. Chlorophyll data are presented fully in Ohman (1983).

Zooplankton abundance at Station D was determined with a 0.5-m diameter, 73-μm mesh net for analysis of *Pseudocalanus* stage structure (Ohman, 1985) and a 1.0-m diameter, 216-μm mesh net for enumeration of predatory zooplankton (on 20 September 1979 a 0.75-m, 110-μm mesh had to be substituted). Replicated (2 – 4) vertical hauls with the 73-μm net were made from 180 – 0 or 150 – 0 m at ~30 m min^{-1}. Replicate (2 – 7) hauls with the 216-μm mesh net were made by lowering the net mouth to within 2 m of the bottom and retrieving vertically at ~45 m min^{-1}. Sampling for *Pseudocalanus* sp. females in 1973 and 1978 and vertically stratified sampling of *Pseudocalanus* sp. females and predatory zooplankton was performed with a 1.0-m, 216-μm modified Juday closing net. Nets were rinsed immediately and zooplankton preserved in a 10% formalin solution buffered with sodium borate. Ionol was added to aid preservation of zooplankton pigments.

Predatory zooplankton and the eggs and copepodids of *Pseudocalanus* were counted in quantitative splits obtained with a Folsom splitter or from entire samples. In the 216-μm mesh series *Pseudocalanus* sp. females and euphausiid furciliae were counted from multiple aliquots subsampled with a Stempel pipet. Euphausiid abundances are based on fewer samples than other zooplankton species; only night hauls were used because of daytime net avoidance by euphausiids (e.g. Brinton, 1967).

Epipelagic fish were sampled near dusk on 10 and 11 July 1979 at Station D. On 10 July fish were dip-netted in surface waters. On 11 July fish were captured with a surface trawl (6.1 m wide, 3.1 m deep; graded mesh from 76 mm at mouth to 6 mm at cod end) towed between two vessels moving at ~3 km h^{-1}. Surface-trawling methods were those used by Bax *et al.* (1980). Three north-to-south transects, each of 10 min duration, were made over Station D. Fish were preserved immediately in 10% formalin. Wet mass of fish was determined by absorbing residual surface water and weighing on a top-loading balance. Standard length was measured to the nearest mm.

Mortality rates

The *Pseudocalanus* population was divided into nine stages as indicated in Table I, with stage durations (τ_x) expressed as a multiple of the egg duration (where k = stage

Table I. Stage structure and relative stage duration used for *Pseudocalanus* mortality calculations.

k	Developmental stage	Stage duration (Multiple of egg duration)
1	Egg	1.00
2	Nauplii	4.09
3	CI	0.96
4	CII	1.01
5	CIII	0.80
6	CIV	0.72
7	CV	1.30
8	CVI-male	—
9	CVI-female	—

number). Egg duration (ED, days) as a function of temperature (T, °C) was obtained from:

$$ED = 1845 \, (11.45 + T)^{-2.05} \tag{1}$$

(Corkett and McLaren, 1978; Thompson, 1982). Predicted values from this relationship agree with measurements of ED of *Pseudocalanus* from Puget Sound within 8.4% at 10°C and 0.9% at 15.5°C (B.W.Frost, personal communication). The constants in Table I are derived from the postembryonic development times reported in Landry (1983).

The day — night average temperature experienced by postembryonic stages through copepodid II (CII), and the daytime temperature experienced by stages CIII through adult were estimated from the temperature in the chlorophyll maximum layer. Stages CIII through adult (and eggs) were assumed to experience a lower temperature by night when vertically migrating. Diel vertical migration behavior of *Pseudocalanus* appears to change at stage CIII (McLaren, 1974; Ohman, 1983). Night temperature was estimated from the temperature at the weighted mean depth where females occurred by night (Ohman, 1983). The fraction of a day spent at the day temperature was estimated from daylight hours. Hours of daylight (HD) at 48°N latitude vary with Julian day (JD) according to:

$$HD = 8.37 + 7.68 \, e^{\frac{(-X - 172)^2}{11327}} \tag{2}$$

where:

$$X = JD \qquad \text{for } JD < 355$$
$$X = JD - 365 \qquad \text{for } JD \geq 355$$

The maximum difference between observed daylength (Anonymous, 1983) and that predicted by this curve is 5.6%.

Mortality varying through time was estimated from a method based on the assumption of continuous recruitment (see Appendix, equations A9, A10). Equation (A9) was solved for mortality of adult males and females over each sampling interval beginning in March 1979. Occasional negative mortality rates were set equal to 0. The recruitment term to the adult stage [term 1, eq. (A9)] approaches 0 at some time in July or August as CV stages enter diapause. The assumption of zero recruitment is therefore incorporated into mortality estimates during late summer through winter. Further

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assumptions include the lack of immigration or emigration, a uniform age distribution within a stage and a 1:1 sex ratio of copepodid stage V.

The mortality of immature stages could not be estimated as a function of time due to their short stage durations. Instead average mortality of immature stages was estimated for the period between March ($t = 1$) and July ($t = x$), the principal period of population growth prior to the onset of diapause of late copepodid stages. For each stage the total number of new recruits (T_k) between March and July was approximated from:

$$T_k = \sum_{t=1}^{x} \frac{(N_{k,t} + N_{k,t+1})\,\Delta t}{2\,\tau_{k,t+\frac{1}{2}}} \tag{3}$$

where N_k is the abundance of stage k at time t and $\tau_{k,t+\frac{1}{2}}$ is the temperature-dependent development time for stage k midway between time t and time $t+1$. Average survivorship to stage k was then estimated from (T_k/T_1), where T_1 is the total number of eggs produced. This average survivorship value approximates survivorship between the midpoints rather than the beginnings of each stage and may best be considered only a qualitative indication of survivorship patterns between successive stages (cf. Hairston and Twombly, 1985). Mortality of stage CV was assumed equal to that of stage CIV. Egg mortality rate was set equal to female mortality since eggs are carried in an attached egg sac. The average mortality of adults was obtained from mean values between March and July, weighted for the length of each sampling interval.

Injury analysis

Copepods were collected in vertical hauls from $\sim 180-0$ m with a 1.0-m diameter, 216-μm mesh net and preserved immediately. Samples for injury analysis were taken within 1 h of midnight except for the May sample which was taken at dusk. Nightime samples were analyzed because *Pseudocalanus* sp. adults encounter predators nocturnally. Specimens were not abraded or disturbed prior to examination. Only individuals collected in 1979 were examined for this purpose. Between 200 and 600 *Pseudocalanus* sp. females were randomly subsampled on each date and scored for injuries according to the criteria in Ohman (1984).

Feeding experiments

The zooplankton used in feeding experiments was collected in Puget Sound using nets with nonfiltering cod ends. Animals were transported to the laboratory then acclimatized for at least 24 h to a suspension of small copepods dominated by *Pseudocalanus* sp. Mature specimens of the hyperiid amphipod *Parathemisto pacifica*, the gammarid amphipod *Cyphocaris challengeri*, the cyclopoid copepod *Corycaeus anglicus* and the calanoid copepod *Metridia lucens* s.l. were then placed in glass-fiber (Gelman A/E) filtered seawater for 24−48 h starvation prior to the experiments. Two to seven predators of a single species and 20−25 *Pseudocalanus* sp. females were added to 1.0-l jars and rotated on a grazing wheel or roller mixing device at ~ 1.5 r.p.m. Experiments were performed at 8°C (15°C in the case of *C. anglicus*) with 7−12 replicate containers. Experiments lasted 24 h except in the case of *M. lucens* s.l. and *C. anglicus* which continued for 3 d to obtain measurable prey depletion. Injured *Pseudocalanus* were recorded and the number of missing plus injured *Pseudocalanus* corrected for recovery in controls.

Chaetognath predation

Sagitta elegans gut contents were analyzed from specimens collected in vertical hauls from ~ 180−0 m on six dates (30 September 1978, 12 April, 7 June, 10 July, 5 December 1979). These dates were selected for adequate seasonal coverge and for occasions when samples were taken for analysis of the vertical disribution of *Pseudocalanus* sp. (Ohman, 1983). The gut region of 2377 *Sagitta elegans* was examined under a dissecting microscope. The developmental stage of each chaetognath was assigned as follows: stage I, juvenile; stage II, ovaries developing, testes present [individuals with rudimentary but visible ovaries, as depicted by Russell (1932) as the upper limit of stage I were assigned to stage II here]; stage III, large ova present. The gut of those *S. elegans* containing prey was dissected under glycerine on a microscope slide. Prey items were often identified from body parts alone, including the exoskeleton, urosome or mandibles. Copepod mandibles were identified from copepods collected in Puget Sound as well as from Minoda (1971) and Sullivan *et al.* (1975). The unusual prey item found in the anterior 1/3 of the chaetognath gut was assumed to have been ingested in the cod end of the net and was discounted from consideration. Measurements of total length (extended specimens) were made of all non-copepod prey items recovered from predator guts. Measurements of the total lengths of copepods were made on intact copepods from Dabob Bay plankton samples.

The turnover rate or gut residence time of prey is needed to estimate predation rates on *Pseudocalanus* from analysis of predator gut contents. It is assumed here that the dominant factor influencing gut residence time (G) is temperature, although G may also depend upon prey species (Feigenbaum and Maris, 1984), the number of prey ingested (Reeve, 1980; Canino and Grant, 1985), the size or age of the predator (Reeve, 1980; but see Feigenbaum and Maris, 1984), and its state of hunger (cf. Murtaugh, 1984). G is expressed as a continuous function of temperature from an exponential curve fitted to the mean values reported in Kuhlmann (1977; 15°C, 2.45 h), Reeve (1980; 3.5 h, and Sullivan's results therein, 4.0 h) and Feigenbaum (1982; 0°C, 10.23 h). Reeve (1980) states that experimental temperatures were close to ambient temperatures in Saanich Inlet (13°C). The curve fitted to these four points is:

$$G = 10.48 \ e^{-0.086 \ T} \qquad (r^2 = 0.954, \ P < 0.05) \qquad (4)$$

Estimates of the temperature experienced by *S. elegans* can be made from knowledge of the vertical distribution of the chaetognath population and vertical profiles of temperature. The following assumptions were made concerning vertical distributions of *S. elegans* in Dabob Bay based on the results of King (1979) and Ohman (1983): (i) stage I *S. elegans* experience near-surface temperatures day and night, estimated from the temperature where *Pseudocalanus* is most concentrated; (ii) stage II and stage III *S. elegans* ingest *Pseudocalanus* near the surface at night; by day they experience lower temperatues (estimated by the temperature at 100 m depth); (iii) feeding rate is constant over the duration of night-time hours, (iv) *S. elegans* contain half the number of prey by day as by night and (v) only stage I *Sagitta* overlap with and consume *Pseudocalanus* diurnally.

Daily consumption of *Pseudocalanus* sp. females by *S. elegans* was obtained from:

$$C = \left\{ \frac{NP}{G_N} + \frac{HD \ P}{2 \ G_D} \right\} S_I + \left\{ \frac{NP}{G_N} \right\} (S_{II} + S_{III}) \qquad (5)$$

where $C = Pseudocalanus$ consumed $m^{-2}\ d^{-1}$

G_N, G_D = gut residence time at night or day temperature

HD = hours of daylight (eq. 2)

$N = 24 - HD$

P = number of *Pseudocalanus* sp. females $Sagitta^{-1}$

S_I, S_{II}, S_{III} = number of *Saggita* m^{-2} in stages I, II, III.

Fish predation

The alimentary canal was dissected from all chum salmon collected and a subsample of 25 stickleback. All prey items ($N = 11\ 957$) were removed to glycerine on microscope slides for identification. Length – frequency distributions of prey were determined from measurements of total length of extended specimens. The total length of *Euphausia pacifica* and of *Parathemisto pacifica* was estimated from the size of the eye, often the structure that is best preserved in fish stomachs. A power curve was used to describe the relationship between eye height (EH; measured perpendicular to the long axis of the body) and total length (TL; extended specimens) for these two species from specimens collected in Dabob Bay (Figure 1):

Euphausia pacifica:
$$TL = 0.0043\ (EH)^{1.192} \qquad (r^2 = 0.975, P < 0.001) \qquad (6)$$

Parathemisto pacifica:
$$TL = 0.0058\ (EH)^{0.963} \qquad (r^2 = 0.781, P < 0.001) \qquad (7)$$

It was assumed that *P. pacifica* smaller than 1.4 mm were ingested while in the marsupium of adult *Parathemisto* and that fish captured the larvacean *Oikopleura dioica* while in its house. The relationship between house length (L) and trunk length (T) for *O. dioica* was approximated from that for *O. rufescens* in Alldredge (1977): $L = 5.6$ $T - 0.4$. *O. dioica* and *O. rufescens* of similar size have houses of similar size (A.Alldredge, personal communication).

The zooplankton composition in fish diets was compared with ambient zooplankton densities using log Q as a measure of electivity (Jacobs, 1974) and the standard error of electivity was estimated from Fleiss (1981).

