

Chapter 5

95320H The Role of Zooplankton

Exxon Valdez Oil Spill
Restoration Project Annual Report

The Role of Zooplankton in the Prince William Sound Ecosystem

Restoration Project 95320-H
Annual Report

This annual report has been prepared for peer review as part of the Exxon Valdez Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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Restoration Project 95320-H Annual Report

Study History: This project was initiated in April, 1994, as part of the multi-disciplinary Sound Ecosystem Assessment (SEA) program studying processes constraining the non-recovery of pink salmon and herring. An annual report was issued in 1995 by Cooney, R. T., under the title The Role of Zooplankton in the Prince William Sound Ecosystem as a chapter contribution to the single compiled report of all SEA94 projects. Two conference presentations were contributed from work sponsored by the EVOS Trustee Council in 1995: 1) Cooney, R. T. and L. Tuttle, Zooplankton in the Prince William Sound Ecosystem: The Role of Size, Species Composition, and Behavior in Mediating Food Web Transfers, Arctic Division, American Association for the Advancement of Science, Annual Meeting, Fairbanks, September, 1995; and 2) Cooney, R. T., Sound Ecosystem Assessment (SEA): Understanding Processes Constraining the Production of Pink Salmon and Herring in Prince William Sound, Alaska, Arctic Division, American Association for the Advancement of Science, Annual Meeting, Fairbanks, September, 1995. 1995 was the second of five anticipated years of funding for zooplankton studies within the SEA program in Prince William Sound. This project is expected to complete its field and modelling work in FY 98, and submit a final report in FY 99 as part of an overall SEA synthesis.

Abstract: Work on zooplankton in 1995 was designed to support studies of juvenile salmon survival in northwestern Prince William Sound, and to examine basin-scale distributions as part of an overall plankton dynamics investigation. Relative to 1994, the early spring zooplankton bloom in 1995 occurred earlier, and stocks at AFK were the highest measured since 1989. For a composite of *Neocalanus plumchrus* and *N. flemingeri*, C1 and C2 copepodite stages were present in March at all locations. By April, all five copepodite stages were present, but stage C3 was numerically dominant. In May, the early stages were diminishing and most of the biomass was centered in the large C5 stage. *Neocalanus* was absent in the surface waters in June except for relatively high numbers at the GOA6 station south of Hinchinbrook Entrance in the open shelf environment. A two-way ANOVA for 6 index stations in the "river region" and 6 in the northern fringe of the Sound demonstrated that *Neocalanus plumchrus/flemingeri* biomass (all stages) was higher in the northern region ($P < 0.05$), and that cruises (March, April, May, and June) were also statistically different. In the vertical sense, C4 *Neocalanus* tended to be twice as abundant in the upper 20 m of the water column than between 20 and 50 m. A small sample of full adult pollock stomachs obtained in late April and May were dominated by stage C4 and C5 *Neocalanus*, prompting us to hypothesize that this large fish filter feeds in dense, seasonally occurring layers of large copepods. Pteropod (*Limicina helicina*) biomass in June was much higher than the previous three months ($P < 0.05$), but there was no north/south gradient evident. This pteropod was very important in the diets of adult pollock in late May and early June of 1995 (see Herring and Salmon Integration report). Surprisingly, *Limicina* biomass was about the same

in 1994 and 1995 during May, but higher in 1994 during early June.

A biomass ranking of the top 15 taxonomic categories collected during the day and at night in March, April, May, June and September demonstrated a shift from a largely euphausiid-dominated community in late winter to large copepods in April and May, then to pteropods and small copepods in June, and finally to jelly plankton (Ctenophora) and large and small copepods in September. The biomass was usually greater at night for these communities, surface populations being supplemented by diel vertical migrators like euphausiids and the copepod *Metridia*. The March and September biomass was low relative to April, May and June.

Key Words: Zooplankton, *Neocalanus*, oceanography, Prince William Sound, copepod, amphipod, euphausiid, *Calanus*, *Pseudocalanus*

Citation: Cooney, R. T. and K. O. Coyle. 1995 The Role of Zooplankton in the Prince William Sound Ecosystem. Exxon Valdez Oil Spill Restoration Project Annual Report (Restoration Project 95320-H), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska 99775-1080.

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Executive Summary

The Sound Ecosystem Assessment (SEA) program was designed to identify and describe the mechanisms influencing survival of juvenile pink salmon and herring in Prince William Sound. This information is presently being used to craft a series of interactive numerical models for management and restoration purposes. Since zooplankton serves as food for young salmon and herring, and for predators (fishes, birds and marine mammals) that also consume juvenile salmon and herring, understanding the interannual, seasonal, and daily dynamics of this important forage element in the pelagic ecosystem is central to the overall SEA synthesis and modelling effort.

A 15-year record of springtime plankton biomass is available from the non-profit salmon hatcheries in the region. For a location in the southern Sound (AFK), annual average settled volumes for April and May are highly correlated ($r^2=0.70$) with the average April/May Bakun Upwelling Index computed for the shelf south of Hinchinbrook Entrance. Zooplankton stocks tend to be greater during years of weak onshore convergence and diminished when the convergence is strongest. This relationship is not apparent for collections at a hatchery in the northwestern part of the Sound (WN). A continuing goal of SEA zooplankton studies is to determine the mechanism(s) establishing this statistical correlation and describe its spatial distribution in the region relative to flow and upper-layer temperature fields.

SEA contends that many of the apex consumers in the Sound, including adult pollock and herring, some sea birds, and marine mammals obtain large portions of their annual rations from zooplankton. This contention is supported by results from diet studies of large fishes captured as part of the SEA salmon and herring predation program. Many zooplankton taxa are important contributors to apex consumer diets including large calanoid copepods, euphausiids, amphipods and pteropods. Some of these taxa occur seasonally as the result of life history patterns keyed to the annual phytoplankton bloom which begins in late March and early April in response to increasing light and shoaling wind-mixed layer (see the SEA modelling and Information Services report). Differences in the timing of the pelagic plant bloom are translated forward to differences in the timing of the spring increase in zooplankton populations. Our examination of a small sample ($n=35$) of full adult pollock stomachs collected from midwater trawl collections in late April and early May, 1995, demonstrate a remarkable dependence on C4 and C5 *Neocalanus* spp. at this time. This dependence was supplanted in 1995 by Pteropoda (*Limacina helicina*) in late May and early June after the large calanoid populations declined (see Herring and Salmon Integration report).

Our studies of large calanoid copepods in the Sound are aided by the ability to separate and enumerate the different copepodite stages. By applying published (Miller, 1993) molting rates for these stages, it is possible to estimate the time required to develop from the smallest C1 to the largest C5 and adult stages. For a composite of *Neocalanus fleminger/plumchrus*, this period is approximately 50-60 days. This means that the C5 stages comprising the late April and May calanoid bloom in the Sound must be residents for at least this time period, or they arise from adjacent shelf populations with inflow at Hinchinbrook Entrance. Overwintering adult

populations have been documented in the deep water of the region (see Role of Zooplankton 1994 annual report) as have upper-layer populations of the C1 stages in March. On the basis of current patterns, it is probable that south-Sound populations are associated with the Alaska Coastal Current (ACC) intrusion, but that most northern populations are produced by local reproduction from the deeper waters of that region. Direct observations of currents indicate that flow fields in the eastern, northern and western parts of the Sound are less organized, weaker, and more variable than flow in the south (see Physical Oceanography report). One of the first experiments using the 3-dimensional eddy-resolving transport model of the Sound (see Modelling and Information Services report) will be to examine the question of retention times of "local populations" molting from C1-C5 in the northern part of the Sound for evidence that resident reproduction, or seeding, or both establishes population biomass each year.

Studies of the vertical distributions of zooplankton in 1995 centered on the life stages of *Neocalanus* because of its importance in the diet of pollock. C1-C3 stages were generally distributed homogeneously from the surface to 50 m. However, the C4 stage tended to be twice as abundant in the upper 20 m than from 20 to 50 m. A stabilizing water column (salinity and temperature) probably focuses the diminishing plant bloom in late April and May at or near the depth of a seasonally developing nutricline. This focus should draw grazers into a relatively narrow zone resulting in "layers and swarms" of zooplankton. An example of this layering was observed for *Neocalanus* C4-C5 size particles in optical plankton counter (OPC) records in late April (see Physical Oceanography report). We surmise this kind of layering may dictate (in part) the distributions of near-surface adult pollock populations during the spring.

A demonstrated influence of tidal range on the survival of hatchery-released pink salmon (see Salmon and Herring Integration report) demonstrates a mechanism that mediates predation on fry. One hypothesis suggests that tidal energy expended in the "edge-zone" of Prince William Sound during spring tides, dilutes layers of zooplankton that feed adult pollock causing a redistribution to deeper-water prey fields and reduced predation on near-surface pink salmon fry. In this regard, we found that *Neocalanus* spp. biomass in the upper 50 m was not correlated with tidal range (May and June), but haste to add our measurements are for integrated densities, not *in situ* concentrations (a consequence of the vertical tow sampling strategy). Layer dilution could have been occurring but not reflected in the integrated vertical tow records. An alternative hypothesis for improved hatchery fry survival during periods of spring tides is that all or most predatory fish cease to feed, or markedly reduce their feeding during periods of strongest monthly tidal currents. This behavior would open "windows" of 3-7 days twice a month during when predation on fry would be minimal.

Differences observed in how alternative prey is utilized each year by adult pollock illustrates the need to monitor zooplankton species composition as one element of future modeling activities supporting nowcasts and forecasts of pink salmon and herring survivals. In 1995, pteropods were more important in diets of adult pollock from mid-May through early June. This switch from large copepods to *Limacina pacifica* may have been initiated by an early decline and low *Neocalanus* biomass in mid-May. May pteropod stocks were about the same in 1994 and 1995

so the switch does not appear to have been initiated by the snails. An examination of the composition of day and night zooplankton communities in the upper 50 from March through September documents seasonal successional patterns. In March, day and night communities were dominated by euphausiids. By April and May, euphausiids were diluted by large calanoid populations, that shifted to small copepods, pteropods, and jelly-plankton in June, and then to jelly plankton (Ctenophora) and large and small copepods in September.

Introduction

The Sound Ecosystem Assessment (SEA) program was designed specifically to determine whether or not the non-recovery of pink salmon and Pacific Herring following the Exxon Valdez oil spill was being constrained partially or wholly by natural mechanisms. Salmon populations in the Gulf of Alaska respond to interannual and decadal-scale variations in environmental conditions influencing their levels of production (Hare and Francis, 1995). The most recent regime shift occurred in the late 1970s and resulted in markedly increased wild production levels in Gulf salmonid populations. This phenomenon is apparent in the production histories of wild pink salmon in the region from ADF&G production records (Figure 1). Wild production peaked in 1984, and with some exceptions, has been declining to pre-regime shift levels each year since. In contrast, the production of hatchery-released pink salmon in Prince William Sound increased steadily after 1976, reaching a peak in 1990. Much of this increase was associated with an increase in the numbers of fry produced each year. A comparison of wild and hatchery marine survivals supports the contention that common factors phased similarly in time effect the production potential for both populations in the region (Figure 2).