Approximations of daily consumption rates by fish were made using the relation:
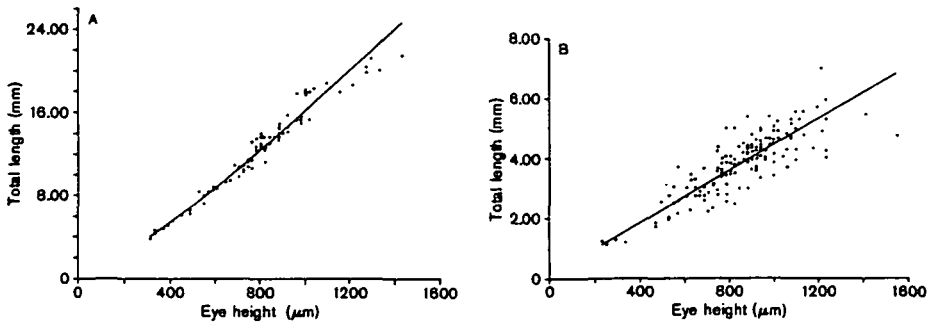

Fig. 1. Relationship between height of the eye and total length for (A) *Euphausia pacifica* and (B) *Parathemisto pacifica*. The fitted curves are obtained from Model I regressions with bias corrected (Beauchamp and Olson, 1973).

$C = 24\ S\alpha$, where C is the consumption rate, S is the 24-h mean abundance of prey in predator guts, and α is the rate of gut evacuation h^{-1} (Eggers, 1977; Simenstad et al., 1980). For application of this simplified equation it was assumed that the 24-h mean food concentration was one-half that found at dusk and that ambient temperature was 15°C. For chum salmon α was estimated from an empirical equation for sockeye salmon (see Simenstad et al., 1980) and for stickleback α was approximated as $0.180\ h^{-1}$ from the data presented in Rajasilta (1980) for three-spined stickleback feeding on Daphnia at 14°C.
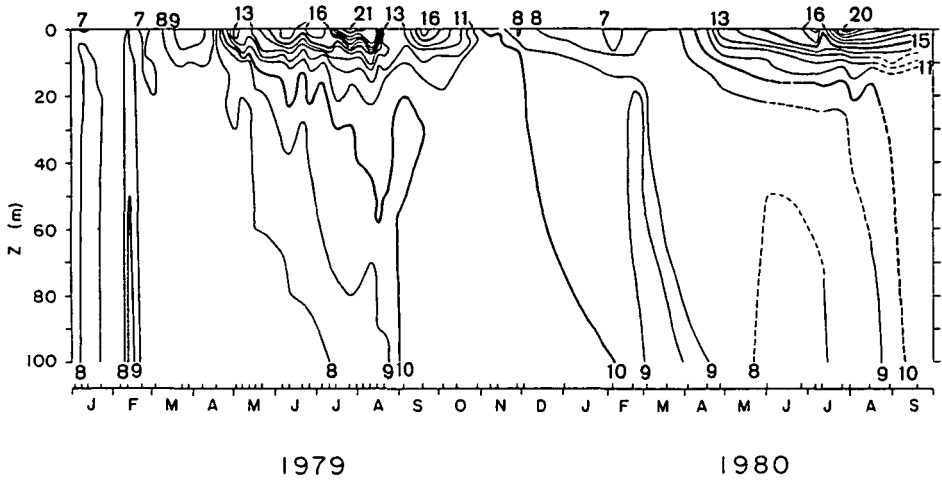

Fig. 2. Temperature (°C) near Station D in Dabob Bay, 1979 — 1980. Upward facing ticks on lower axis indicate intervals when temperature data were taken (see Methods). Dashed regions indicate uncertain contours.
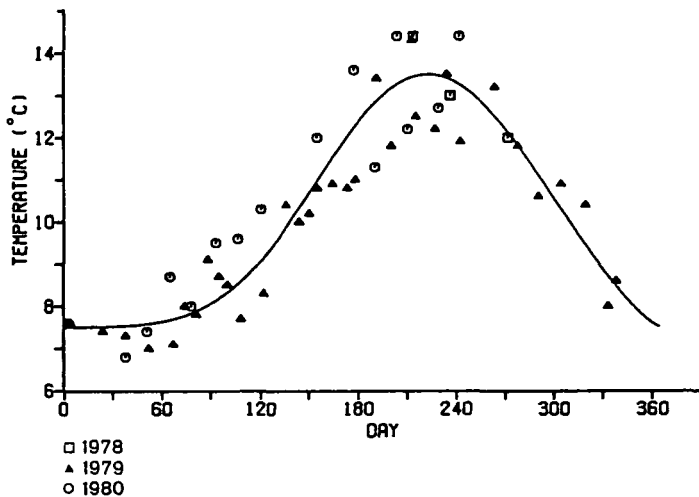

□ 1978
▲ 1979
○ 1980

Fig. 3. Temperature at the depth of the chlorophyll maximum, from vertical profiles of temperature and Chl a made at Station D during 1978 — 1980 (see text eq. 8).

Results

Mortality

Temperature in Dabob Bay varied as illustrated in Figure 2, and the temperature at the depth of the chlorophyll maximum (TC_{max}) changed as in Figure 3. In winter the chlorophyll maximum was poorly defined but the euphotic zone was nearly isothermal. Seasonal changes in TC_{max} can be described by the function:

$$TC_{max} = 7.5 + 6.0 \ X^{1.319} \ e^{0.385(1 \ - \ X^{3.426})} \tag{8}$$

where

$$X = \frac{(365 - JD)}{143}$$

Seasonal changes in TC_{max} approximate seasonal changes in temperature at the median daytime depth of the *Pseudocalanus* population (Ohman, 1983), although this empirical relation does not require that the copepods are orienting specifically to the chlorophyll maximum layer.

Temperature-dependent development times were used to estimate survivorship and mortality of *Pseudocalanus* sp. (see Methods). The average survivorship of *Pseudocalanus* sp. varied among developmental stages and between years (Figure 4). The two principal episodes of mortality in the life history of *Pseudocalanus* sp. occurred in the naupliar and the late copepodid stages. In both years a plateau region of low mortality occurred in the young copepodid stages, between CI or CII and CIV. Higher mortality of late copepodid stages in 1979 than in 1980 resulted in approximately one-half the survivorship through the adult stage in 1979 by comparison with 1980. Daily mortality
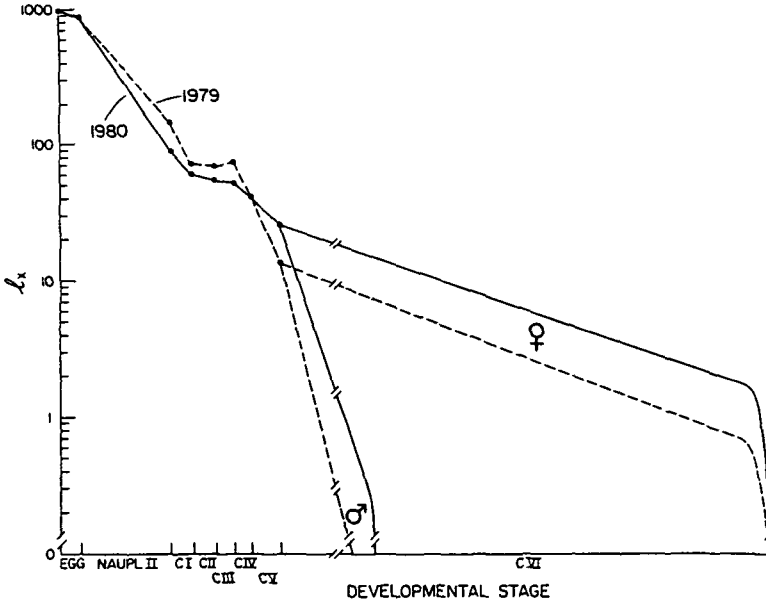

Fig. 4. Stage-specific survivorship of *Pseudocalanus* sp. during 1979 and 1980. The curves reflect average survivorship from March to July, the primary period of population growth. The width of each segment on the abscissa is proportional to the stage duration, except for the CVI stage which is not of fixed duration.
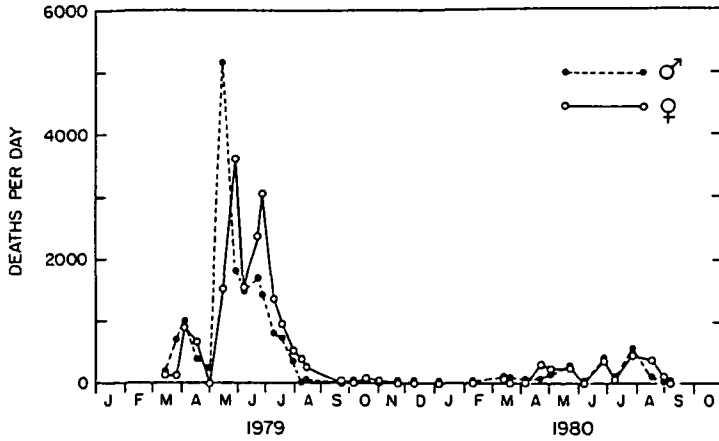
Fig. 5. Seasonal variation in mortality of adult male and adult female *Pseudocalanus* sp.
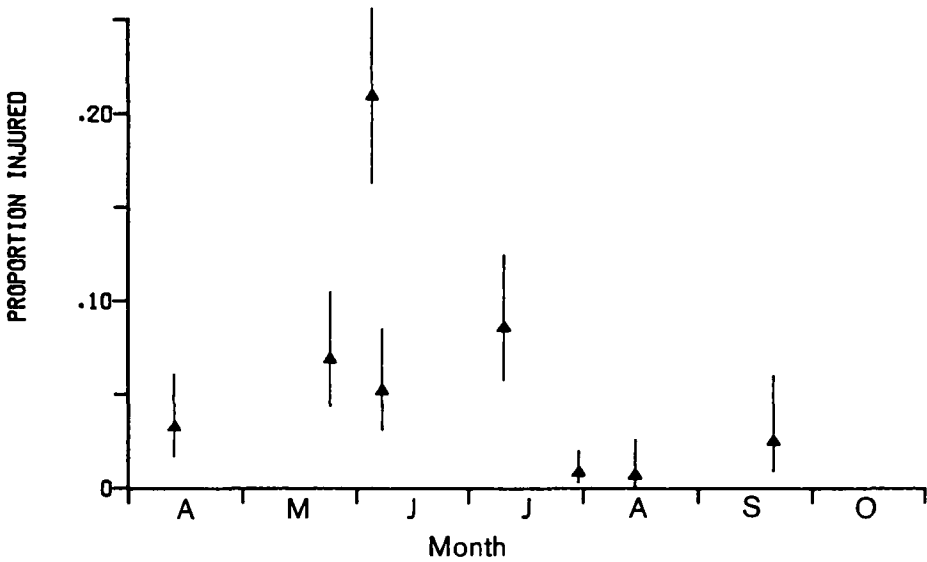

Fig. 6. Proportion of injured *Pseudocalanus* sp. females in field samples from Station D in Babob Bay during 1979. ($x \pm 95\%$ C.L. for a binomial distribution.)

of both adult male and adult female *Pseudocalanus* exhibited a seasonal increase, with maximum values in summer and lower values in winter (Figure 5). Adult males experienced substantially higher mortality than females. Peak daily deaths for both males and females were higher in 1979 than 1980, by a factor of 9.2 for males and 8.0 for females. The weighted mean instantaneous mortality rate between March and early July, the interval of sustained population growth, was also higher in 1979 than 1980 for males (0.454 d^{-1} versus 0.307 d^{-1} for the two years) and females (0.040 d^{-1} versus 0.036 d^{-1}). Based on these mortality rates, the average half-life of adults (time to 50% mortality) was 1.5 and 2.3 days for males in 1979 and 1980, respectively, and 17.3 and 19.2 days for females.

Table II. Summary of predation rates on *Pseudocalanus* spp. Unless otherwise noted experiments were performed with mature developmental stages of predators, at 8°C, at a prey density of 20 – 30 *Pseudocalanus* l^{-1}.

Predator	Prey predator^{-1} d^{-1} ($\bar{x}$ ± 95%)	Comments
Euchaeta elongata	14.45 ± 1.86	Yen (1983)
Pleurobrachia bachei (6 mm)	6.2	Reeve *et al.* (1978); 13°C
Sagitta elegans	2.51 ± 0.50	Reeve (1980); 13°C
Euphausia pacifica	2.39 ± 2.22	Ohman (1984)
Parathemisto pacifica	0.56 ± 0.72	Present study
Cyphocaris challengeri	0.44 ± 0.40	Present study
Metridia lucens s.l.	0.09 ± 0.06	Present study
Corycaeus anglicus	0.07 ± 0.13	Present study; 15°C

Injury analysis

The frequency of injured *Pseudocalanus* sp. females varied among sampling dates (Figure 6). Injury frequencies were highest in May through early July and declined markedly in late July. The seasonal trend in frequency of injured females paralleled the trend in mortality rate of females (Figure 5).