The salmon literature proposes that salmon marine survival is established each year during early marine residence, perhaps during the first few weeks in the coastal ocean (Bax, 1983; Hargreaves and LeBrasseur, 1985; Hartt, 1980; Healey, 1982; Parker, 1971). The mechanism for loss is believed to be predation, and the rate of loss is thought to be modified by the growth rate of the fry during this critical period. The slowest growing fish probably experience the highest rates of mortality since they remain at risk longer in the smallest, presumably weakest sizes. Temperature and food have been implicated as the major factors influencing growth rates (Healey, 1991; Mortensen, 1983; Walters et al., 1978). Locally, Willette (1985), and Willette and Cooney, (1991) found that production levels of odd and even year southcentral Alaska pink salmon stocks are sensitive to fry-year spring-time ocean temperatures, and that the odd brood lines are also influenced by ocean temperatures during the late maturing and adult stage.

Wild juvenile pink salmon in the northern Gulf of Alaska begin emerging into the nearshore tidally-mixed zone in late March. The outmigration from natal habitats is usually completed by early June (Taylor 1988). Cooney et al., (1995), demonstrated close correspondence between the timing of wild pink salmon ocean entry and the timing and duration of a coastal springtime zooplankton bloom in Prince William Sound. This correspondence suggested that fry benefit by emerging during this period. In fact, marine survival estimates from the hatchery program

demonstrate that fry released into the bloom perform better than fry released prior to, or after the peak of zooplankton biomass. Until recently, this observation seemed to confirm food-limited growth dependence for fry since juvenile pink salmon are immediate consumers of pelagic food in the deep, nearshore waters of the region (Urquhart, 1979). However, more recent studies (Willette, 1996), demonstrate pink salmon fry growth rates (determined from post-release recaptures of wire tagged fry) are predicted by springtime temperatures, but not by levels of food. This surprising result means that either zooplankton is rarely growth-rate limiting for fry, or that plankton plays some as yet-to-be-determined role in modifying hatchery and (presumably) wild stock production.

The zooplankton component of the SEA program is attempting to understand the coupling between zooplankton as forage for fry and juvenile herring, and zooplankton as alternative prey for predators that also consume juvenile salmon and herring. This work is being undertaken as a SEA collaboration in each of the present field/modelling focus groups; Ocean State and Plankton Dynamics, Pink Salmon Recruitment Dynamics, and Pacific Herring Recruitment Dynamics. In a sense, zooplankton forms one important "bridge" between bottom-up oceanographic forcing and subsequent "effects" at higher trophic levels. Understanding the time/space mechanics of this "bridge" will provide the means to simulate these processes for the kinds of numerical tools SEA is producing for the Trustee Council and its member agencies.

Objectives

Each year, the timing, numbers, biomass and species composition of zooplankton populations are expected to differ in response to interannual and decadal-level shifts in oceanographic and meteorological forcing influencing the northern Gulf of Alaska and Prince William Sound. Understanding how this variability translates to juvenile fish survival requires the careful interpretation of the outcomes of natural experiments staged each year. Accomplishing this requires standardized monitoring techniques and focused process studies. The following represent objectives identified for 1995 zooplankton data bases contributing to collaborative studies of juvenile pink salmon and Pacific herring survival:

1. Use hatchery annual Plankton Watch and SEA shipboard collections to describe the timing, duration, magnitude, and species composition of spring-time upper-layer zooplankton stocks in northern and southern Prince William Sound.
2. Utilize shipboard samples of zooplankton to describe how ontogenetic and diel shifts in distribution and species composition influence trophic coupling between juvenile salmon and herring and their predators.
3. Provide direct measures of community composition, and indices of abundance and size for macrozooplankton occurring in layers and swarms that are also being sampled with optical and acoustic means.

4. Describe how the timing and magnitude of the phytoplankton bloom each year influences the timing and magnitude of subsequent zooplankton populations.
5. Work cooperatively with other components of SEA to test the Lake/River, Prey Switching, and herring Overwintering hypotheses.
6. Provide that means to supply zooplankton for stable isotope analyses.

Methods

Zooplankton stocks in Prince William Sound were sampled in 1995 with simple ring nets, 0.5-m diameter (0.335-mm Nitex) fished vertically in the upper 20 or 50 m of the water column. Hatchery collections follow procedures established for the PWSAC Plankton Watch. This includes twice-weekly sampling at specified locations near each hatchery. Hatchery nets (0.5-m diameter; 0.250-mm) are lowered by hand and retrieved vertically in the upper 20 m. Three or fewer samples are composited in a daily collection at each station to provide sufficient material for settled volume measurements. Following a hatchery determination of settled volume, the samples are stored for processing later at UAF. It is assumed that 3.9 m³ of water are filtered in each vertical tow from 20 m to the surface, although there is no way to determine how much water is actually sampled per tow. Filtering more water (common result with hand-held operations) will result in over estimates of zooplankton stocks.

Zooplankton collections from the R/V *Bering Explorer* and F/V *Alaska Beauty* were obtained in 50-m (occasionally deeper) vertical tows integrating the upper layers of the water column. Samples were collected at SEA core stations and from other locations as needed to support the juvenile salmon work. Aboard ship, the net was fished using a meter-block and light-wire hydrographic winch. The net was weighted with a thirty-lb. canon ball, lowered quickly to depth (20-m, 50-m, deeper sea bed) and immediately retrieved at 1.0 m/sec. A wire angle was estimated during the retrieval to judge error in volumes filtered. Using the winch and heavy terminal weight, most tows from 20 or 50-m to the surface were completed in less than 5 min. However, there were times when excessive wind-drifting introduced large wire angles and increased the volumes being filtered. Samples resulting from extreme wire angles can be excluded from analyses.

Because the schedule of occupying SEA oceanographic stations was not stratified by time of day, zooplankton tows were collected at all hours during the day and after dark. Inspection of data from these different collections indicates a general increase in upper-layer biomass after dark, presumably caused by diel migration of some taxa. This component of variance will reduce the precision of data for certain taxa including euphausiids, amphipods, some copepods and total estimates of biomass, if not taken into account. Most analyses reported here are for daytime collections.

Zooplankton collections are processed in the laboratory using standard oceanographic

procedures. The entire sample is scanned for large or otherwise obvious animals which are counted directly. The remainder of each collection is then subsampled for the numerically dominant species. About 100 to 150 specimens are counted and identified in subsamples. Subsamples are obtained using a stemple pipet or Folsom plankton splitter or combination of both.

Results

Lake/River Considerations: Macrozooplankton stocks measured in the southern Sound at the AFK Hatchery were the highest since 1989, the last "lake" year (Figure 3). Compared with 1994, the calanoid bloom at AFK in 1995 began and ended earlier than the previous year (Figure 4). The relationship with Hinchinbrook Entrance Bakun wind forcing (upwelling index) remained consistent, Although we found no relationship between the upwelling index and settled volumes measured at the WN Hatchery in the northwest corner of the Sound (Figure 5). A regression of *Neocalanus plumchrus/flemingeri* (all stages combined) on total zooplankton for April and May (slope=0.68) suggested that during the period of wild and hatchery fry entry into the Sound in 1995, about 70% of the measured settled volumes from the hatchery plankton watch was probably *Neocalanus* (Figure 6). With the exception of one measurement, zooplankton stocks at the WN Hatchery at Esther Island were weaker than in 1994, and like AFK, began and ended earlier in the year (Figure 7). These observations have obvious ramifications for juvenile pink salmon survival differences between these two hatcheries in 1995 that may be evident in the 1996 returns.

Results from a two-way ANOVA testing the main effects of month (March-June) and location (north and south) for a subset of six index stations representative of the ACC intrusion and six across the northern deep-water Sound demonstrated seasonality ($P < 0.05$) for all categories except euphausiids (composite of all species). North/south gradients emerged for *Neocalanus* spp. (composite of *plumchrus/flemingeri*; all stages) and euphausiids; both taxonomic groups demonstrated higher stocks over the deeper northern region (Table 1). Taxa for this analysis were selected because some are important in pollock diets, while others are abundant but not eaten. The *Neocalanus* pattern is suggestive of consistent north/south differences in the historical plankton records from AFK and WN. While total zooplankton also tended to be higher in the north, observed north/south differences were not statistically significant ($P > 0.05$).

Basin-Scale Patterns: A ranking of the top 15 taxa by day and night from all samples collected on Bering Explorer cruises in March, April, May, June and September demonstrates major shifts in near-surface zooplankton community composition from late winter to summer and early fall. In March, the biomass was low and both day and night communities were dominated by euphausiids and the large copepod, *Metridia okhotensis* (Table 2). By April and May, dominance in biomass shifted to *Neocalanus plumchrus/flemingeri* and *Calanus marshallae* (Table 3,4). In early summer, the pteropod *Limacina helicina*, small copepods (*Pseudocalanus* spp. and *Acartia longiremis*), and jelly-plankton were dominating the animal plankton, while by September, jelly-plankton, and large and small copepods were the obvious components (Table 5,6). The

occurrence of CV *Neocalanus flemingri* and *N. plumchrus* in June results mostly from one sample acquired outside the Sound over the adjacent shelf. *Calanus pacificus* was only present in September in the surface waters.

An examination of time-space patterns in the numerical distribution of northern and southern stocks of *Neocalanus plumchrus/flemingri* by copepodite stage (March-May) illustrates the development from C1 through C5 in approximately 60 days (Figure 8). Seasonal differences for the stages are real ($P < 0.05$) but north/south gradients, though suggestive, are not ($P > 0.05$). For this analysis, core stations were arbitrarily partitioned north and south of 60.5 degrees north Latitude in the region.

When the inter-stage molt frequency is set at 15 days (a reasonable value), changes in numbers within stages and the overall biomass of the population can simply modeled. Using a daily mortality rate suggested by Miller (1993) and average wet weights for each stage, a hypothetical cohort can be followed in time with a 30-day arrival of C1 stages at the surface beginning on March 1 (Figure 9). Because the CIV and CV stages are so massive, relative to the younger stages, the bloom in biomass occurs in the older stages despite their much reduced numbers. This crude model accurately predicts the general timing of the macroplankton bloom observed by the hatcheries in the region.

Selected Comparisons Between 1994 and 1995 in the Northwestern Region: Zooplankton studies aboard the F/V Alaska Beauty were conducted to support juvenile salmon survival studies being conducted near the WN Hatchery at Esther Island. A late April through mid-June study period was common for both years and was selected for comparative purposes (Figure 10). For Copepoda, the May increase observed in 1994 was not apparent in 1995. Instead, large copepods, including *Neocalanus plumchrus/flemingri* declined steadily through the period, not peaking in mid-May as generally expected (Figure 11). Larvacean (*Oikopleura* spp.) stocks were higher in 1995, but Gasropoda (*Limacina helicina*) was not, despite the fact they were apparently more important in the diets of adult pollock in 1995 (Figure 12, 13). The overall relationship between large and small copepods during this period appears to be similar for both years (Figure 14). Amphipods and euphausiids, two taxa found commonly in adult pollock stomachs appear to be more abundant in 1994, but no statistical tests were performed to evaluate year-to-year differences (Figure 14, 15).

Vertical Distribution Patterns: Although most of the emphasis for zooplankton work has centered on regional-scale patterns, and seasonal and ontogenetic behavior, there was some work undertaken in 1995 to examine vertical patterns in the upper 50 m. Much of this work is being reported as results from Plankton Acoustics and optical plankton counting (OPC) surveys (see Physical Oceanography and Plankton and Nekton Acoustics reports). Plankton samples were collected during OPC and acoustic surveys to describe species composition, numbers and sizes of plankters present in layers and swarms. In addition, 50 and 20-m vertical tows were obtained at all oceanographic core stations in April, May and June. For stages of *Neocalanus* spp. (C1-CV), the abundance of individuals in the upper 20-m was regressed on total numbers in the upper 50 m.

A slope of 0.40 occurs with homogeneous distributions in the upper 50 m. If all the *Neocalanus* are above 20 m, the slope of the regression will be 1.0. For the case of no *Neocalanus* in the upper 20 m, the slope of the regression will be zero. Plots for these regressions suggest that stage CI *Neocalanus* were most abundant below 20 m, that stages CII and CIII were generally homogeneous from 50 m to the surface, but that the CIV stage was about twice as abundant in the upper 20 m (Figure 17, 18, 19). The CV stage demonstrated a tendency to be more abundant above 20 m, but the difference was slight. This approach is crude, but the results hint at movement toward the surface by the younger stages, some compression near the surface in the older stages, and a possible redistribution as older CV animals begin leaving the surface for overwintering depths (reported in FY94). A short OPC record for 28 April along a transect from Hinchinbrook Entrance to Valdez Arm, illustrates a layer of "*Neocalanus* C4 and C5-size" particles in a dense layer centered at about 30 m (see Physical Oceanography report). Net samples taken at this time verified the presence of abundant C4 and C5 *Neocalanus*. The potentially important layers will be the focus of coordinated OPC, acoustic and MOCNESS sampling in May, 1996.

Pollock Stomach Contents: Although it is not the task of this project to undertake stomach analyses of the diets of pelagic fishes in the region, an opportunity was taken in late April and early May to examine a small sub-set (n=70) of full adult pollock stomachs to ascertain which components of the zooplankton community were being utilized at that time. A subsequent laboratory analysis of half of this collection (5 stomachs from 7 different trawl hauls) revealed that large copepods were being taken almost exclusively (biomass), and that the majority of these were C4 and C5 *Neocalanus plumchrus/flemingeri* (Figure 20). An examination of the gill rakers of these fish, suggested they are superbly adapted for filtering large zooplankton (probably in layers).

Tidal Influence on Zooplankton Biomass: A reduction in pollock catch near the middle of May in 1995 near the WN Hatchery appears to be associated with a redistribution of adults during a period of strong spring-tides in 1995. While we do not understand the mechanism for this redistribution, it seems logical that the monthly tidal cycle might influence the amounts and distributions of forage available to the adult pollock. However, we found no relationship between stocks of *Neocalanus* during April and May and tidal range ($r^2=-0.047$). This does not mean that dilution of *in situ* concentrations possibly associated with increased vertical mixing during spring tides was not occurring, only that the vertically integrated biomass (50 m) was not related to the tidal cycle during this time. Since this also seemed to be a period when *Neocalanus* was beginning to leave the upper layers, the ontogenetic migration may have confounded any tidal relationship. The vertical distribution of layered zooplankton relative to tidal range will be examined as part of the FY96 zooplankton field work.

Discussion

After two years of study, our work, coupled with that of others, is demonstrating a complex role for zooplankton in Prince William Sound. Traditionally, zooplankters have been considered a critical link between phytoplankton and higher level consumers, both pelagic and benthic. Our

observations conform to this model, but also provide insight into local mechanisms that create webs rather than simple food chains in the region. The initial carbon budget that SEA prepared as part of its proposal for pink salmon and herring-related studies suggested that zooplankton would serve as food for not only 0-age fish (including pink salmon and herring), but for older juvenile and adult fishes, seabirds and marine mammals as well. These trophic transfers become important because of the life history strategies, behaviors and sizes of the zooplankters in the Sound. Several calanoid copepods, including *Calanus*, *Neocalanus*, *Metridia*, *Eucalanus* and *Euchaeta* are among the largest in the world's ocean. In the Subarctic Pacific, compression of the shelf and coastal production cycles into 2 or 3 month periods each year focuses the reproductive and growth of many species into relatively narrow temporal and spatial (upper ocean) windows. These "peaks" in local population biomass become focal points for all consumers.

We now have evidence that the Prince William Sound pelagic environment is partitioned into two regions; 1) a northern deep-water region of generally weak and variable upper-layer currents, and 2) a southern region associated with inflow of shelf and Alaska Coastal Current water. Since there seems to be no correlation between wind-forced flow over the shelf and zooplankton stocks in the northern area of the Sound, it seems likely the northern Sound is "buffered" from effects associated with the ACC. We now suspect that differences in residence times in these two regions may hold the key for interpreting differences between the generally larger north Sound *Neocalanus* stocks, and those in the south. Understanding these differences, particularly the sources for zooplankton for each region (local reproduction, seeding from outside the Sound) is critical to ideas about interannual differences that were originally described in the context of "lake" or "river". The 3-dimensional circulation model for the Sound is being employed in 1996 to determine relationships between local stock size (*Neocalanus*) and sources and residence times (inside the Sound) of zooplankton in the two main flow regimes.

Mackas et al. (1993) on the large calanoids in the adjacent deep Subarctic ocean finds their distributions are associated primarily with seasonally changing physical strata in the upper-layer of the ocean (0-100 m). Developing *Neocalanus flemingii* and *N. plumchrus* exploit the wind-mixed surface layer above seasonally developing thermoclines. *Neocalanus cristatus* is found below this layer. If these observations are confirmed for Prince William Sound, and we have some evidence to support this now, interannual differences in the timing and degree of upper-layer seasonal stratification should be predictive of the strength of springtime zooplankton layering in the region. We contend that *Calanus* and *Neocalanus* move into the surface layers to feed each spring. Since the photic zone may initially be broad and without nutrient limitation, vertical focusing of the early life stages (C1-C3) may not be as apparent as for the later C4 and C5 stages seeking food during formation of the seasonal nutricline. Most of the annual biomass of these copepods is established in the older, much larger stages, so substantial swarms and layers of "forage" for pelagic consumers will be limited in time and space. Further, since energy for growth comes from each year's phytoplankton bloom, the timing, magnitude and duration of this event is important as well. It is becoming increasingly obvious to us that the alignment in time and space of fry food and fry predators will set the potential for fry losses each year. The evolved strategy of juvenile pink salmon entering the coastal waters in the northern Gulf each year in April

and May is apparently designed to optimize survival relative to fry food, but also to take advantage of predation sheltering by the accompanying zooplankton bloom at this same time.

Identifying the "trigger" mechanisms that couple juvenile pink salmon and their predators has proven to be difficult. If the majority of the large calanoid biomass in April and May is confined to the upper 20-30 m of the water column, stocks in the tidally-mixed nearshore zone could be diluted by a factor of 2 or more. This gradient may be sufficient to keep adult pollock filter feeding outside fry nursery areas most of the time, but may draw juveniles into deeper water where the risk of predation may be greater. For the case of older juvenile pollock feeding on pink salmon in shallow water nursery areas, the trigger may be associated more with environmental constraints, like water temperature (see Salmon and Herring Integration report). We also wonder whether the practice of feeding fry near hatcheries during the spring may provide cues for pollock and other predators that may follow "scent" trails right to each hatchery.

Since adult pollock can, and do prey on juvenile pollock, the appearance of juveniles in fry nursery zones in mid to late May may also be related to avoiding adult populations near the surface. In years of weak zooplankton, adults may not be able to filter feed broadly in the region and avoid large areas of the Sound. Under these conditions, juvenile pollock could invade the near-shore fry nurseries sooner, and remain longer than years of higher adult biomass. In a very general sense, the time-series of zooplankton measured at AFK tracks the wild stock success in the region since 1981 suggesting a relationship between fry survival and zooplankton (Figure 21). This new notion transfers the impact of predation on fry mostly away from adults (some impact already demonstrated) to juvenile pollock. It seems reasonable to assume that populations of 1 and 2-year old pollock will generally be more abundant than surviving adults, so that losses of fry to younger pollock could potentially be much greater than losses to adults. If this is true, fry might do better during years of higher-than-average zooplankton biomass because the adult pollock filter-feeding in adjacent waters restrict the timing and duration of juvenile invasions of the nearshore fry nursery areas. These and other complex relationships between juvenile pink salmon and herring, zooplankton, and salmon and herring predator seek collaborative resolution in continuing SEA field and modelling studies.

Conclusions

1. Zooplankton stocks measured at the AFK hatchery in 1995 were the highest since 1989. In this regard, that region was more lake-like than the previous 5 years with obvious implications for salmon returns in the summer of 1996.
2. Regional scale studies of large calanoid distributions demonstrated the presence of all copepodite stages from March through May. The youngest stages were present in both north and south regions. Development from C1 to C5 was completed in about 60 days. For a small set of northern and southern index stations, *Neocalanus* was found to be higher ($P < 0.05$) in the northern region.

3. The biomass structure in the upper 50 m shifted from a euphausiid dominated community in March, to large calanoids in April and May, to pteropods, small copepods and jelly plankton in June. Jelly plankton and large and small copepods (some not observed in other seasons) dominated the September upper-layer zooplankton biomass.
4. Adult pollock feeding at the peak of the *Neocalanus* bloom exhibited a strong selection for C4 and C5 stages in 1995.