Feeding experiments

Feeding experiments were used to identify predators responsible for the mortality and injury of adult *Pseudocalanus* sp. Quantification of sources of predation on naupliar stages of *Pseudocalanus* sp. was not attempted because of the large number of omnivorous and predatory zooplankton species which could contribute to naupliar mortality. In Table II the results of the survey predation experiments performed here are compared with those of other predation experiments where *Pseudocalanus* sp. adults were used as prey. All predators or omnivores are species of zooplankton with which *Pseudocalanus* sp. co-occurs in Dabob Bay and in other temperate regions of the northeastern Pacific. The predatory copepod *Euchaeta elongata* shows substantially higher daily predation rates than the other species. In addition, *P. bachei*, *S. elegans* and *Euphausia pacifica* have relatively high per capita attack rates on *Pseudocalanus* adults. [The rank order of predators would change if maximum predation rates were compared rather than rates at an intermediate prey density, since *P. bachei* can capture at least 100 *Pseudocalanus* d^{-1} at swarm densities of prey (Reeve *et al.*, 1978).] The low attack rates by the last four species in Table II and the high variance of those rates suggest that the latter four species do not efficiently handle and capture adult *Pseudocalanus*.

Pleurobrachia bachei and other ctenophore species occurred only in low abundance in Dabob Bay during this study (Ohman, 1983), despite their proliferation in CEPEX enclosures in Saanich Inlet (Harris *et al.*, 1982) and other regions nearby. Low ctenophore abundance may have been due to the year-round presence of large-bodied suspension-feeding zooplankton in Dabob Bay (Damkaer, 1964; Runge, 1985). Suspension-feeding copepods fatally injure cydippid larvae of ctenophores in culture thus suppressing recruitment of adult ctenophores (Greve, 1972; Stanlaw *et al.*, 1981). In addition to the predatory zooplankton treated here, other taxa including medusae, siphonophores and amphipods will also make some contribution to the mortality of adult
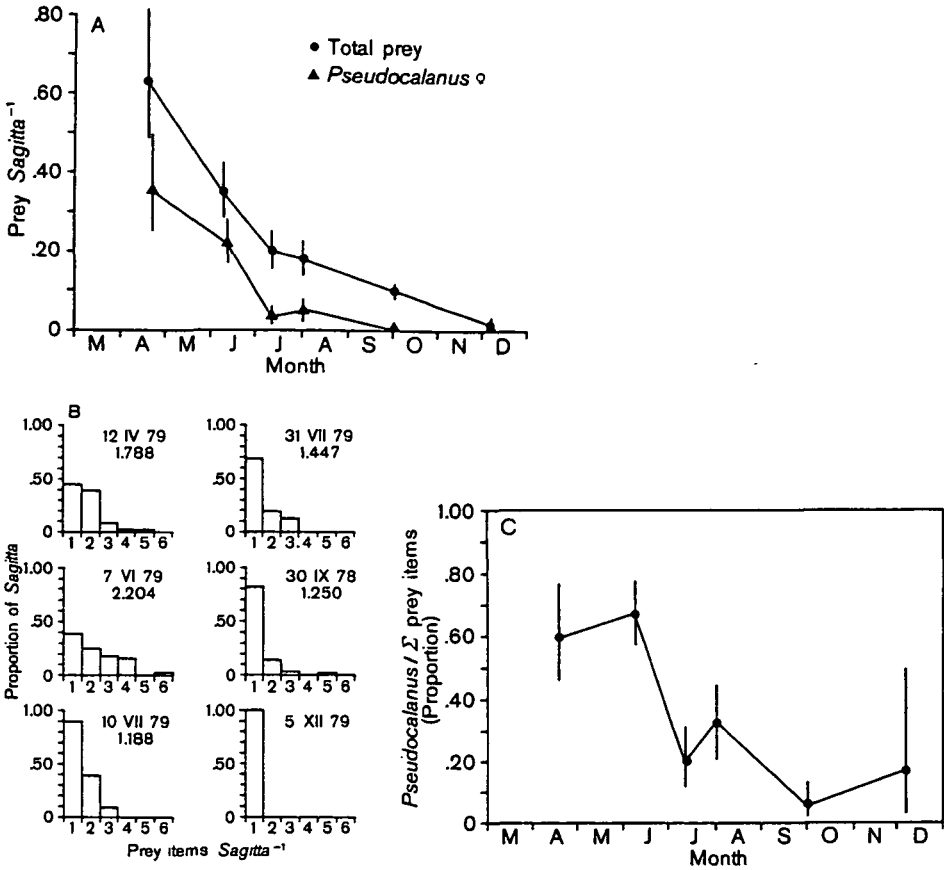
Fig. 7. Seasonal variation in prey ingested by *Sagitta elegans* at Station D in Dabob Bay. (A) Number of prey items per *S. elegans* ($x \pm 95\%$ C.L. for a Poisson distribution). April and June points offset for clarity. (upper curve with circles = total prey; lower curve with triangles = *Pseudocalanus* sp. feamales.) (B) Frequency distribution of number of prey per *S. elegans* on six sampling dates. The mean number of prey per chaetognath is indicated beneath the sampling date. (C) Proportion *Pseudocalanus* sp. of total prey items ($x \pm 95\%$ C.L. for a binomial distribution).

Pseudocalanus in Dabob Bay. Their contribution appears to be relatively minor, however, because of low abundance (Ohman, 1985), low feeding rates or apparent preferences for other prey organisms. To a first approximation the principal predation risk to adult *Pseudocalanus* sp. is from the predatory copepod *Euchaeta elongata*, the chaetognath *Sagitta elegans* and the euphausiid *Euphausia pacifica*.

Predation by Sagitta elegans

The number of *Pseudocalanus* females and total prey items ingested by *S. elegans* in Dabob Bay changed seasonally (Figure 7A). Considering only those chaetognaths containing prey, seasonal differences were detected in the number of prey per chaetognath ($P < 0.001$; G test of independence, Model I; Figure 7B). Multiple prey per chaetognath were found more frequently in April and June than at other times of the year.
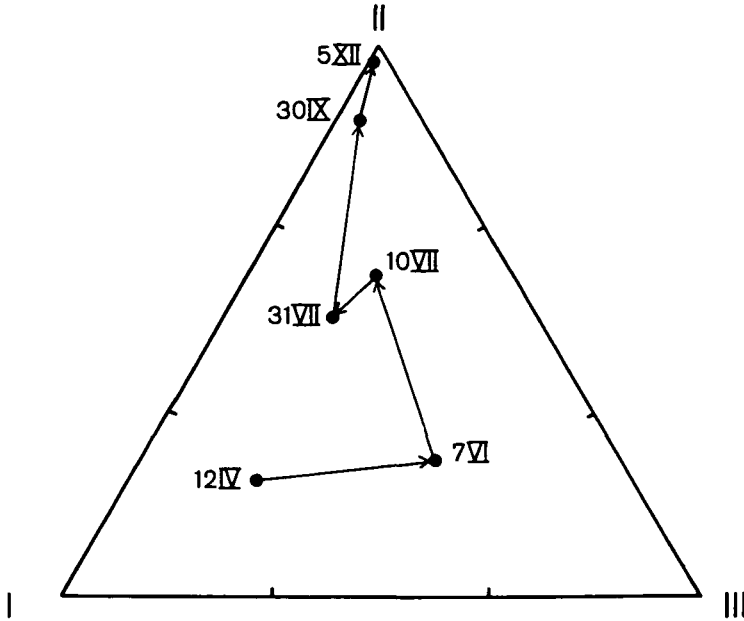
Fig. 8. Seasonal variation of the stage composition of *Sagitta elegans* in Dabob Bay from six dates on which the diet of *S. elegans* was analyzed. Dots indicate the proportion in each chaetognath developmental stage (stage I, II, III). The September sample was taken in 1978 and all others in 1979.

Pseudocalanus copepodids comprised 61.0% of the prey items of *S. elegans* in April and 67.0% in June, thereafter declining to a significantly smaller percentage (Figure 7C). Beginning in July other prey increased in relative importance in the diet of *Sagitta*, although no single prey taxon reached the dominance shown by *Pseudocalanus* earlier in the year (Table III). Substantial contributors to the diet of *S. elegans* in July and September, in addition to *Pseudocalanus* sp. were *Calanus* spp. (*C. marshallae* and *C. pacificus*) and cyclopoid copepods: *Oithona similis*, *Oncaea* spp. and *Corycaeus anglicus*. Few prey items were found in *Sagitta* guts in December. Overall, 96.0% of the prey items were copepods.

The developmental stage structure of the *S. elegans* population shifted seasonally from 21.2% stage II in April to 95.6% stage II in December (Figure 8). Comparison of the stage structure of all *S. elegans* collected in the water column with that of prey-containing *Sagitta* revealed a significant difference between them ($P < 0.001$, Table IV). Analysis of the six dates individually showed significant differences at all times of year ($P < 0.05$). On each date there was an excess of stage III *S. elegans* containing prey by comparison with the relative abundance of this stage in the water column. Except for the samples in April, there were fewer stage II individuals containing prey than expected. Developmental stages I and III chaetognaths accounted for a disproportionate share of the prey consumed by the *S. elegans* population.

The diel vertical migration behavior of *S. elegans* was analyzed on three dates along with the nocturnal distribution of prey-containing chaetognaths (Figure 9). A progressively larger fraction of the *S. elegans* population is found at a deeper daytime and night-

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Table IIIA. Seasonal change in diet of *Sagitta elegans* collected near midnight at Station D, Dabob Bay. Copepod prey taxa listed in approximate sequence of ascending total length. Entries in each column indicate the proportion each prey item represented of total prey on that date. The three most abundant prey categories are underlined.

Prey		Prey composition					
		12 April 79	7 June 79	10 July 79	31 July 79	30 Sept 78	5 Dec 79
Copepoda							
Oithona similis	♀	0.034	0.113	0.053	0.235	0.056	0.000
	copepodids	0.034	0.010	0.026	0.059	0.078	0.083
Paracalanus parvus	♀	0.000	0.000	0.013	0.015	0.044	0.000
	CV	0.000	0.021	0.026	0.015	0.056	0.000
Oncaea spp.	♂ + ♀	0.017	0.031	0.197	0.029	0.056	0.000
Corycaeus anglicus	♀	0.000	0.000	0.040	0.015	0.222	0.000
	♂	0.000	0.000	0.013	0.000	0.056	0.000
Unident. small copepod		0.085	0.031	0.079	0.103	0.044	0.083
Pseudocalanus spp.	♀	0.559	0.629	0.171	0.279	0.044	0.167
	CV	0.017	0.021	0.013	0.000	0.011	0.000
	CIV	0.034	0.010	0.000	0.015	0.000	0.000
	CIII	0.000	0.010	0.000	0.015	0.000	0.000
	CII	0.000	0.000	0.013	0.015	0.000	0.000
Acartia longiremis	♀	0.034	0.000	0.000	0.000	0.000	0.000
	CV	0.017	0.000	0.000	0.000	0.000	0.000
Oithona spinirostris	♀	0.017	0.010	0.000	0.000	0.022	0.000
	copepodids	0.000	0.000	0.000	0.000	0.022	0.000
Centropages abdominalis	♀	0.017	0.000	0.000	0.000	0.000	0.000
Tortanus discaudatus	♂	0.000	0.000	0.000	0.000	0.000	0.000
Metridia lucens s.l.	♀	0.000	0.000	0.000	0.000	0.011	0.250
	CV	0.000	0.000	0.000	0.000	0.011	0.083

Table IIIB. Seasonal change in diet of S. elegans from station D, Dabob Bay. Prey other than Copepoda, listed in approximate sequence of increasing total length.

Prey		12 April 79	7 June 79	10 July 79	31 July 79	30 Sept 78	5 Dec 79
Calanus spp.	♀	0.034	0.052	0.145	0.103	0.056	0.083
	CV	0.000	0.021	0.197	0.059	0.100	0.083
	CIV	0.000	0.000	0.013	0.000	0.033	0.000
	CIII	0.000	0.000	0.000	0.000	0.011	0.000
	CIV	0.000	0.000	0.000	0.029	0.011	0.000
Euchaeta elongata							
Prey composition							
Microzooplankton							
Nauplii		0.068	0.000	0.000	0.000	0.000	0.000
Tintinnida		0.017	0.000	0.000	0.000	0.000	0.000
Trocophores		0.017	0.000	0.000	0.000	0.000	0.000
Bivalve larvae		0.000	0.000	0.000	0.000	0.011	0.000
Polychaete larvae		0.000	0.000	0.000	0.000	0.022	0.000
Pteropoda							
Limacina sp.		0.000	0.010	0.000	0.000	0.011	0.000
Amphipoda							
Parathemisto pacifica		0.000	0.000	0.000	0.015	0.000	0.000
Euphausiacea							
Euphausiid furcilia		0.000	0.010	0.000	0.000	0.000	0.000
Chaetognatha							
Sagitta elegans		0.000	0.021	0.000	0.000	0.011	0.000
No. Sagitta examined		93	278	378	374	620	634
Proportion containing prey		0.355	0.158	0.180	0.126	0.083	0.019
Length (mm) range of Sagitta containing prey		6.4 – 22.9	6.6 – 23.7	8.2 – 21.7	9.3 – 22.5	6.8 – 25.0	18.4 – 26.2

Table IV. Developmental stage composition of prey-containing *Sagitta elegans* and of total *S. elegans* sampled. Data for six sampling dates pooled.