Acknowledgements: This work would not have been possible without the able assistance of cooperating SEA personnel in the field and laboratory representing the Prince William Sound Science Center, Alaska Department of Fish and Game, the University of Alaska Fairbanks, and the Prince William Sound Aquaculture Corporation. I am also indebted to the captains and crews of the R/V Bering Explorer and F/V Alaska Beauty. Their inventiveness, professionalism and desire to "get the job done" was crucial to the completion of our work.

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Table 1. Analysis of Variance (ANOVA) for two locations (north and south) and four times (March, April, May, and June) for biomass of seven categories of large zooplankton collected in 1995

Taxonomic Category	Source of Variability		
	Location	Month	Location x Month
Total zooplankton	NS	**	NS
<i>Neocalanus plumchrus/flemingeri</i>	*	**	NS
<i>Pseudocalanus</i> spp.	NS	**	NS
<i>Limicina helicina</i>	NS	**	NS
Euphausiacea	*	NS	NS
Amphipoda	NS	**	NS
Larvacea	NS	**	NS

NS = P>0.05

* = P<0.05

** = P<0.01

Table 2. Ranking the top 15 zooplankton taxa by biomass from samples collected during the daytime and at night in March, 1995; R/V Bering Explorer

Daytime Samples

Taxonomic Category	Rank	Biomass (mg/m ³)	Cumulative %
<i>Metridia okhotensis</i>	1	18.15	23.7
<i>Thysanoessa spinifera</i>	2	13.31	41.1
<i>Thysanoessa inermis</i>	3	5.27	47.9
<i>Thysanoessa longipes</i>	4	3.65	52.7
<i>Euphausia pacifica</i>	5	3.51	57.3
<i>Pseudocalanus</i> spp. AF	6	2.50	60.5
<i>Calanus marshallae</i> AF	7	2.37	63.6
<i>Thysanoessa raschii</i>	8	2.16	66.5
Barnacle nauplii	9	1.88	68.9
<i>Metridia pacifica</i> AF	10	1.75	71.2
<i>Sagitta elegans</i>	11	1.72	73.4
Calanidae CII	12	1.32	75.2
Calanidae CI	13	1.19	76.7
<i>Pseudocalanus</i> spp. CV	14	1.06	78.1
<i>Thysanoessa raschii</i> WS	15	0.94	79.3

Nighttime Samples

<i>Metridia okhotensis</i> AF	1	74.40	43.0
<i>Thysanoessa longipes</i>	2	19.15	54.1
<i>Thysanoessa inermis</i>	3	8.10	58.8
<i>Calanus marshallae</i> AF	4	6.25	62.4
<i>Thysanoessa spinifera</i>	5	5.86	65.8
<i>Metridia pacifica</i> AF	6	4.89	68.6
<i>Aglantha digitale</i>	7	4.86	71.4
<i>Euphausia pacifica</i>	8	4.61	74.1
<i>Thysanoessa raschii</i> WS	9	3.63	76.2
<i>Sagitta elegans</i>	10	3.62	78.3
<i>Pseudocalanus</i> spp. AF	11	3.28	80.2
Squid larvae	12	2.29	81.5
<i>Calanus marschallae</i> CV	13	2.21	82.8
<i>Neocalanus cristatus</i> CIII	14	2.20	84.0
<i>Metridia</i> spp. CV	15	1.97	85.2

AF designates adult female; C is copepodite stage; WS is without spermatophore

Table 3. Ranking the top 15 zooplankton taxa by biomass from samples collected during the daytime and at night in April, 1995; R/V Bering Explorer

Daytime Samples

Taxonomic Category	Rank	Biomass (mg/m ³)	Cumulative %
<i>Neocalanus</i> spp. CIV	1	55.52	15.7
<i>Neocalanus</i> spp. CIII	2	33.58	25.5
<i>Eirene indicans</i>	3	30.35	33.8
<i>Neocalanus flemingeri</i> CV	4	18.43	39.1
<i>Neocalanus plumchrus</i> CV	5	17.66	44.1
<i>Calanus marshallae</i> AF	6	15.33	48.4
<i>Thysanoessa inermis</i>	7	14.46	52.5
<i>Metridia okhotensis</i> AF	8	12.78	56.2
<i>Clione limicina</i>	9	9.98	59.0
<i>Sagitta elegans</i>	10	7.96	61.2
<i>Thysanoessa longipes</i>	11	7.17	63.3
Calanidae CII	12	6.46	65.1
Octopus larvae	13	5.73	66.7
Barnacle nauplii	14	5.61	68.3
Fish larvae	15	5.29	69.8

Nighttime Samples

<i>Metridia okhotensis</i> AF	1	89.03	19.2
<i>Neocalanus</i> spp. CIV	2	42.01	28.2
<i>Neocalanus</i> spp. CIII	3	31.01	34.8
<i>Calanus marshallae</i> AF	4	21.41	39.5
<i>Metridia okhotensis</i> AM	5	18.35	43.4
<i>Neocalanus plumchrus</i> CV	6	15.36	46.7
<i>Conchoecia</i> spp.	7	14.22	49.8
<i>Sagitta elegans</i>	8	12.54	52.5
<i>Thysanoessa spinifera</i>	9	11.86	55.0
<i>Neocalanus cristatus</i> CV	10	11.57	57.5
Barnacle nauplii	11	9.83	59.6
<i>Euphausia pacifica</i>	12	9.77	61.7
<i>Thysanoessa inermis</i>	13	9.16	63.7
<i>Thysanoessa longipes</i>	14	9.14	65.6
<i>Metridia</i> spp. CV	15	8.42	67.5

AF designates adult female; AM is adult male;

Table 4. Ranking the top 15 zooplankton taxa by biomass from samples collected during the daytime and at night in May, 1995; R/V Bering Explorer

Daytime Samples

Taxonomic Category	Rank	Biomass (mg/m ³)	Cumulative %
<i>Neocalanus plumchrus</i> CV	1	250.42	34.9
<i>Neocalanus flemingeri</i> CV	2	73.72	45.2
<i>Pseudocalanus</i> spp. CV	3	39.44	50.7
<i>Neocalanus</i> spp. CIV	4	39.29	56.2
<i>Eirene indicans</i>	5	39.00	61.6
<i>Calanus marshallae</i> CV	6	18.34	64.2
<i>Calanus marshallae</i> AF	7	17.37	66.6
<i>Calanus marshallae</i> CIV	8	14.64	68.7
<i>Coryne principis</i>	9	14.08	70.6
<i>Pseudocalanus</i> spp. CIV	10	14.05	72.6
<i>Calanus marshallae</i> AM	11	10.80	74.1
<i>Pseudocalanus</i> spp. AF	12	10.47	75.6
<i>Clione limicina</i>	13	9.70	76.9
Hippolytidae zoea	14	8.97	78.2
<i>Oikopleura</i> sp.	15	8.12	79.3

Nighttime Samples

<i>Neocalanus plumchrus</i> CV	1	316.01	31.1
<i>Metridia okhotensis</i> AF	2	107.26	41.7
<i>Neocalanus</i> spp. CIV	3	74.59	49.0
<i>Neocalanus flemingeri</i> CV	4	73.72	56.3
<i>Thysanoessa longipes</i>	5	34.76	59.7
<i>Metridia pacifica</i> AF	6	29.99	62.7
<i>Pseudocalanus</i> spp. CV	7	28.51	65.5
<i>Metridia</i> spp. CV	8	23.46	67.8
<i>Neocalanus cristatus</i> CV	9	17.79	69.5
<i>Metridia okhotensis</i> AM	10	17.27	71.2
<i>Pseudocalanus</i> spp. CIV	11	16.64	72.9
<i>Metridia</i> spp. CII	12	15.79	74.4
<i>Metridia</i> spp. CIV	13	15.60	76.0
<i>Calanus marshallae</i> AF	14	15.46	77.5
<i>Neocalanus cristatus</i> CIV	15	14.85	78.9

AF designates adult female; AM is adult male; C is copepodite stage

Table 5. Ranking the top 15 zooplankton taxa by biomass from samples collected during the daytime and at night in June, 1995; R/V Bering Explorer

Daytime Samples

Taxonomic Category	Rank	Biomass (mg/m ³)	Cumulative %
<i>Limacina helicina</i>	1	142.32	21.2
<i>Pseudocalanus</i> spp. CV	2	74.46	32.3
<i>Pseudocalanus</i> spp. AF	3	69.95	42.7
<i>Coryne principis</i>	4	53.36	50.6
<i>Sagitta elegans</i>	5	42.45	57.0
<i>Calanus marshallae</i> CV	6	42.09	63.2
<i>Oikopleura</i> sp.	7	41.95	69.5
<i>Limacina helicina</i> SM	8	39.68	75.4
<i>Clione limicina</i>	9	13.88	77.5
<i>Oikopleura</i> sp. SM	10	11.45	79.2
<i>Calanus marshallae</i> AF	11	10.59	80.7
<i>Acartia longiremis</i> AF	12	10.30	82.3
Barnacle cyprid	13	7.82	83.4
<i>Neocalanus flemingeri</i> CV	14	7.37	84.5
<i>Pseudocalanus</i> spp. AM	15	6.62	85.5

Nighttime Samples

<i>Limacina helicina</i>	1	341.44	30.6
<i>Neocalanus flemingeri</i> CV	2	184.30	47.1
<i>Metridia</i> spp. CV	3	117.91	57.8
<i>Metridia pacifica</i> AF	4	64.28	63.5
<i>Sagitta elegans</i>	5	46.16	67.7
<i>Pseudocalanus</i> spp. CV	6	41.67	71.4
<i>Neocalanus plumchrus</i> CV	7	35.32	74.6
<i>Pseudocalanus</i> spp. AF	8	33.89	77.6
<i>Thysanoessa inermis</i>	9	25.05	79.8
<i>Calanus marshallae</i> CV	10	21.73	81.8
<i>Neocalanus cristatus</i> CV	11	15.19	83.2
<i>Calanus marshallae</i> AF	12	13.40	84.4
<i>Eirene indicans</i>	13	11.72	85.4
<i>Thysanoessa longipes</i>	14	11.66	85.5
<i>Metridia</i> spp. CIV	15	10.91	87.4

AF designates adult female; AM is adult male; SM is small

Table 6. Ranking the top 15 zooplankton taxa by biomass for samples collected during the day in September, 1994; R/V Bering Explorer