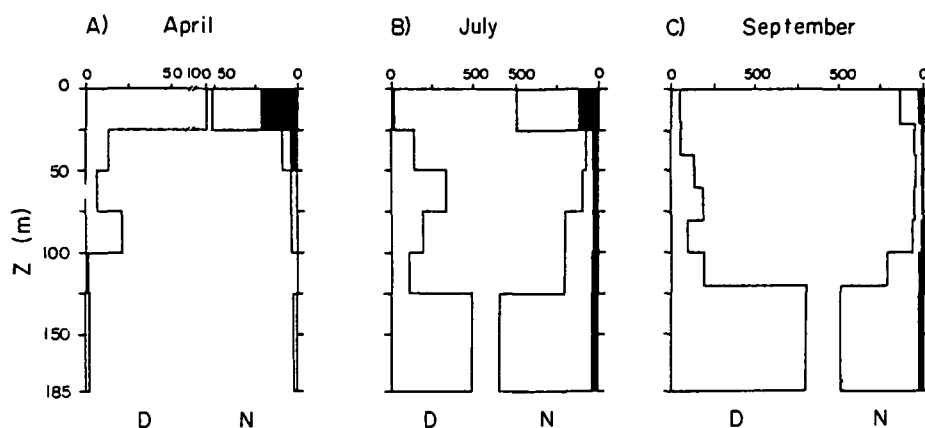| S. elegans	N	Stage I	Stage II	Stage III
Prey-containing	294	0.282	0.439	0.279
Total	3684	0.143	0.764	0.093

$x_2^2 = 161.31$ $P < 0.001$

Fig. 9. Seasonal change in vertical distribution of *Sagitta elegans* and in the nocturnal vertical distribution of prey-containing *Sagitta*. Abundances expressed as number of chaetognaths per sample by day (D) and by night (N) with shaded region on night panels indicating the number of *Sagitta* containing prey. Sampling was carried out on (A) 12 April 1979, (B) 25 – 30 July 1979, and (C) 28 – 29 September 1978.

Table V. Day – night difference in the proportion of *S. elegans* containing prey.

Date	Time	N	Containing prey (proportion)
11 April 1979	Night	93	0.355
	Day	143	0.133
	$x_1^2 = 16.16$	$P < 0.001$	
30 July 1979	Night	1359	0.153
	Day	1226	0.095
	$x_1^2 = 20.08$	$P < 0.001$	

time depth as the year progresses. Concurrently with the seasonal submergence of *Saggita* is the shift to predominance of stage II individuals (Figure 8), a decrease in the proportion of *Sagitta* which exhibit feeding activity and a larger proportion of *Sagitta* containing prey at depth (Figure 9). In autumn and winter most stage II *S. elegans* appear to cease vertical migration behavior, reduce feeding activity and enter diapause in deeper strata.

A higher proportion·of *S. elegans* contain prey during night than day (Table V). Those chaetognaths analyzed for night/day comparisons were scrutinized carefully for evidence of prey remains but their guts were not always dissected.

Table VI. Comparison of observed and expected feeding rates of *Sagitta elegans*. Expected rates of consumption are projected from ambient *Pseudocalanus* densities and the feeding experiments of Reeve (1980). Observed feeding rates are based on stomach content analysis and gut residence times.

Date	Peak density *Pseudocalanus* ♀[a] (No. l⁻¹)	Feeding rate (prey *Sagitta*⁻¹ d⁻¹)		Observed/ expected	Inferred density of *Pseudocalanus* ♀[d] (No. l⁻¹)	Patch Factor[e]
		Expected[b]	Observed[c]			
12 April	1.71	0.22	0.71	3.2	5.94	3.5
7 June	0.82	0.11	0.64	5.8	5.28	6.4
10 July	0.88	0.12	0.19	1.6	1.44	1.6
31 July	0.20	0.03	0.24	8.0	1.83	9.2
30 September	0.04	0.01	0.06	6.0	0.44	11.0
5 December	0.24.	0.03	0.21	7.0	1.60	6.7

[a]Night estimate; vertically stratified hauls with 1-m, 216-μm net.

[b]Estimated from: $Y = \dfrac{0.137\,X}{1 + 0.024\,X}$ where X is prey density and Y is daily predation rate.

[c]Only *Sagitta* in upper 50–60 m included, except upper 100 m on 31 July.

[d]Obtained by solving the equation in note b for X, where Y is the observed predation rate.

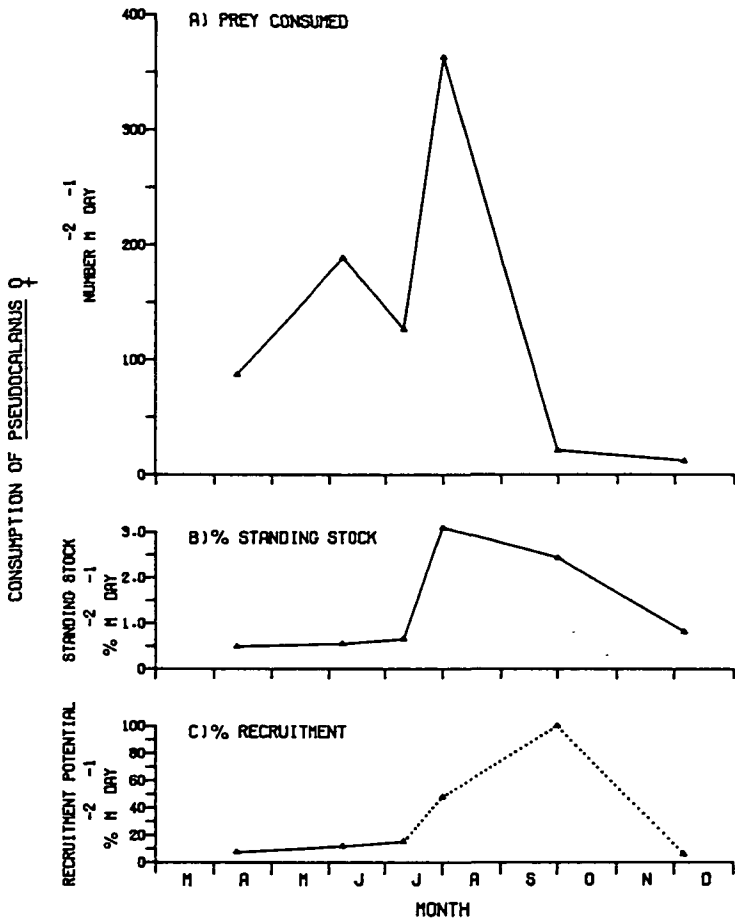[e](Inferred/peak) density of *Pseudocalanus*.

Fig. 10. Seasonal change in predation on *Pseudocalanus* sp. adults by *Sagitta elegans*. (A) *Pseudocalanus* sp. females consumed $m^{-2} d^{-1}$, (B) percentage of standing stock of females removed daily and (C) percentage of recruitment to adult female stage removed daily.

Estimates of *in situ* consumption rates of *Pseudocalanus* sp. by *S. elegans* are shown in Table VI. These estimates can be compared with rates predicted from laboratory feeding experiments, which vary with prey density (Reeve, 1980). Conversely, by comparison of observed *in situ* feeding rates with the expected feeding rates from the measured prey denisty and the laboratory-determined functional response, the density of prey actually encountered by *Sagitta* can be inferred.

The maximum population density of *Pseudocalanus* sp. females in the water column was determined from vertically stratified samples taken at 20 – 25 m intervals at night on each of the dates for which *S. elegans* gut contents were analyzed. The dependence of *Sagitta* feeding rate on *Pseudocalanus* density was described by fitting a Holling type II curve to the data of experimental data of Reeve (1980) using a nonlinear least

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squares estimation procedure employing Marquardt's method:

$$Y = \frac{0.137\ X}{1\ +\ 0.024\ X} \tag{9}$$

where Y = daily predation rate $Sagitta^{-1}$
$\quad X$ = concentration of *Pseudocalanus* $(N\ l^{-1})$

With the estimate of Y obtained from the above analysis of *in situ* consumption, equation (9) can then be solved for X. The result is the density of *Pseudocalanus* sp. females in Dabob Bay necessary to produce the observed feeding rate, or the 'inferred prey density', for comparison with the observed prey density from net samples. This analysis assumes that the feeding behavior of *S. elegans* in the field is comparable to that in the laboratory and that predators attain their daily ration in a night-time feeding bout.

In Table VI the inferred density of *Pseudocalanus* sp. consistently exceeds the population density obtained from net samples. An estimated patch factor was calculated from the ratio of the inferred *Pseudocalanus* sp. density to the maximum observed *Pseudocalanus* sp. density. This patch factor is an indication of the extent to which *Pseudocalanus* sp. aggregated within the sampled depth strata. The patch factor ranged from 1.7 to 9.6 (median = 6.4).

Figure 10A illustrates the total daily water column consumption of *Pseudocalanus* sp. by *S. elegans*. Even the maximum rate of consumption, 360 *Pseudocalanus* sp. $m^{-2}\ d^{-1}$, reflects a low predation rate. This predatory impact was also expressed as the proportion of standing stock and recruitment of adult female *Pseudocalanus* sp. removed daily (Figure 10B, C). Potential recruitment of CVI females was estimated from the number of copepodid stage V present, the assumption of a 1:1 CV sex ratio and the temperature-dependent stage duration. Standing stock removal rates were low all year round (maximum 3.0% d^{-1}) as was consumption of newly recruited adults through mid-July. Calculation of adult recruitment becomes uncertain after July because most copepodid V *Pseudocalanus* sp. enter diapause and recruitment to the adult stage is therefore restricted.

Predation by Euchaeta elongata and Euphausia pacifica

To compare the predation rates by *Euchaeta elongata* and *Euphausia pacifica* on *Pseudocalanus* sp. females with predation by *S. elegans*, the abundance and vertical distribution of the former two species were also determined in Dabob Bay. Abundance data are illustrated in Figures 15 and 16 and seasonal changes in vertical distribution are discussed in Ohman (1983). Predation rates by *Euchaeta elongata* were estimated from Yen (1983) assuming that CV and CVI female *Euchaeta* were the principal stages ingesting *Pseudocalanus* adults. Only those predators in the upper 50−60 m at night were assumed to overlap with and attack *Pseudocalanus* sp. Experimental work has shown that *Pseudocalanus* sp. adults are the preferred prey of *E. elongata* adults in the laboratory (Yen, 1983) as well as in natural mixtures of prey from Dabob Bay (Yen, 1985). Consumption by *Euphausia pacifica* was estimated from the functional response in Ohman (1984) assuming that only those *E. pacifica* > 10.5 mm total length occupying the upper 50−60 m nocturnally attacked adult *Pseudocalanus*. Although *E. pacifica*
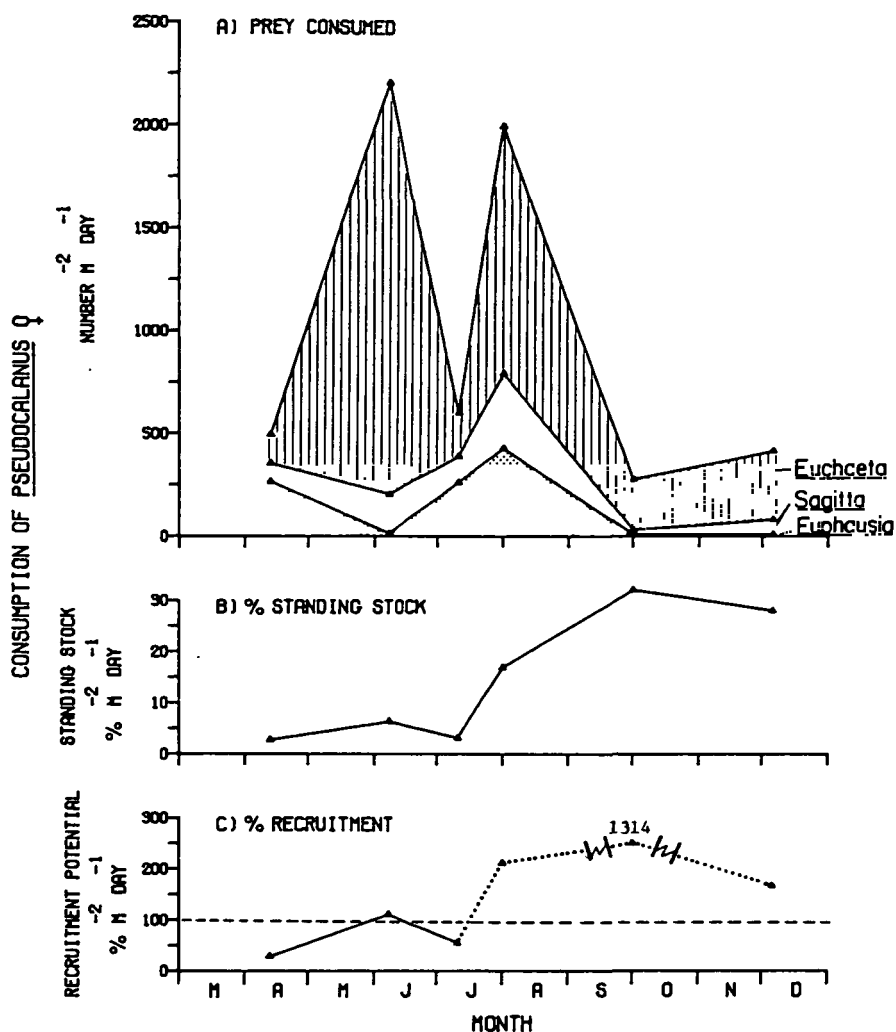
Fig. 11. Seasonal change in predation on *Pseudocalanus* sp. adults by three species of predatory or omnivorous zooplankton (*Euchaeta elongata*, *Euphausia pacifica*, *Sagitta elegans*). (A) *Pseudocalanus* sp. females consumed $m^{-2} d^{-1}$, (B) percentage of standing stock of females removed daily, and (C) percentage of recruitment to adult female stage removed daily.

adults ingest diatoms at higher rates than they attack copepods, the presence of diatom prey does not depress attack rates on copepods (Ohman, 1983). Prey concentrations were estimated from the inferred prey densities in Table VI.