Daytime Samples

Taxonomic Category	Rank	Biomass (mg/m ³)	Cumulative %
Ctenophora	1	16.52	31.6
<i>Pseudocalanus</i> spp. AF	2	13.20	56.9
Euphausiacea JUV	3	2.44	61.6
<i>Limacina helicina</i> SM	4	2.16	65.7
<i>Eirene indicans</i>	5	1.89	69.3
<i>Calanus marshallae</i> CIV	6	1.73	72.6
<i>Neocalanus</i> spp. CIII	7	1.09	74.7
<i>Acartia longiremis</i> AF	8	0.93	76.5
<i>Pseudocalanus</i> spp. CV	9	0.93	78.3
<i>Calanus pacificus</i> CV	10	0.90	80.0
<i>Calanus marshallae</i> CV	11	0.85	81.6
Euphausiid CPS	12	0.81	83.2
<i>Mesocalanus tenuicornis</i>	13	0.80	84.7
<i>Neocalanus</i> spp. CIV	14	0.67	86.0
<i>Calanus pacificus</i> CIV	15	0.65	87.2

Nighttime Samples - no night sampling

AF designates adult female; JUV is juvenile; C is copepodite stage; CPS is calyptopis stage

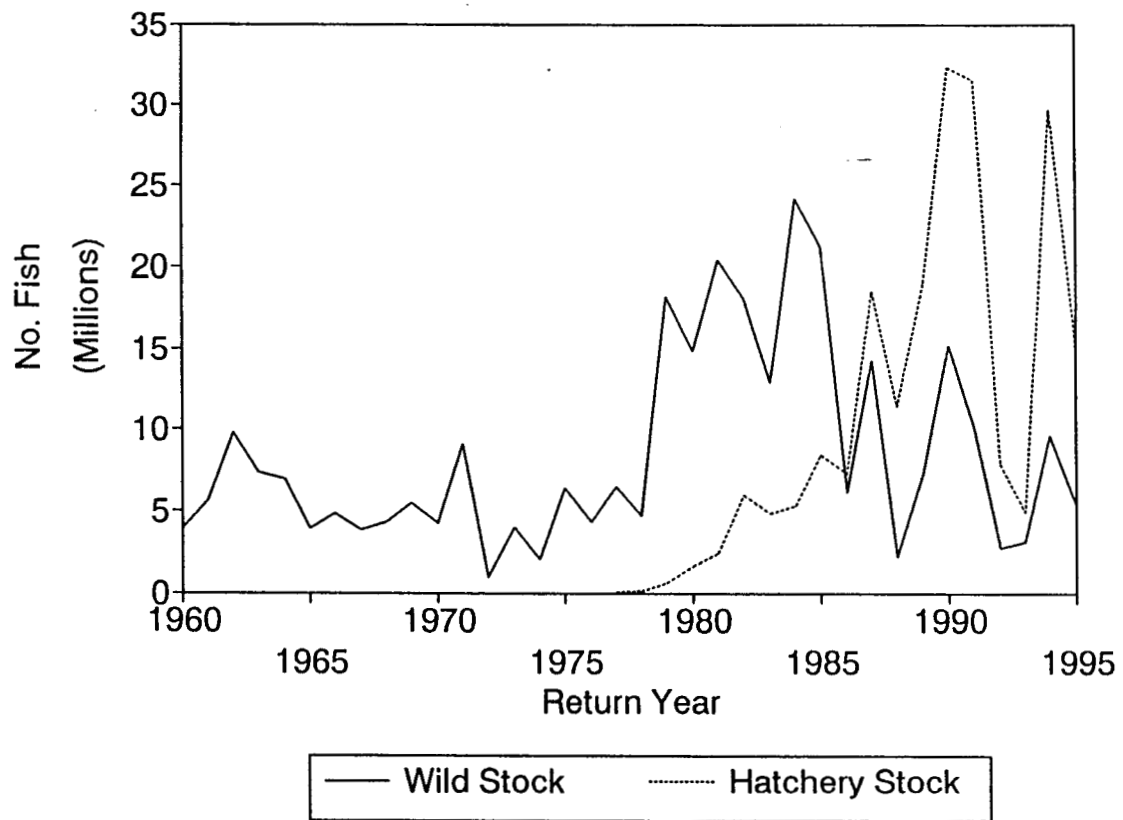


Figure 1. Wild and hatchery historical adult pink salmon returns to Prince William Sound.

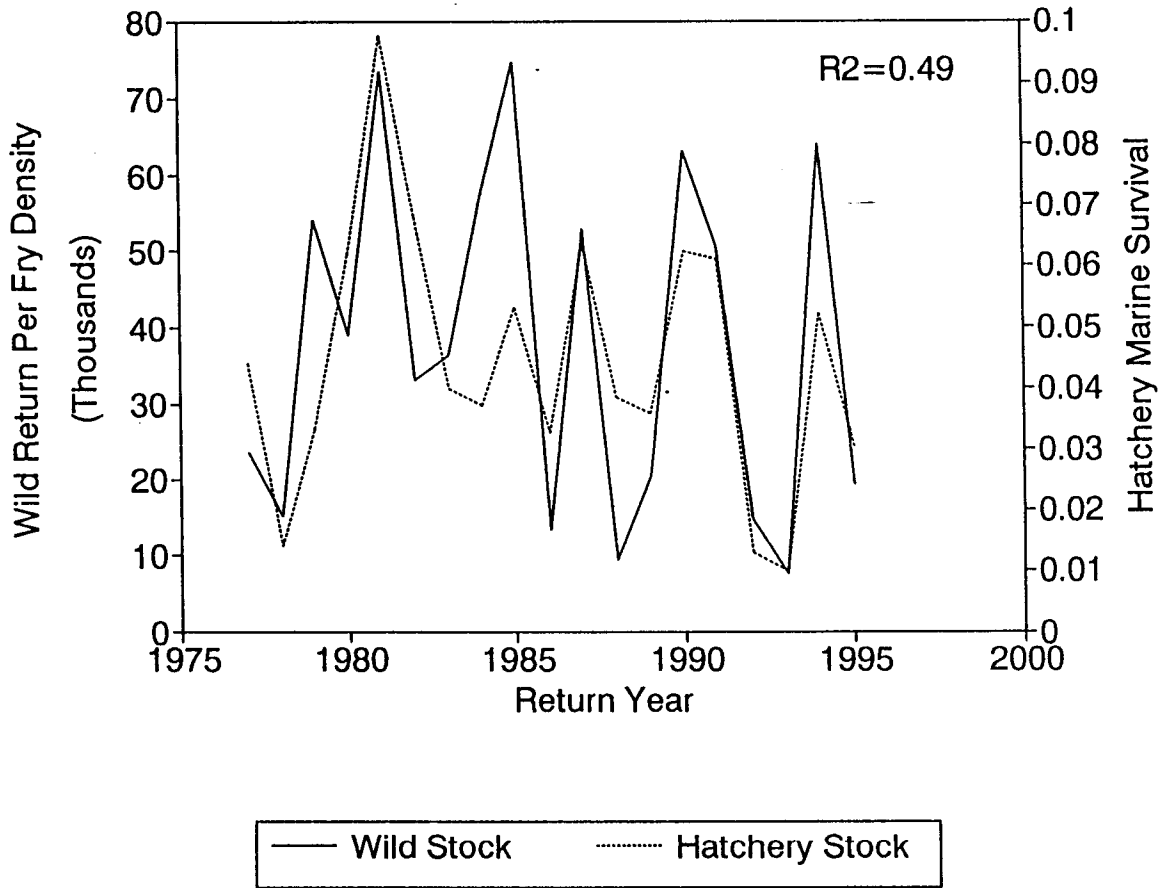


Figure 2. Annual marine survivals for wild and hatchery pink salmon populations in Prince William Sound.

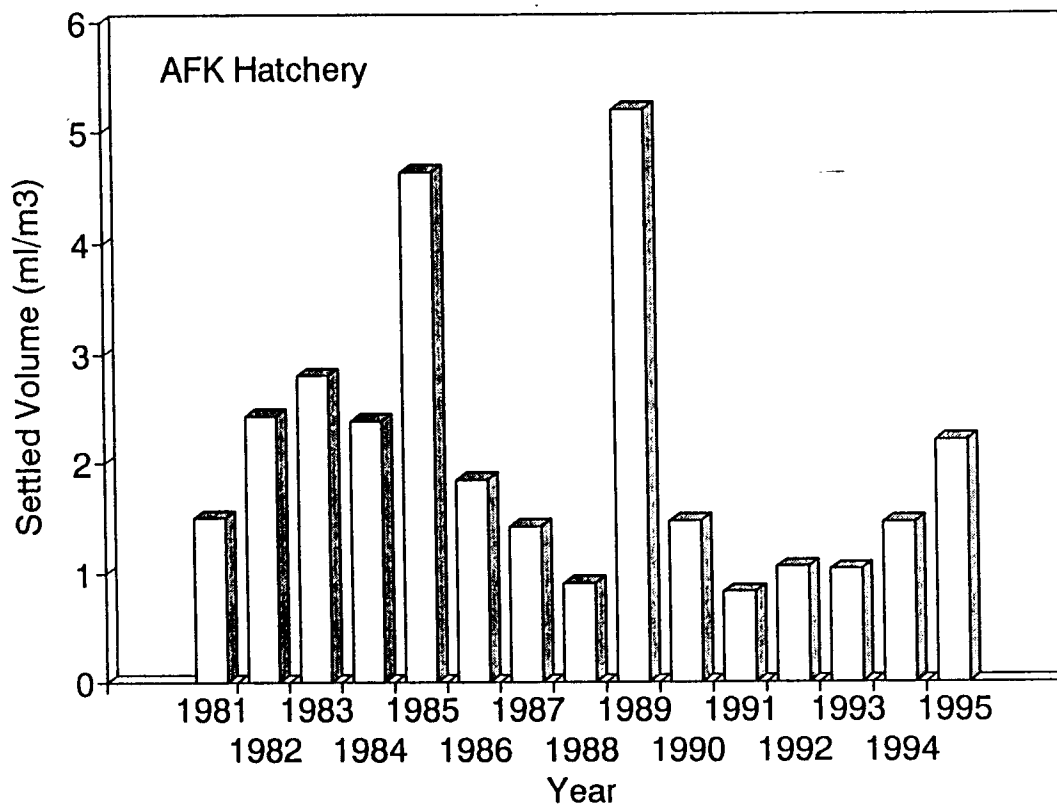


Figure 3. Average annual zooplankton stocks reported for the Elrington Passage station near the AFK Hatchery in Prince William Sound.