The daily prey consumption by *S. elegans*, *Euchaeta elongata* and *Euphausia pacifica* combined is shown in Figure 11A. The maximum consumption rate occurs in early June and is due primarily to predation by *Euchaeta elongata*. The contribution of *S. elegans* to the total predation on *Pseudocalanus* is small and is usually exceeded by euphausiid predation. Seasonal changes in daily consumption of *Pseudocalanus* sp.

Table VII. Abundance and size composition of planktivorous fish collected in Dabob Bay, 10 – 11 July 1979. Abundance estimates are from surface trawl samples. Length and weight measurements are from dip net and surface trawl samples.

	Stickleback (*Gasterosteus aculeatus*) ($\bar{x} \pm$ SD)	Chum salmon (*Oncorhynchus keta*) ($\bar{x} \pm$ SD)	
		Small mode	Large mode
No. fish trawl^{-1}	9.33 ± 4.66		5.33 ± 4.16
Estimated no. m^{-2}	0.043*		0.025*
Standard length	72.7 ± 3.7 mm	73.1 ± 4.7 mm	97.3 ± 1.2 mm
(range; *n*)	(61 – 83; 35)	(63 – 83; 14)	(96 – 98; 3)
Wet weight	4.76 ± 0.95 g	4.19 ± 1.17 g	8.67 ± 0.87 g
(range, *n*)	(2.8 – 6.8; 35)	(2.6 – 6.8; 14)	(7.7 – 9.4; 3)

*Assuming tow length averaged 460 m, effective net area = 16.1 m^2 and capture efficiency for 75-mm fish if 9.0% (N.Bax, personal communication).

females (Figure 11A) parallel changes in daily mortality (Figure 5), with seasonal maxima occurring in May – July and sharp declines by September. Removal of standing stock and of recruitment potential of *Pseudocalanus* sp. females peaks later in the year (in late September, Figure 11B, C) than the maximum in consumption rate (June; Figure 11A). (Again note that recruitment after July is uncertain, reflected by the dotted line in Figure 11C). Most importantly, predators have the capability to suppress recruitment of *Pseudocalanus* sp. females beginning as early as June (i.e. the predation rate exceeds 100% of the recruitment potential).

The maximum early summer daily consumption (2200 *Pseudocalanus* females d^{-1}; Figure 11) is somewhat lower than the maximum daily mortality (3610 *Pseudocalanus* sp. females d^{-1}; Figure 5). Estimated predation on *Pseudocalanus* females in December is higher than the estimated mortality, perhaps because predators have switched to alternate prey.

Fish predation

For comparison with zooplankton predation, a 'snapshot' was made of the abundance and diet of planktivorous fish in early July, a time of high mortality of *Pseudocalanus* (Figure 5). Analysis of temporal changes in fish predation was beyond the scope of this investigation. Sampling with a surface trawl at Station D resulted in capture of adult three-spine stickleback (*Gasterosteus aculeatus*) and juvenile chum salmon (*Oncorhynchus keta*). No other species were captured. An estimation of the abundance of fish m^{-2} is made in Table VII, although this is only an approximation because of the unknown capture efficiency of the net for stickleback (here assumed equal to that for chum salmon of the same size) and to the unknown schooling behavior or larger-scale distribution pattern of the fish. Few fish larvae were observed in the 216-μm mesh plankton samples taken at Station D in July.

Qualitative differences in the diet of stickleback and salmon are reflected in the predominance of copepods as prey for stickleback (62.5% of total prey items; see Figure 12) in contrast to the small contribution of copepods to the diet of chum salmon collected concurrently (2.6% of total prey items, both salmon size classes combined).

Table VIII. Diet of planktivorous fish. Entries in each column indicate the mean (±SD) abundance of each prey item in the stomachs of stickleback (61–83 mm; $N = 25$), small chum salmon (63–83 mm; $N = 14$) and larger chum salmon (96–98 mm; $N = 3$). Copepod prey taxa are listed in approximate sequence of increasing total length. If not noted, copepod developmental stages are adults. The three most abundant prey categories are underlined in each column.

Prey		Number of prey items ($\bar{x}$ ± SD)		
		Stickleback	Chum salmon	
		(61–83 mm)	(63–83 mm)	(96–98 mm)
Copepoda				
Oithona similis	♀	0.4 ± 0.9	—	—
Paracalanus parvus	♀	47.4 ± 101.2	—	—
	♂	1.2 ± 2.4	—	—
	CV	9.5 ± 15.2	—	0.3 ± 0.6
	CIV	0.2 ± 0.5	—	—
	CIII	0.1 ± 0.2	—	—
Corycaeus anglicus		19.9 ± 33.4	—	—
Unidentified small copepod		0.2 ± 0.4	—	—
Pseudocalanus sp.	♀	18.5 ± 36.5	—	—
	♂	0.4 ± 0.9	—	—
	CV	0.7 ± 1.5	—	—
	CIII	0.1 ± 0.3	—	—
	CII	0.1 ± 0.2	—	—
Oithona spinirostris		0.1 ± 0.4	—	—
Centropages abdominalis		0.2 ± 0.4	—	—
Scolecithricella minor		0.1 ± 0.4	—	—
Aetideus divergens		0.6 ± 1.3	—	—
Metridia lucens s.l.	♀	1.8 ± 2.4	—	0.3 ± 0.6
	♂	0.2 ± 0.5	—	—
	CV	0.9 ± 3.2	—	—
Calanus spp.	♀	12.6 ± 15.8	0.4 ± 0.6	1.0 ± 1.7
	♂	52.0 ± 45.5	0.2 ± 0.4	3.3 ± 5.8
	CV	13.3 ± 19.5	0.6 ± 0.9	0.3 ± 0.6
	CIV	0.9 ± 1.6	—	—

|			
Candacia columbiae	CIII	0.8 ± 1.8	—	—
	CII	0.5 ± 1.5	—	—
	CI	1.4 ± 2.7	—	—
		2.1 ± 4.8	—	0.3 ± 0.6
Epilabidocera longipedata	CV	46.1 ± 40.4	0.3 ± 0.6	1.0 ± 1.7
Metridia okhotensis	σ	0.1 ± 0.2	—	—
Euchaeta elongata		0.4 ± 0.6	1.3 ± 1.8	—
Cladocera		0.4 ± 1.6	—	—
Ostracoda		0.1 ± 0.2	—	—
Insecta		7.9 ± 28.4	113.6 ± 112.8	—
Decapoda (larvae)		4.1 ± 5.0	0.4 ± 1.1	0.7 ± 0.6
Appendicularia				
Oikopleura dioica		45.8 ± 83.7	21.0 ± 51.9	22.7 ± 19.7
Amphipoda				
Parathemisto pacifica		102.0 ± 159.0	1.8 ± 2.3	10.7 ± 18.5
Gammaridea		0.5 ± 0.9	0.8 ± 1.0	—
Vertebrata				
Fish eggs		3.6 ± 4.9	1.3 ± 2.8	0.3 ± 0.6
Fish larvae		0.4 ± 0.7	0.1 ± 0.3	4.0 ± 6.9
Cnidaria (medusae)		0.1 ± 0.2	—	—
Euphausiacea				
Nauplii		1.1 ± 3.1	—	—
Euphausia pacifica furciliae		1.4 ± 1.7	0.6 ± 1.2	—
Chaetognatha				
Sagitta elegans		0.2 ± 0.5	0.3 ± 0.8	0.3 ± 0.6
Total prey fish^{-1}		400 ± 253	143 ± 112	45 ± 47

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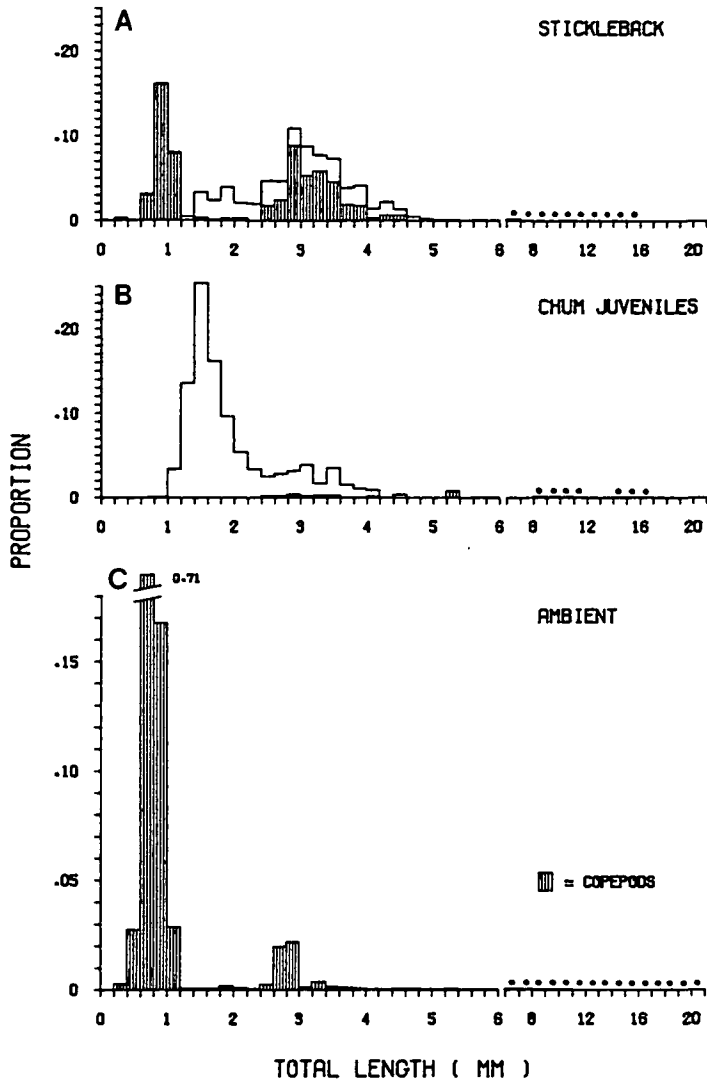
Fig. 12. Length — frequency distribution of prey recovered from (A) adult three-spine stickleback, (B) juvenile chum salmon and (C) from the near-surface zooplankton in Dabob Bay. Shaded region indicates Copepoda. Abscissa scale changes at 6 mm; above this size dots indicate nonzero proportions < 0.002.