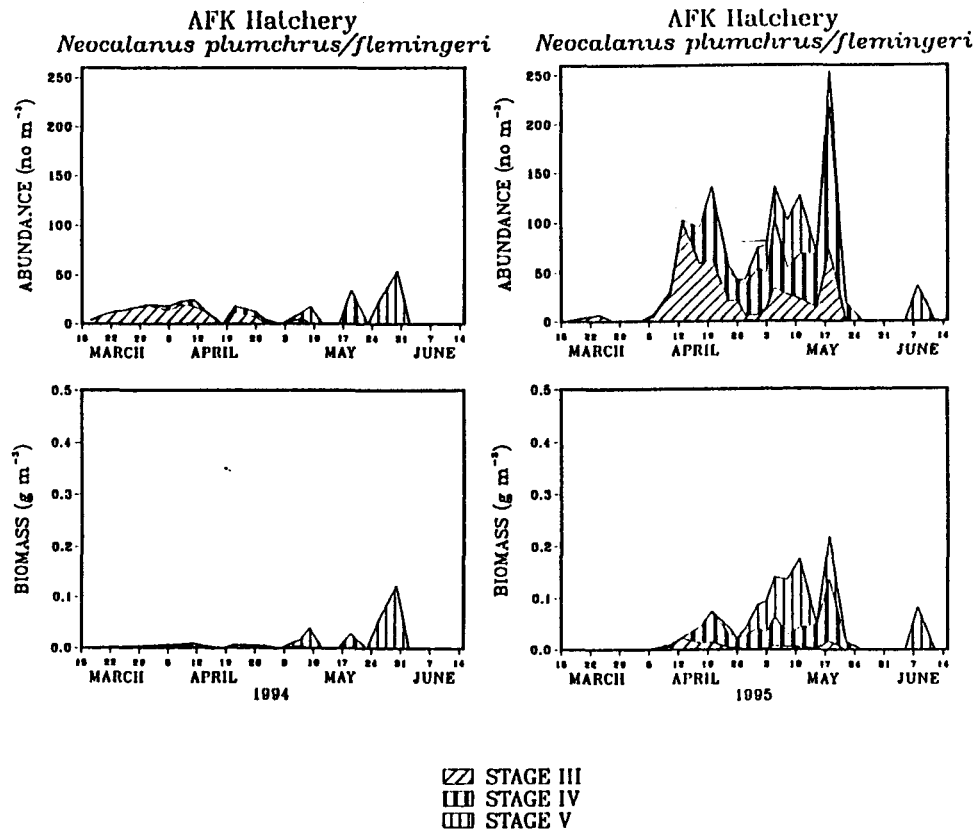


Figure 4. Seasonality in the abundance and biomass of a composite of C3-C4 *Neocalanus plumchrus/flemingeri* from the AFK Hatchery.

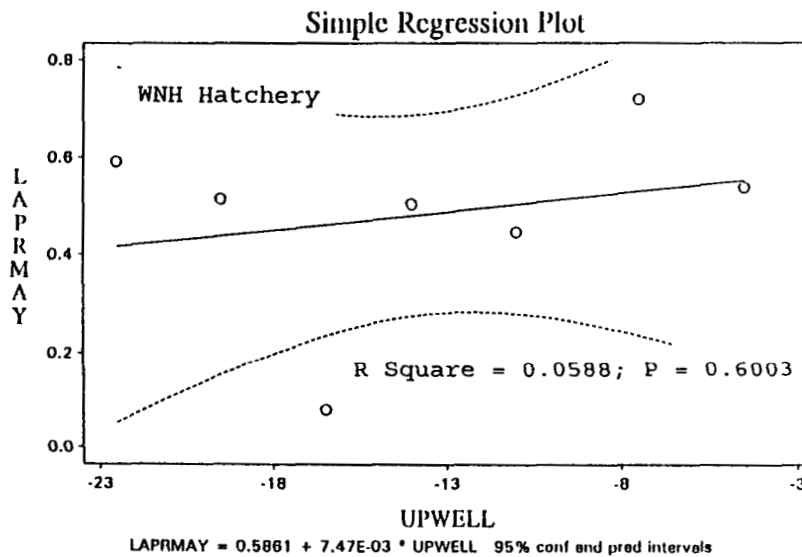
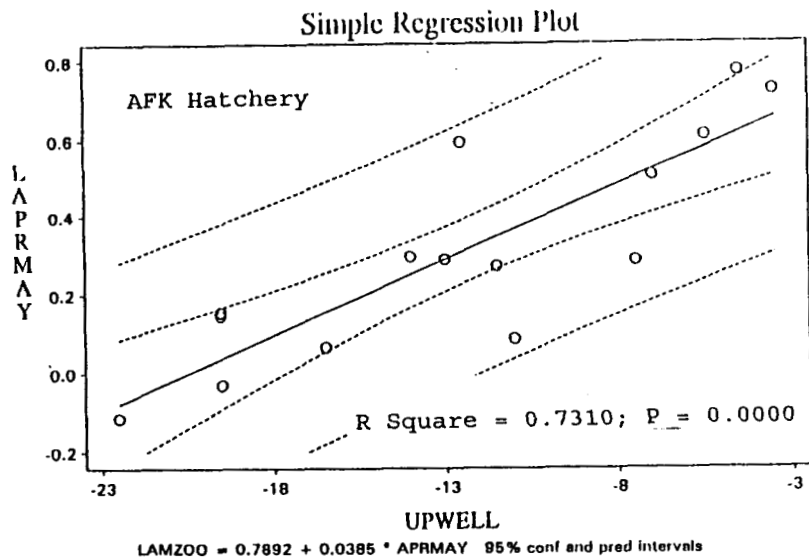


Figure 5. Regressions of hatchery zooplankton settled volumes (April and May) on the average April/May Bakun upwelling index computed for a location near Hinchinbrook Entrance.

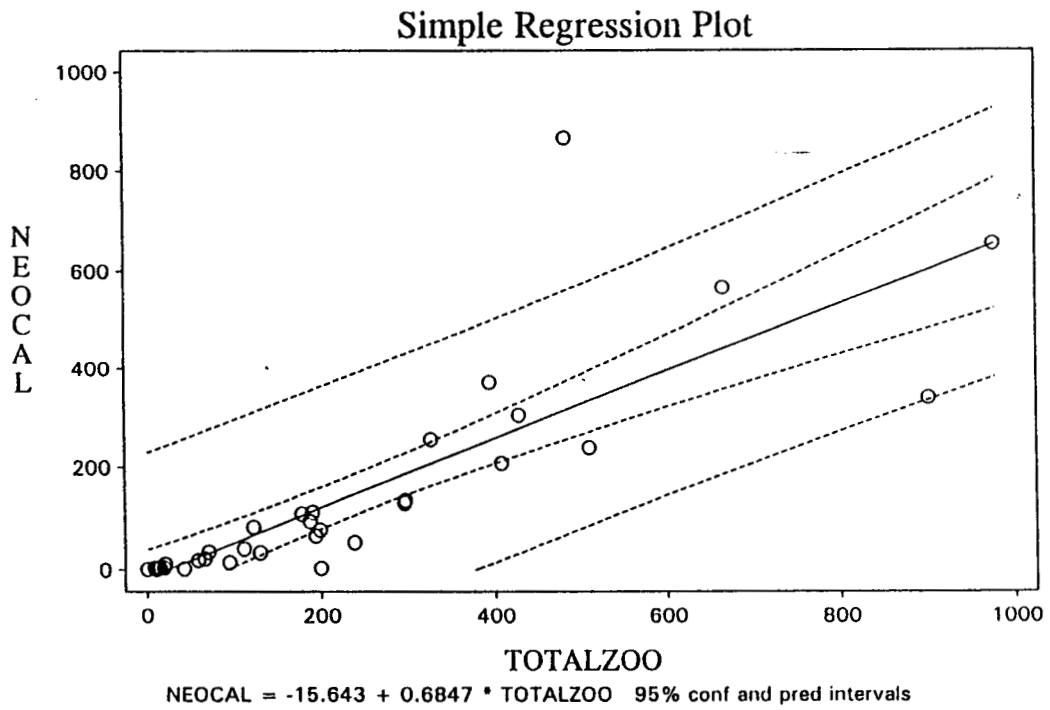


Figure 6. A regression of *Neocalanus plumchrus/flemingeri* biomass (all copepodite stages) on total zooplankton biomass.

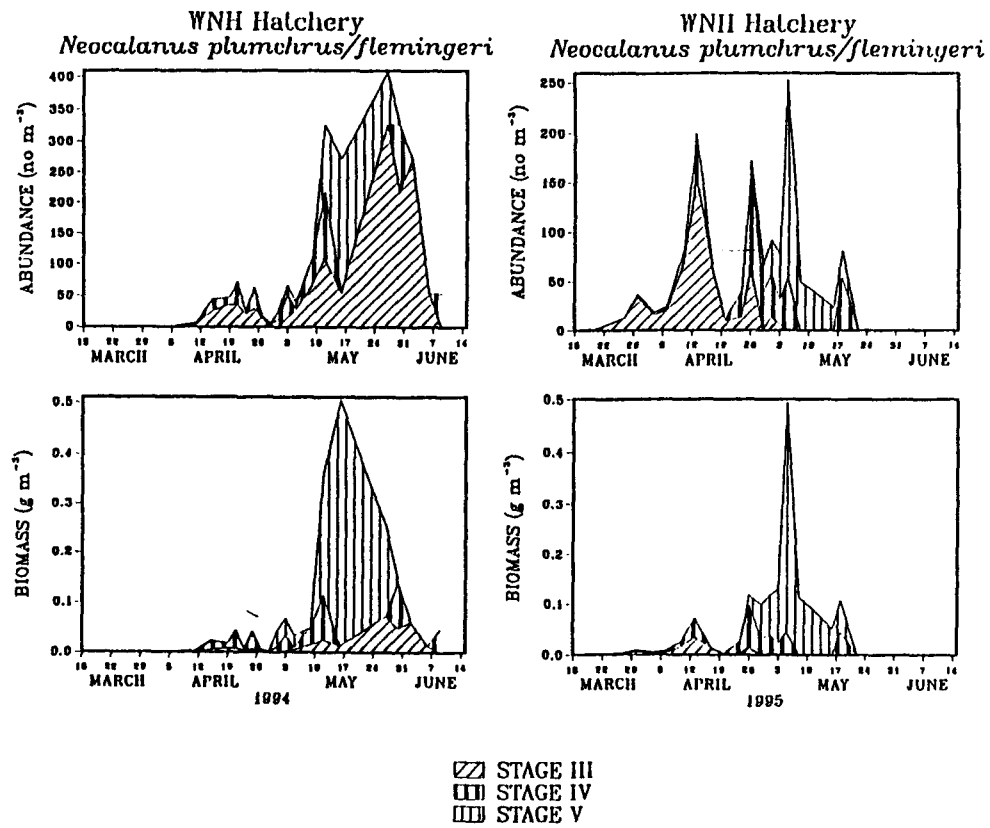


Figure 7. Seasonality in the abundance and biomass of a composite of C3-C5 *Neocalanus plumchrus/flemingeri* from the WN Hatchery.

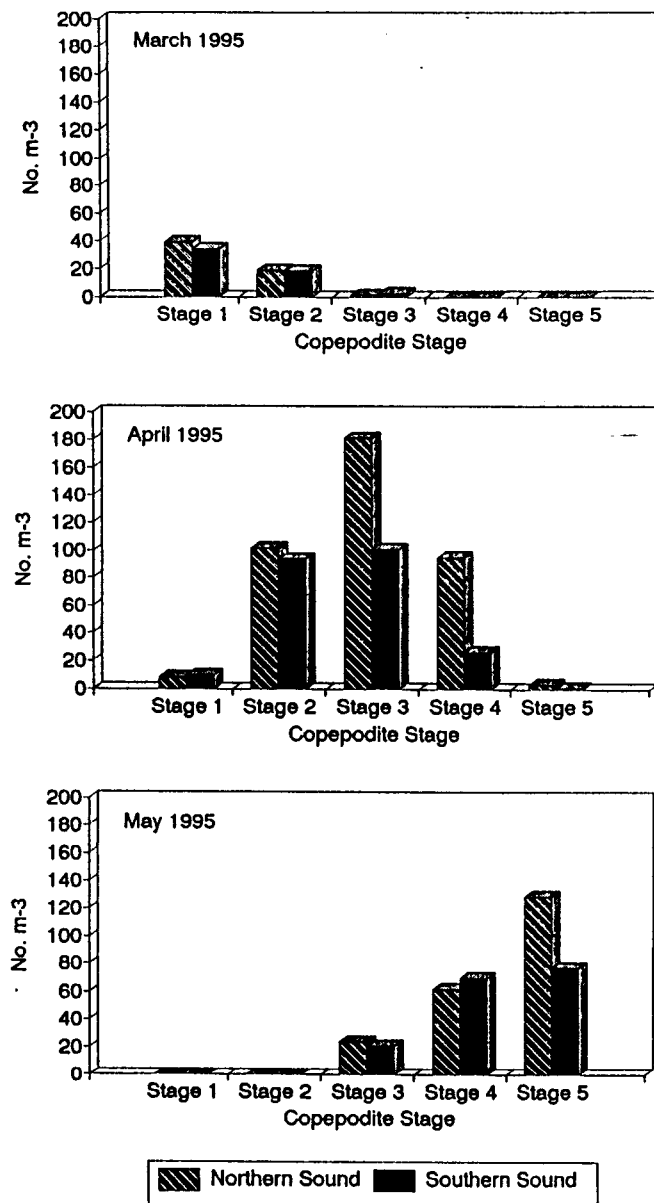
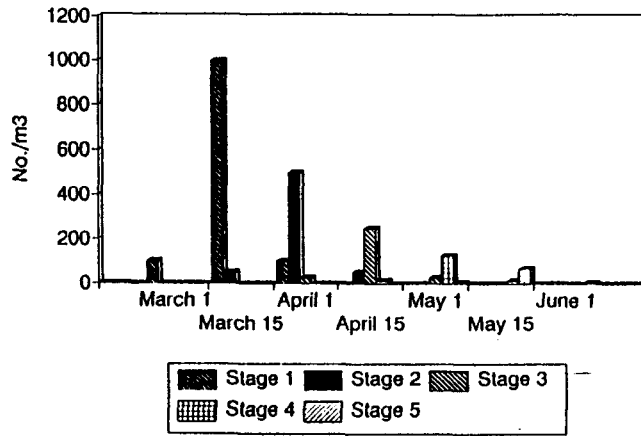


Figure 8. Monthly composition by stage for *Neocalanus plumchrus/flemingeri* partitioned arbitrarily into north and south Sound collections.

Phasing of Copepodite Stages Neocalanus spp.; 30 Day Spawning Period



Modelling Neocalanus spp. in PWS Assumes a 30 Day Spawning Period

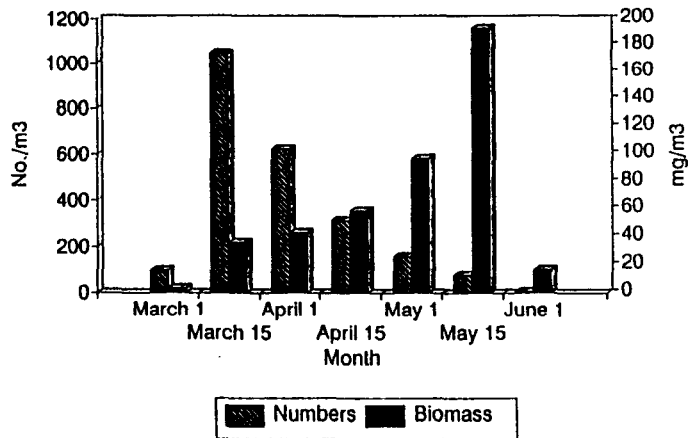


Figure 9. The hypothetical phasing of copepodite stages for *Neocalanus* assuming a 30 day spawning period, C1 stages beginning to arrive at the surface on 1 March, and a 15-day inter-molt period. The bottom panel depicts the composite biomass by month.

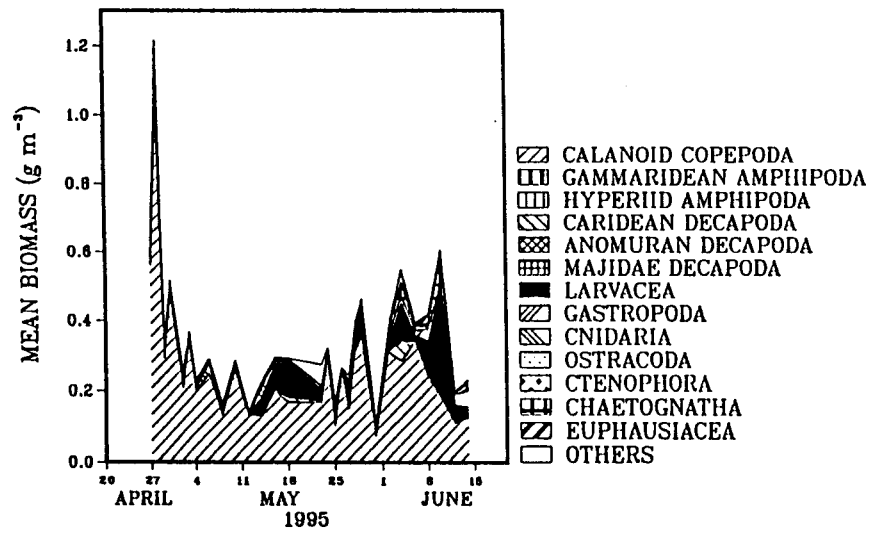
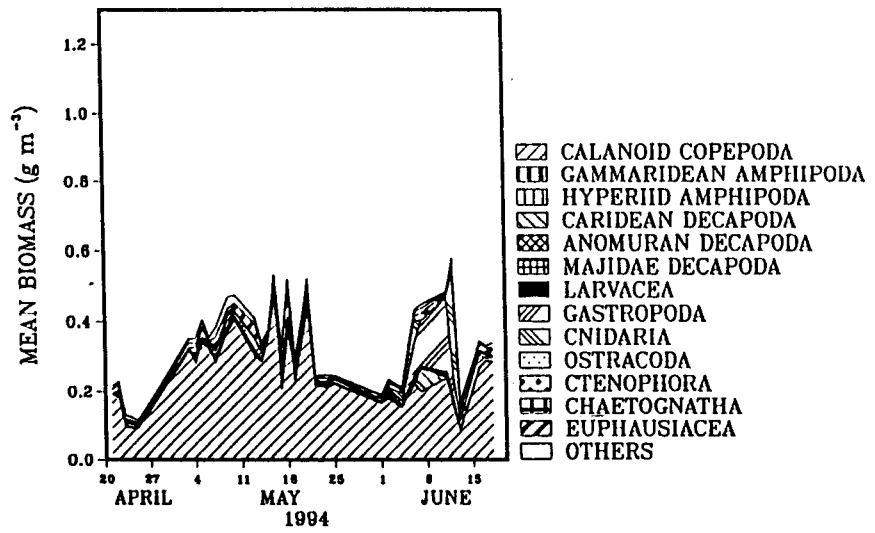


Figure 10. Variability in the community composition of major pelagic taxa during the spring in 1994 and 1995.

Neocalanus plumchrus/flemingeri

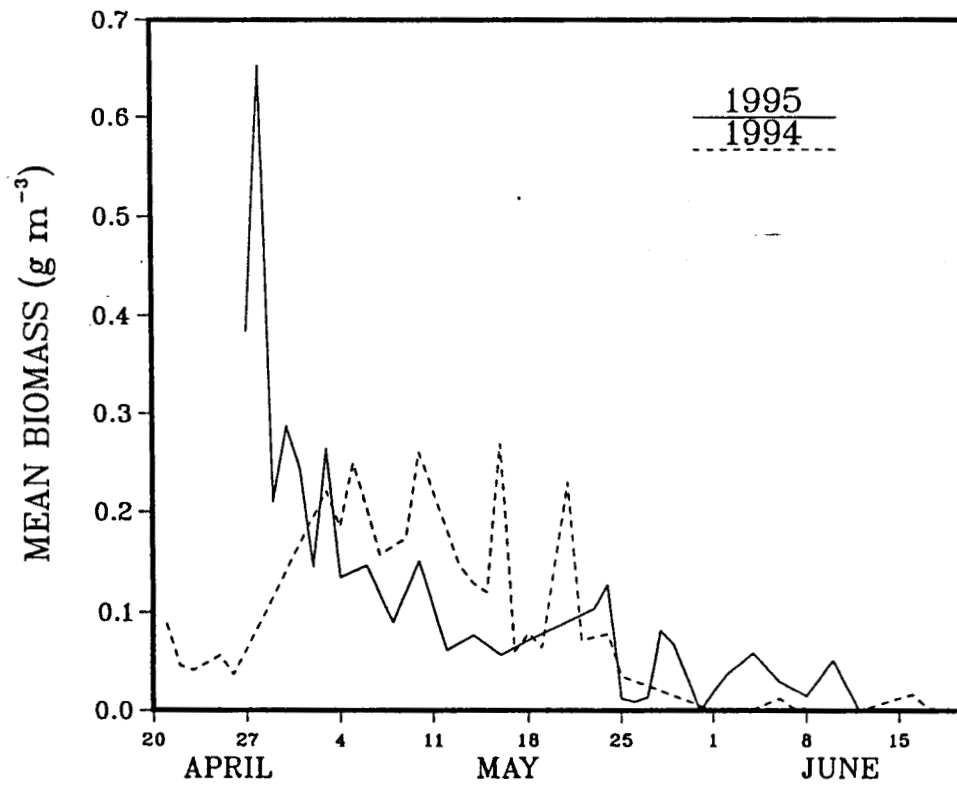


Figure 11. Variability in the *Neocalanus plumchrus/flemingeri* during the spring in 1994 and 1995.