Pseudocalanus sp. females were captured by stickleback but not by juvenile chum salmon (Table VIII). Other differences in the spectrum of prey captured are illustrated in Table VIII. Sizes, as well as species, of prey ingested by stickleback and salmon differed (*P* < 0.01, Kolmogorov — Smirnoff test, 2-tailed; Figure 12A, B). Chums ingested a larger proportion of intermediate-sized prey, primarily Insecta (Diptera and Hemiptera, 1.2 — 3.2 mm total length). The spectrum of prey observed suggested that fish were feeding in the surface stratum where they were caught. A comparison of the size distribution of prey in the upper 5 m of the water column (Figure 12C) with that recovered
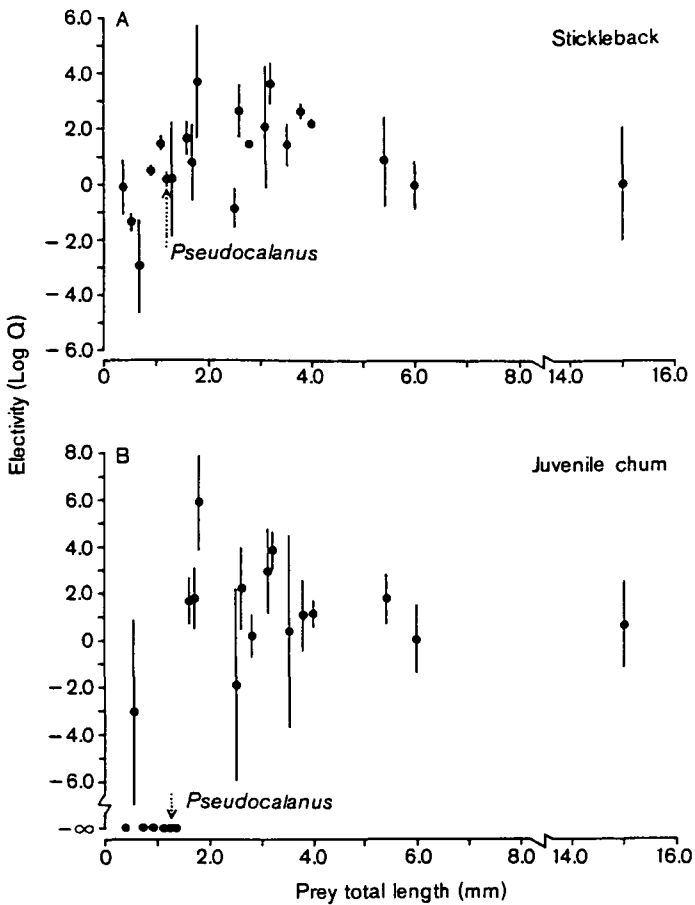
Fig. 13. Electivity (log Q; Jacobs, 1974) with standard error for different prey taxa, by (A) adult three-spine stickleback and (B) juvenile chum salmon. Prey taxa, from left to right in both panels: (1) nauplii, (2) subadult copepodids of *Pseudocalanus* sp. and *Paracalanus parvus*, (3) *Oithona similis*, (4) *Paracalanus parvus*, (5) *Corycaeus anglicus*, (6) *Pseudocalanus* sp., (7) *Centropages abdominalis*, (8) fish eggs, (9) Gammaridea, (10) Insecta, (11) *Metridia lucens* s.l., (12) decapod larvae, (13) *Calanus marshallae* and *C. pacificus*, (14) fish larvae, (15) *Oikopleura dioica*, (16) *Candacia columbiae*, (17) *Epilabidocera longipedata*, (18) *Parathemisto pacifica*, (19) *Euchaeta elongata*, (20) *Euphasia pacifica*, (21) *Sagitta elegans*. Prey are adult stages unless otherwise identified.

from fish stomachs indicated little utilization by either predator species of the smallest available prey and a disproportionate representation of most larger and pigmented prey species. Electivity calculations indicate that *Pseudocalanus* sp. adults were ingested by adult stickleback in the same proportion as their relative abundance in the water column. Larger or more highly pigmented prey formed a disproportionate share of the stickleback diet (Figure 13).

Electivity for *Pseudocalanus* copepodids by stickleback increased with increasing prey stage and size (Figure 14; $r^2 = 0.87$, $P < 0.05$; Spearman's rank). Juvenile chum salmon showed an extreme negative electivity for *Pseudocalanus* sp. and other small
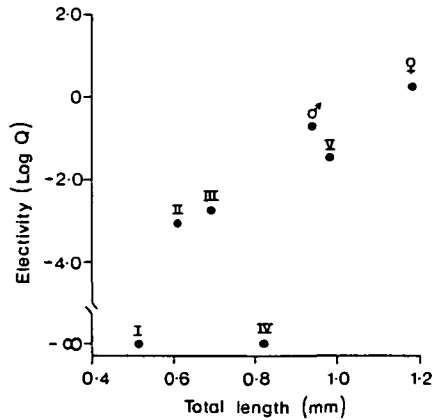
Fig. 14. Electivity for different copepodid stages of *Pseudocalanus* sp. by adult three-spine stickleback.

Table IX. Daily predation on *Pseudocalanus* sp. and predatory zooplankton by three species of zooplankton (*Euchaeta elongata*, *Sagitta elegans* and *Euphausia pacifica*) and by two species of planktivorous fish (stickleback and juvenile chum salmon) on 10–11 July 1979. Estimates of consumption by *S. elegans* and fish are based on stomach content analyses; those by *E. elongata* and *E. pacifica* are projections from laboratory feeding experiments.

Prey	(% standing stock consumed d^{-1})	
	Predatory zooplankton	Fish
Pseudocalanus sp. ♀	3.06	0.01
E. elongata ♀, ♂	0.00[a]	0.03
S. elegans	0.00[a]	0.01
E. pacifica	0.00[a]	0.01

[a]Consumption by *S. elegans* alone.

copepods, peak positive electivity for insects and larvaceans and intermediate electivities for other prey. Both fish species expressed a stronger preference for larger prey, including predatory zooplankton, than for *Pseudocalanus* sp. Positive electivities were shown for *Euchaeta elongata* adults by both fish species; positive electivity for *Sagitta elegans* by chum salmon and neutral electivity for euphausiids by both species.

Consumption of *Pseudocalanus* sp. by adult stickleback and juvenile chum salmon was compared with consumption of *Pseudocalanus* sp. by predatory zooplankton. On this date in July stickleback and juvenile chum salmon removed an estimated 0.01% of standing stock of adult female *Pseudocalanus* daily, in contrast with 3.06% removed daily by predatory zooplankton, a value 300 times greater (Table IX). Table IX also shows that fish predation on carnivorous zooplankton has a greater impact than consumption by predatory zooplankton. Thus, from comparison of the effect of those predators listed in Table IX, the risk to *Pseudocalanus* sp. is greatest from predatory zooplankton while the greater risk to these species of predatory zooplankton is from planktivorous fish.
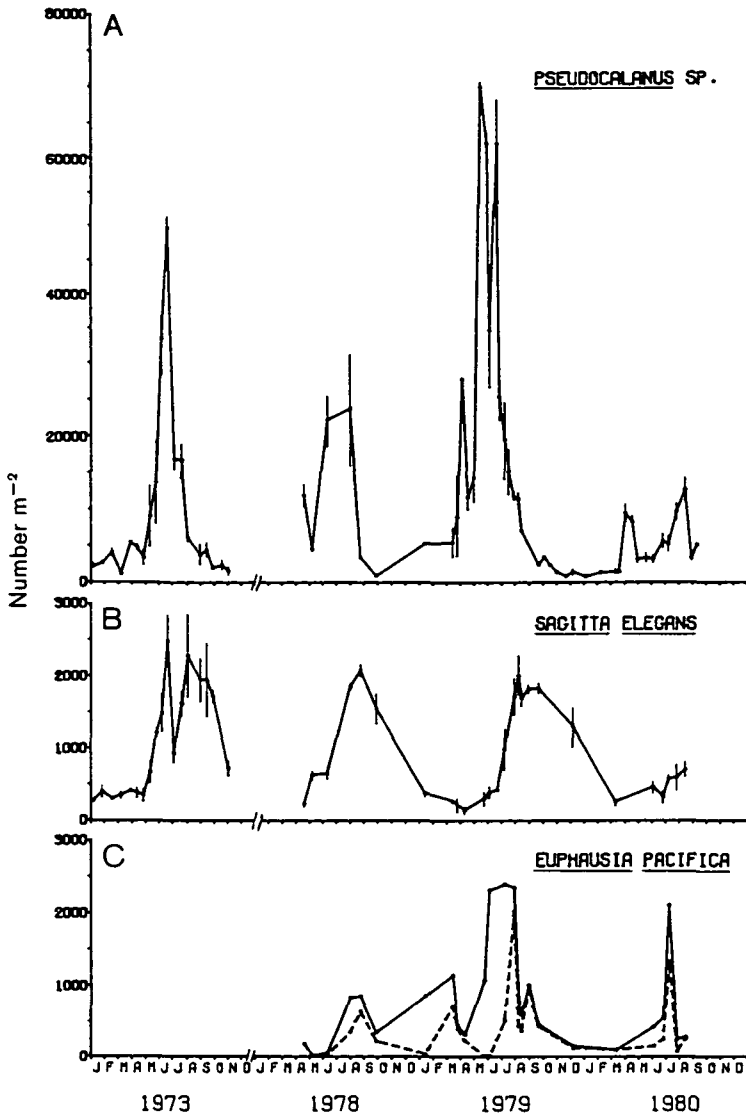
Fig. 15. Interannual variation in abundance of (A) *Pseudocalanus* sp. females, (B) *Sagitta elegans* and (C) *Euphausia pacifica* at Station D in Dabob Bay. Panels (A) and (B) illustrate $\bar{x} \pm$ sd; panel (C) illustrates the median only, due to high sampling variability and fewer replicate samples for euphausiids (solid line = total *E. pacifica*; dashed line = *E. pacifica* > 10.5 mm total length). Data for *S. elegans* for 1973 from King (1979).

Interannual variability

The abundance of *Pseudocalanus* sp. varied considerably among four years when seasonal sampling was conducted (Figure 15A). Note the marked decrease in abundance in 1980 by comparison with 1979 and concomitant decrease in mortality (Figure 5). The abundance of *Sagitta elegans* (Figure 15B) and *Euchaeta elongata* (Figure 16)
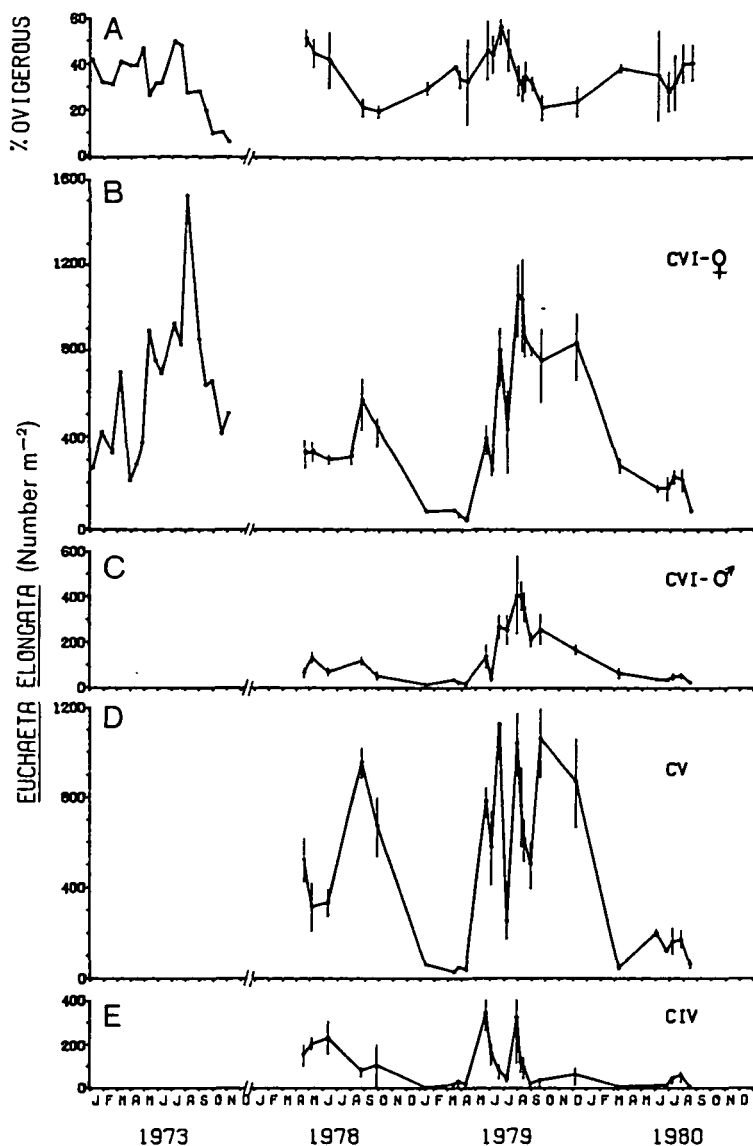
Fig. 16 Interannual variation in fecundity and abundance of *Euchaeta elongata* ($x \pm$ sd). (A) Percentage of females carrying egg sacs and (B) abundance of CVI females, (C) of CVI males, (D) of CV and (E) of CIV. Data for 1973 from Yen (1985).

showed a parallel decline in the same year; this was less evident in the census of the *Euphausia pacifica* population (Figure 15C). In each of the four years sampled the abundance of *Pseudocalanus* sp. and the two species of obligate predators (*S. elegans*, *Euchaeta elongata*) suggested a prey – predator oscillation. The seasonal timing of maximum fecundity of *E. elongata* (as percent of females ovigerous; Figure 16A) typically coincided with or lagged slightly behind the maximum in abundance of *Pseudocalanus*
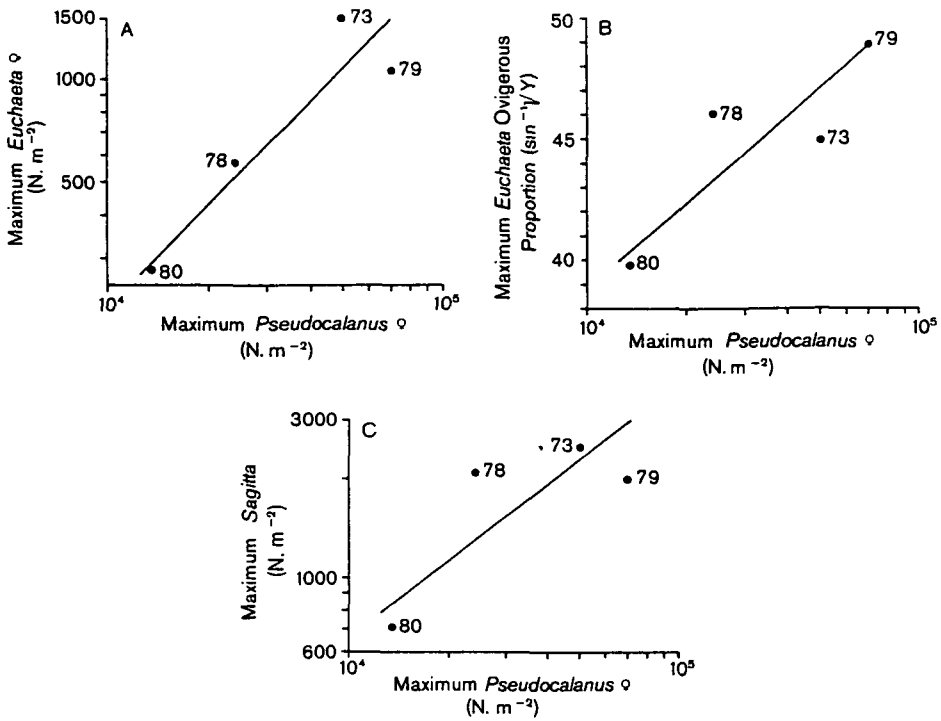
Fig. 17. Relationship between the annual maximum abundance of *Pseudocalanus* sp. females and (A) the maximum abundance of *Euchaeta elongata* females, (B) maximum proportion of ovigerous females of *E. elongata* or (C) the maximum abundance of *Sagitta elegans*.

sp. females (Figure 15A). The timing and magnitude of successive generations of *E. elongata* (Figure 16B – E) were associated with fluctuations in *Pseudocalanus* sp. abundance (Figure 15A). In 1979, the year of maximum abundance of *Pseudocalanus* sp., two generations of *E. elongata* occurred (Figure 16D, E). There may have been a single generation of *E. elongata* in the years of lower abundance of *Pseudocalanus* sp. (1978, 1980). Interannual variations in maximum abundance of *Pseudocalanus* sp. females appeared to be associated with peak abundance of *E. elongata* females ($r^2 = 0.855$, Figure 17A), with maximum proportion of ovigerous females of *E. elongata* ($r^2 = 0.739$, Figure 17B) and with the peak abundance of *S. elegans* ($r^2 = 0.628$, Figure 17C). *Euphausia pacifica* showed no association with *Pseudocalanus* sp. abundance ($r^2 = 0.083$; 1978 – 1980 only). Although a 4-year time series is wholly inadequate to establish such correlations rigorously, the positive relationship between *Pseudocalanus* and *Euchaeta elongata*, and to a lesser extent between *Pseudocalanus* and *S. elegans*, suggests that on time scales longer than the seasonal population growth of *Pseudocalanus* sp. may influence growth and recruitment of its major predators.

Despite similar development rates, adult body size and fecundity of *Pseudocalanus* sp. in 1979 and 1980, a pronounced difference between years occurred in the 'initial conditions' (i.e. the abundance of overwintering CIV and CV stages; Ohman, 1985)
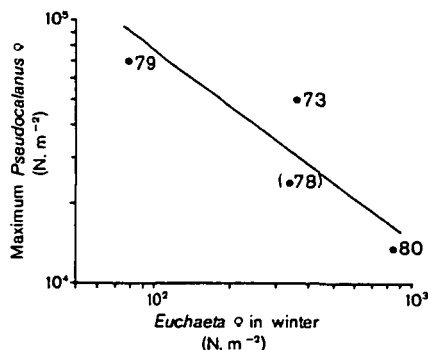
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Fig. 18. Annual maximum of *Pseudocalanus* sp. females versus the abundance of *Euchaeta elongata* females in the previous winter (December – January). The point for 1978 was not included in the regression because it indicates the abundance of *E. elongata* in April; no winter data were available for that year.

and in subsequent survivorship within each year (Figure 4). Both the winter initial conditions and the within-year survivorship appear to be dependent upon mortality due to predatory zooplankton. An indirect measure of predation in winter is provided by the abundance of predatory zooplankton at that time of year. There is an inverse relationship between the abundance of *E. elongata* in winter (December – January) and the subsequent population maximum of *Pseudocalanus* females (Figure 18). Although based on a time series of short duration this relation suggests that winter predation on CIV and CV stages of *Pseudocalanus* sp. affects the initial conditions for population growth, which in turn is a prime determinant of subsequent abundance (cf. Colebrook, 1985).

Discussion

Effects of predation

Parallel studies of mortality rates in a natural population of *Pseudocalanus* sp. and of predation rates by its principal consumers suggest that population growth of this copepod becomes seasonally predator-limited in Dabob Bay. Evidence in support of this conclusion includes: (i) mortality rates of adult female *Pseudocalanus* sp. vary seasonally in association with changes in predation pressure; (ii) frequency of injured adult females track seasonal changes in predation pressure; (iii) calculated daily consumption rates by three species of predatory or omnivorous zooplankton are sufficient to suppress recruitment to the adult stage and restrict population growth early in summer; (iv) between-year differences in summer mortality of *Pseudocalanus* sp. adults are associated with between-year differences in abundance of predators. Moreover, a 2-year study of the effects of resource-limitation on *Pseudocalanus* sp. in Dabob Bay suggested that fluctuations in phytoplankton resources do not markedly affect *Pseudocalanus* sp. population growth rates (Ohman, 1983, 1985). Egg production and recruitment to the adult stage continued during the early summer period of peak mortality noted here, and growth and development of sequential generations occurred at food-satiated rates. Combined with the present study of mortality, injury and predation pressure, results indicate that population fluctuations of *Pseudocalanus* sp. in this study site were primarily restricted

by predators, not by the phytoplankton production cycle.

The results from Dabob Bay do not preclude greater susceptibility of species of *Pseudocalanus* to resource fluctuations in other locations. However, evidence from Loch Striven, Scotland all year round (McLaren, 1978), Georges Bank in February and October (Davis, 1984b) and possibly the Bering Sea continental shelf during April and May (Cooney and Coyle, 1982) also suggest that for the duration of the study periods resources probably permitted maximum reproduction, development or ingestion of species of *Pseudocalanus*. In addition, for a population of *Pseudocalanus* sp. on Georges Bank, computed predation potential appeared sufficient to restrict copepod growth (Davis, 1984a). However, the latter calculations rest on the assumptions that predation rates were independent of prey density and that prey and predator populations overlapped completely in the vertical plane.

Mortality patterns

The changes in survivorship with ontogeny of *Pseudocalanus* sp. parallels mortality changes during the life history of other marine calanoid copepods. Lower survivorship in the naupliar than early copepodid stages has been observed previously in other field populations (Heinle, 1966; Mullin and Brooks, 1970; Landry, 1978; Parslow *et al.*, 1979; Sonntag and Parslow, 1981). Notably, a contrasting pattern was seen in Yen's (1985) study of predation by late developmental stages of *Euchaeta elongata* on different developmental stages of *Calanus pacificus* in the laboratory. Attack rates by *E. elongata* were highest on CI−CII stages of *C. pacificus* and lower on both naupliar and late copepodid stages. This contrast suggests that predators other than late copepodids of *E. elongata* are responsible for the mortality of *Pseudocalanus* nauplii. Because numerous taxa could contribute to naupliar mortality (including juvenile chaetognaths, ctenophores, medusae, siphohophores, calanoid and cyclopoid copepods, euphausiids) specific identification of these predators was not attempted, but needs to be addressed in future studies.

Although mortality rates of adult stages of other species of marine copepods enclose those rates calculated here for adult *Pseudocalanus* sp. (Mullin and Brooks, 1970; Matthews *et al.*, 1978; Landry, 1978; Sonntag and Parslow, 1981; Johnson, 1981; Uye, 1982; Harris *et al.*, 1982) mortality rates reported here and in previous studies may best be viewed as approximations. Mortality rates are highly sensitive to sampling error, sampling interval and to model assumptions (e.g. Parslow *et al.*, 1979; Hairston and Twombly, 1985). In particular, the assumption of a uniform age distribution within copepodid stage V was almost certainly not rigorously met in this study, although it appears to have been approximately met since abundance did not change quickly and the mortality rate of CV was relatively low. Two fundamental assumptions did appear to be well satisfied by this population, namely that a single population was sampled and that recruitment occurred continuously (between March and July). The observable sequence of generations, the relative stability of CV numbers over time and the female egg ratio are in support of these assumptions (Ohman, 1985). One exception occurred in May 1979 when a pulse of CV *Pseudocalanus* sp. was observed (Ohman, 1985), thus violating the assumption of continuous recruitment to the adult stage. Hence adult mortality calculations that include this date should be considered less accurate than those for other dates.

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The higher mortality rate of adult male *Pseudocalanus* sp. by comparison with adult females is probably accounted for by the lack of functional mouthparts in adult males and their inabiliy to feed. In the laboratory (Corkett and McLaren, 1978) as well as in the field adult males have substantially shorter lifetimes than adult females. The importance of predators to the mortality of adult males is not clear since *Pseudocalanus* males were not detected in chaetognath or in chum salmon guts and were only an occasional item in the diet of stickleback.

Sources of mortality other than predation include starvation, parasitism and senescence. Because *Pseudocalanus* sp. females have low food requirements in the laboratory (e.g. Frost, 1974, 1980; Paffenhöfer and Harris, 1976; Vidal 1980a, b; Klein-Breteler and Gonzalez, 1982; Klein-Breteler *et al.*, 1982) and these requirements are typically met in the field (Ohman, 1985), starvation is unlikely to have contributed significantly to the observed mortality patterns. Additionally, half-day intervals of starvation appear not to depress survivorship or fecundity (Dagg, 1977). Attachment of stalked diatoms or an ectoparasitic isopod to the exoskeleton of *Pseudocalanus* was observed with low incidence in the population. The impact of parasites on *Pseudocalanus* populations is thought to be small (Corkett and McLaren, 1978) although parasitic attack has been found to depress birth rates in a freshwater copepod population (Burns, 1985).

Senescence appears not to have been a major cause of seasonal mortality increases since the average half-life of female *Pseudocalanus* sp. in Dabob Bay was 17 – 19 days, a fraction of the 79 – 107 day lifespan observed in the laboratory (Corkett and McLaren, 1978). Additionally, sediment traps deployed in Dabob Bay (by C.J.Lorenzen and associates) were sampled for evidence of *Pseudocalanus* remains, a possible indication of non-predatory mortality. Material was examined from sediment traps deployed in summer 1980 at 70, 80 and 90 m depth at a 105-m deep station located 6 km north of Station D. Virtually no identifiable *Pseudocalanus* remains were found, suggesting that *Pseudocalanus* experiences mortality and consumption above 70 m and that *Pseudocalanus* exoskeletons do not accumulate in Dabob Bay sediments.

Injury patterns

The high incidence of injuries observed suggests that grasping predatory zooplankton, rather than predators which engulf their prey whole, are the primary predators on *Pseudocalanus* sp. This conclusion is consistent with estimates indicating that *Euchaeta elongata* made the largest contribution to *Pseudocalanus* mortality with a measurable contribution from euphausiids. Both predatory copepods (Yen, 1983) and euphausiids (Ohman, 1984) show incomplete consumption of *Pseudocalanus* in laboratory feeding experiments.

Pseudocalanus injury patterns could be influenced by two sources of bias, i.e. damage by the net during collection and attacks by zooplankton in the cod end during retrieval. However, minor damage that occurs in nets, such as loss of apical spines on swimming legs, caudal setae or antennules, could readily be distinguished from more severe signs of attack (see Ohman, 1984). Attacks during retrieval of the net were minimized by rapidly recovering and preserving the samples. Furthermore, there was no correlation between the incidence of injured *Pseudocalanus* sp. females and the total abundance of the three most abundant grasping predatory zooplankton (*E. elongata, Euphausia*

pacifica and *Parathemisto pacifica*) in the same samples ($r^2 = 0.096$, $P > 0.05$) or with any of these three predators separately ($P > 0.10$). Indeed, the lowest proportion of injured *Pseudocalanus* occurred in late July when the abundance of predators was at its annual maximum. No attempt was made to infer rates of predation from the observed injury frequencies (cf. Murtaugh, 1981) because of the unknown duration of survival of injured individuals.

Sagitta elegans

Pseudocalanus was the principal prey item of *S. elegans* during April – June, the season of maximum recruitment of *S. elegans* in Dabob Bay (King, 1979). The decline in numerical importance of *Pseudocalanus* sp. as a prey item beginning in July may be due to the decrease in abundance of *Pseudocalanus* sp. in the water column, an increase in relative abundance of other copepods, or to the reverse diel vertical migration by the *Pseudocalanus* sp. population beginning in July. Reverse migration behavior reduces nocturnal overlap of *Pseudocalanus* sp. and predators (Ohman *et al.*, 1983).

Pseudocalanus has been found to be the principal prey of *S. elegans* elsewhere in north temperate ocean regions. In the seas around the British Isles *Pseudocalanus* sp. formed 48.0% (median rank = 1) of the identifiable prey items in summer and 9.7% (median rank = 4; from data in Rakusa-Suszczewski, 1969) in autumn, a seasonal shift comparable to that observed in Dabob Bay. In Bedford Basin, Nova Scotia, *Pseudocalanus* was the principal prey of *S. elegans* in both July and December (Pearre, 1973) but formed a lower percentage of total prey numbers (29.1% in both seasons) than in Dabob Bay or the British Isles. In CEPEX enclosures in Saanich Inlet in summer copepodids and adults of *Paracalanus* plus *Pseudocalanus* comprised 82% of the prey of those *S. elegans* > 12 mm total length (Harris *et al.*, 1982). *Pseudocalanus* sp. was not a significant component of the diet of *S. elegans* in the open subarctic Pacific in summer (Sullivan, 1980), where the absolute and relative abundance of *Pseudocalanus* sp. is low (Marlowe and Miller, 1975).

Dietary importance might also be assessed from energetic value, rather than prey numbers. Although the energetic value of prey such as *Calanus pacficus* is much greater than that of *Pseudocalanus* sp. (~ 10-fold by carbon content; Frost, 1980), the median contribution of *Calanus* to total prey of *Sagitta* was 16% (maximum = 36%; $N = 6$ dates). The nutritional subsidy for those *Sagitta* which do capture *Calanus* is substantial, but this is a relatively small proportion of feeding *Sagitta* and a still smaller proportion of the total *S. elegans* population.

The estimated daily consumption rates ranged from 1.4 to 2.1 total prey per feeding *Sagitta* per day. This estimate is within the range of values summarized by Feigenbaum and Maris (1984) for *Sagitta* spp. feeding on copepod prey at $10-15°C$. That the daily ration may be obtained largely from nocturnal feeding has been repeatedly documented (Feigenbaum and Maris, 1984; Canino and Grant, 1985). In addition, some previous authors have concluded that a chaetognath's daily ration is obtained in localized patches although others suggest that patch feeding is not necessary to account for observed daily ingestion (see Feigenbaum and Maris, 1984). Comparisons made herein of observed and expected rations in Dabob Bay, as well as observations of multiple prey per chaetognath, suggest that patch feeding has occurred. Indeed, the patch factors calculated here probably underestimate prey concentrations occurring *in situ*.

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The prey — predator interaction between *Pseudocalanus* sp. and *S. elegans* is asymmetrical. Predation by *S. elegans* had limited impact on adult *Pseudocalanus* sp., though *Pseudocalanus* sp. appears to be a prime determinant of seasonal growth of chaetognaths and of interannual changes in their abundance. Hence calculations which assume symmetrical density-dependent control of copepod prey and chaetognath predators in the manner of Volterra (1926) will probably be in error. In contrast to early opinion stressing the voracity of chaetognaths as predators, more quantitative studies suggest that chaetognaths may have relatively minor impact on prey populations (Feigenbaum and Maris, 1984; Canino and Grant, 1985).

Fish predation

Estimates suggest that the impact of zooplankton predation on *Pseudocalanus* sp. adult females is two orders of magnitude greater than that of fish predation, at a deep water station in Dabob Bay in July. Planktivorous fish predation may be of greater consequence during April — May when more larval stages occur in the Puget Sound region (Wailes, 1936; Barraclough *et al.*, 1968; Hart, 1973; Bax *et al.*, 1980; Hay, 1985). Fish predation may also be more significant in shallow water environments close to shore where schools of planktivorous fish seek refuge from larger piscivores (cf. Kerfoot, 1975). Since sampling in this study was not appropriate for larval and smaller juvenile fish (cf. Wurtsbaugh *et al.*, 1981; re: Lane, 1979), it was not possible to evaluate Cushing's (1983) argument that larval fish, in early phases, are too dilute to depress prey abundance.

Pseudocalanus copepodids are susceptible to predation by intermediate-sized herring larvae (Hardy, 1924; Checkley, 1982; Cohen and Lough, 1983) which peak in abundance in April — May in this region (Wailes, 1936; Barraclough *et al.*, 1968). Marine populations of stickleback ingest small copepods when no other prey are present (Landry, 1978) but from the present study appear to select larger or more pigmented prey species when alternate prey are available. Of those stages of *Pseudocalanus* sp. which are captured, predation by adult stickleback falls disproportionately on adult *Pseudocalanus*. Larval, juvenile and possibly adult sandlance (*Ammodytes hexapterus*) may also contribute to *Pseudocalanus* mortality (e.g. Barraclough *et al.*, 1968) in May — June. Juvenile salmonids do not appear to be a major source of predation on *Pseudocalanus* sp. in Dabob Bay, despite the ingestion of *Pseudocalanus* by juvenile salmon in closed experimental containers (Volk *et al.*, 1984). As juvenile chum salmon grow to ~45 — 55 mm length they undergo a shift in habitat from the nearshore littoral zone, where they feed on epibenthic prey (Feller and Kaczynski, 1975), to the pelagic zone (LeBrasseur and Parker, 1964; Salo *et al.*, 1980) where they feed on zooplankton prey larger or more visible than *Pseudocalanus* sp. (Barraclough *et al.*, 1968; Simenstad *et al.*, 1980).

Quantitative studies are needed to enable better estimates to be made of the impact of fish predation on marine zooplankton assemblages. Particular attention needs to be given to seasonal fluctuations and to onshore — offshore gradients in fish predation.

Prey dispersion and mortality

Despite the apparent impact of predatory zooplankton on *Pseudocalanus* sp. population growth, there is a discrepancy between the estimated maximum rate of predation

on *Pseudocalanus* females and the estimated maximum daily mortality. However, predation rates were probably underestimated in this study because predators in Dabob Bay frequently fed at higher temperatures than in the feeding experiments of Yen (1983) and Ohman (1984) and additional predator species would have augmented consumption rates. Also, attack rates by predatory zooplankton are highly density-dependent (Reeve, 1980; Purcell, 1982; Yen, 1983) and thus sensitive to estimates of ambient prey densities. If predators were able locate prey aggregations of 7.5 *Pseudocalanus* l^{-1} in 1979 and 2.5 l^{-1} in 1980, then *Euchaeta elongata, Sagitta elegans* and *Euphausia pacifica* alone would account for more than the observed mortality of *Pseudocalanus* on each date in both years. Hence these predators can suppress population growth and account for observed mortality, though this outcome depends primarily on the prey concentrations that predators encounter *in situ*.

Vertical layers or aggregations of prey may be of greater significance to invertebrate predators than are horizontal aggregations. Densities of *Pseudocalanus* may change 50-fold or more over a vertical range of 100 m on the same date that they vary by less than a factor of 2 over a horizontal range of 10 km (Ohman, 1983). Direct visual observations from submersibles confirm the aggregation of copepods within vertical strata. In the Black Sea (Vinogradov and Shushkina, 1982; Vinogradov *et al.*, 1985), Saanich Inlet (Mackie and Mills, 1983; Yen, 1983; Mackie, 1985), and in the Santa Barbara basin (Alldredge *et al.*, 1984) copepods and other macrozooplankton taxa have been observed in aggregations in vertical layers in the water column on the scale of a few to 10−20 m.

The ability of predators to detect and exploit such vertical layers can have significant consequences for mortality of the prey. Although the importance for predators of ver-
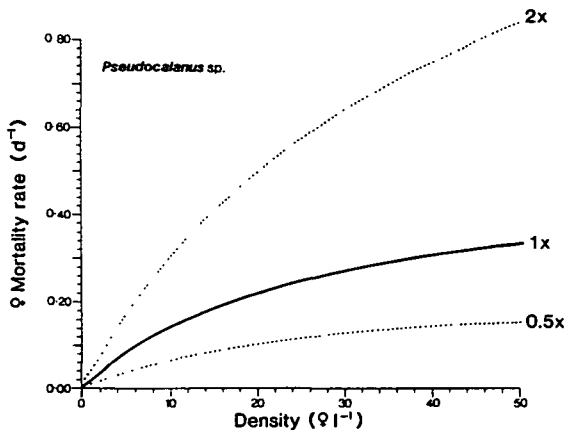

Fig. 19. Dependence of the instantaneous mortality rate of *Pseudocalanus* sp. females (due to consumption by predators) on the population density of *Pseudocalanus* sp. females. The three curves show mortality for the predator densities measured on 4−7 June 1979 in the upper 50 m at night; for twice the measured predator densities; and for one half the measured predator densities. Five hundred *Pseudocalanus* sp. females contained within 1 m³ were assumed to cluster in localized patches; prey densities could thus vary from 0.5 l^{-1} to 50.0 l^{-1}. Predator attack rates as a function of prey concentration were determined from Reeve (1980), Yen (1983) and Ohman (1984).

tical layers of prey is well recognized (Mullin *et al.*, 1985 and references therein), the consequences for prey populations has not been fully explored. The magnitude of this effect is demonstrated in Figure 19 where the abundance of predators (*Euchaeta elongata, S. elegans* and *Euphausia pacifica*) in early summer is combined with their feeding rates (from Reeve, 1980; Yen, 1983; Ohman, 1984) to estimate the mortality of *Pseudocalanus* sp. Where layers of higher-than-average prey concentrations can be located by predators the mortality of prey rises steeply. For example, an increase in prey concentration from 1 to 2 *Pseudocalanus* sp. 1^{-1} results in a nearly 2-fold increase in mortality rate (Figure 19). Furthermore, if predators aggregate in regions of higher prey concentrations (e.g. 2X curve in Figure 19) prey mortality rises even more steeply. (The density-dependence of prey mortality declines at high predator densities due to the saturation of predators.) Because of the sensitivity of both predation and mortality rates to prey density, accurate assessments of vertical layering of prey will be particularly important in future studies of prey — predator interactions.

Conclusions

Population growth of *Pseudocalanus* sp. is seasonally predator-limited in Dabob Bay. Predatory zooplankton rather than planktivorous fish are the principal source of mortality of adult *Pseudocalanus* sp. in a deep water region during summer. The impact of planktivorous fish may be greater during spring and in shallow water regions. The calanoid copepod *Euchaeta elongata* is the principal source of predation pressure on adult *Pseudocalanus* sp.; chaetognaths (*Sagitta elegans*) have a relatively minor impact on standing stock and recruitment of adult *Pseudocalanus* sp. The omnivorous euphausiid *Euphausia pacifica* makes an additional contribution to mortality.

Predator feeding behavior varies with predator developmental stage, seasonal diapause and diel vertical migration behavior, not size structure alone. Since predation rates are highly density-dependent, prey dispersion patterns — particularly layering in the vertical plane — strongly affect prey mortality. Asymmetries may occur in planktonic prey — predator interactions: as illustrated by *Pseudocalanus* sp. and *S. elegans*, predator abundance may be coupled to prey population growth without symmetrical effects of the predator population on the prey.

Acknowledgements

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Appendix I

Mortality rates were estimated by a method suitable for populations experiencing continuous recruitment (cf. Argentesi *et al.*, 1974).

For a stage-structured population with n developmental stages, where n is the adult female stage:

$$\frac{dN_k}{dt} = R_k - R_{k+1} - m_k N_k \qquad \text{for } k = 1, \ldots, n \qquad \text{(A1)}$$

and

$$\frac{dN_k}{dt} = r_k N_k \qquad \text{(A2)}$$

where, for stage k at time t: N_k = abundance, R_k = recruitment rate, m_k = mortality rate, r_k = observed rate of change.

The recruitment rate can be expressed as:

$$R_1 = b N_n \qquad \text{for } k = 1 \qquad \text{(A3)}$$
$$R_k = p_{k-1} N_{k-1} \qquad \text{for } k = 2, \ldots, n \qquad \text{(A4)}$$

where: b = birth rate of stage 1 (egg), p_{k-1} = per capita molting rate from stage $k-1$ to stage k.

If τ_k, the duration of stage k, is short by comparison with the time scale of changes in the recruitment rate, then:

$$p_k \approx \frac{1}{\tau_k} \qquad \text{(A5)}$$

(Parslow *et al.*, 1979) and equation (A4) can be expressed as:

$$R_k = \frac{N_{k-1}}{\tau_{k-1}} \qquad \text{(A6)}$$

Then r_k, the observed rate of change at time t, can be approximated from:

$$\hat{r}_k = \frac{\ln\left(\frac{N_{k, t+1}}{N_{k, t-1}}\right)}{\Delta t} \qquad \text{(A7)}$$

where Δt = time in days. By substitution, m_k can be expressed as:

$$\hat{m}_k = \frac{1}{N_k}\left(\frac{N_{k-1}}{\tau_{k-1}}\right) - \frac{1}{\tau_k} - \frac{\ln\left(\frac{N_{k, t+1}}{N_{k, t-1}}\right)}{\Delta t} \qquad \text{(A8)}$$

For mortality of adults the second term in equation (A8) goes to 0 and the first term is halved to account for a 1:1 sex ratio of copepodid stage V:

$$m_k = \frac{1}{N_k}\left(\frac{N_{k-1}}{2\tau_{k-1}}\right) - \frac{\ln\left(\frac{N_{k, t+1}}{N_{k, t-1}}\right)}{\Delta t} \qquad \text{(A9)}$$

The average number of daily deaths (D_k) is obtained from

$$D_k = \hat{m}_k N_k \qquad \text{(A10)}$$