Larvaceans

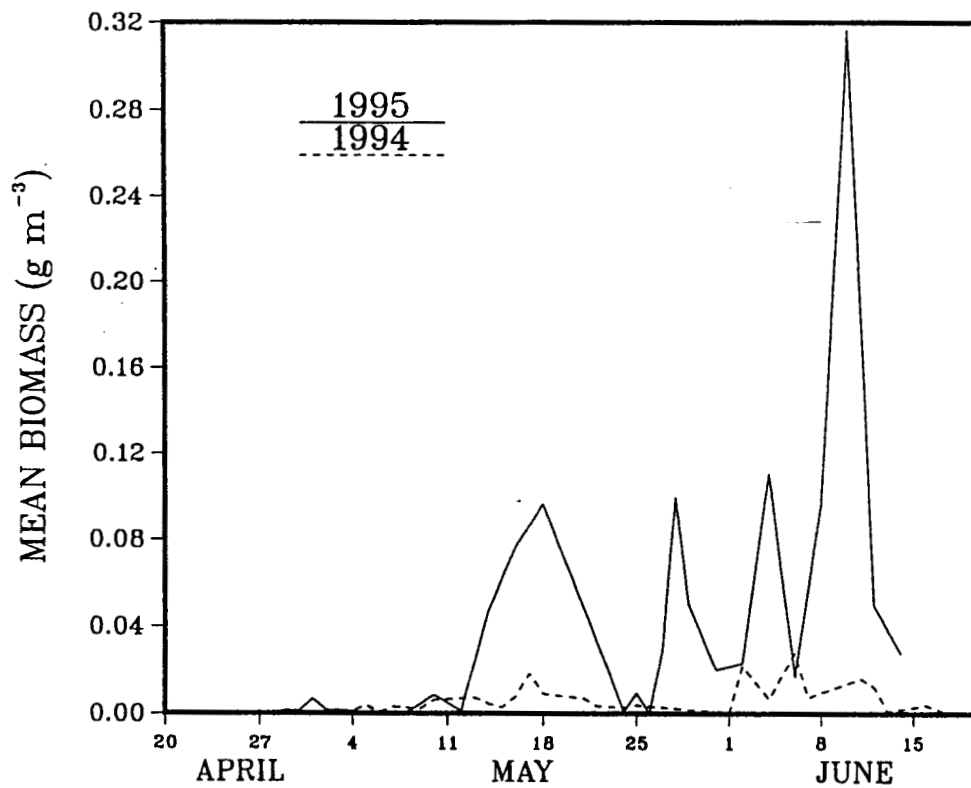


Figure 12. Variability in larvaceans during the spring in 1994 and 1995.

Limacina helicina

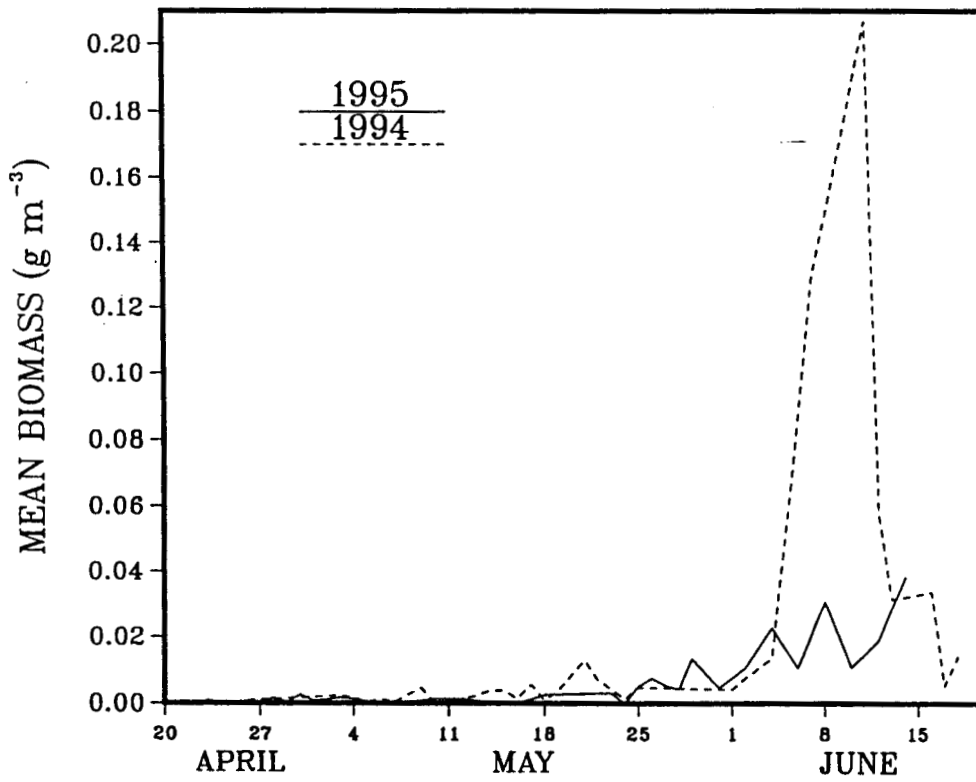


Figure 13. Variability in *Limacina helicina* during the spring in 1994 and 1995.

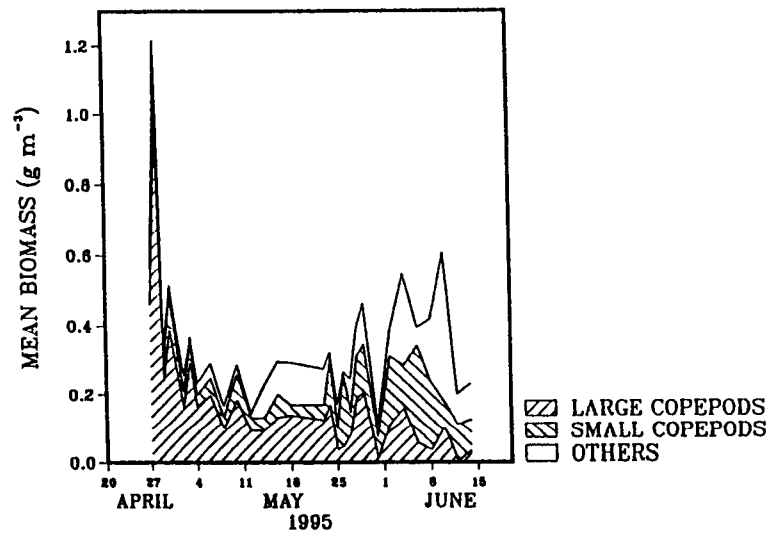
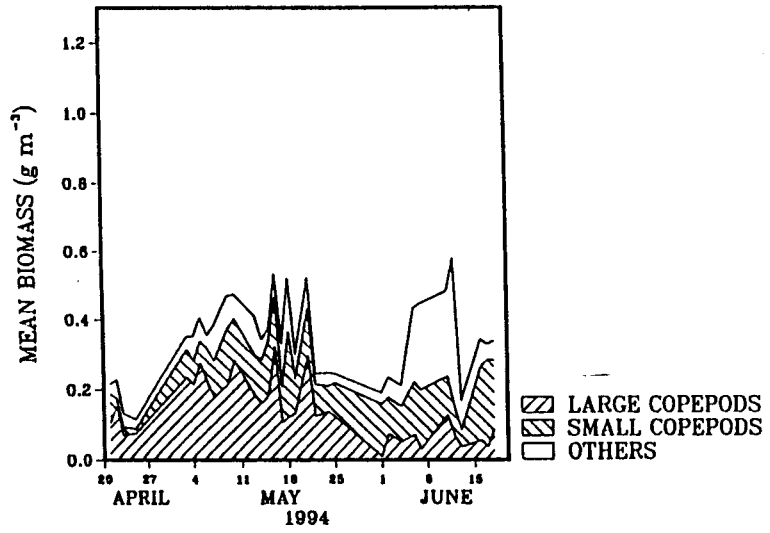


Figure 14. Variability in the large and small copepods and other taxa during the spring in 1994 and 1995.

Amphipoda

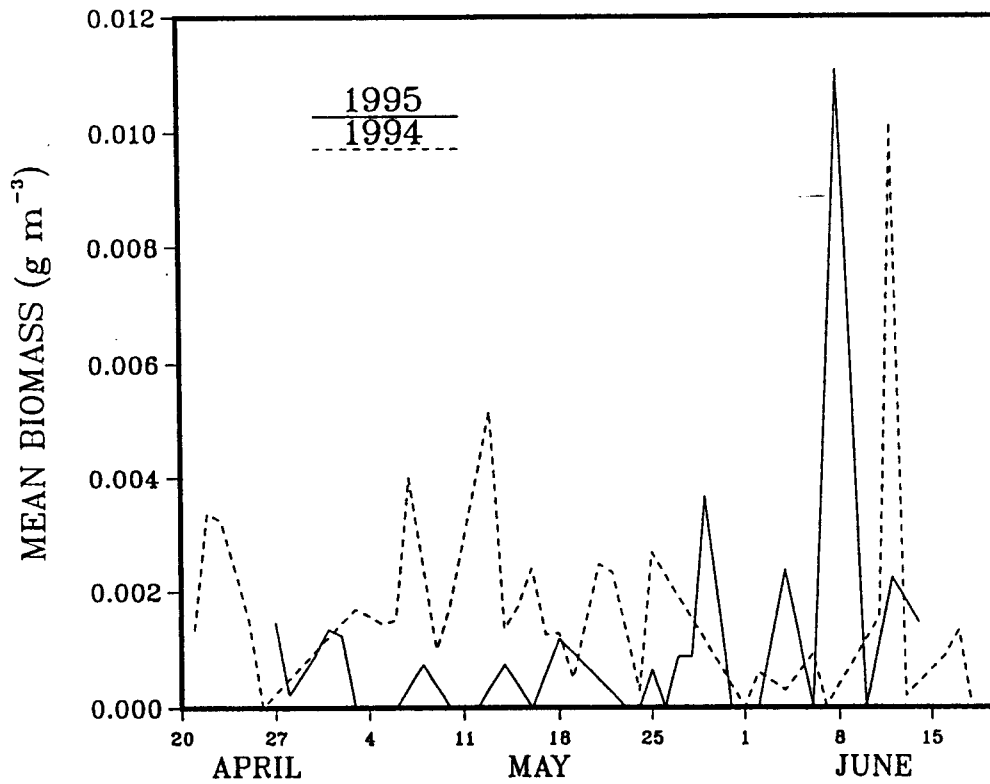


Figure 15. Variability in Amphipoda during spring in 1994 and 1995.

Euphausiacea

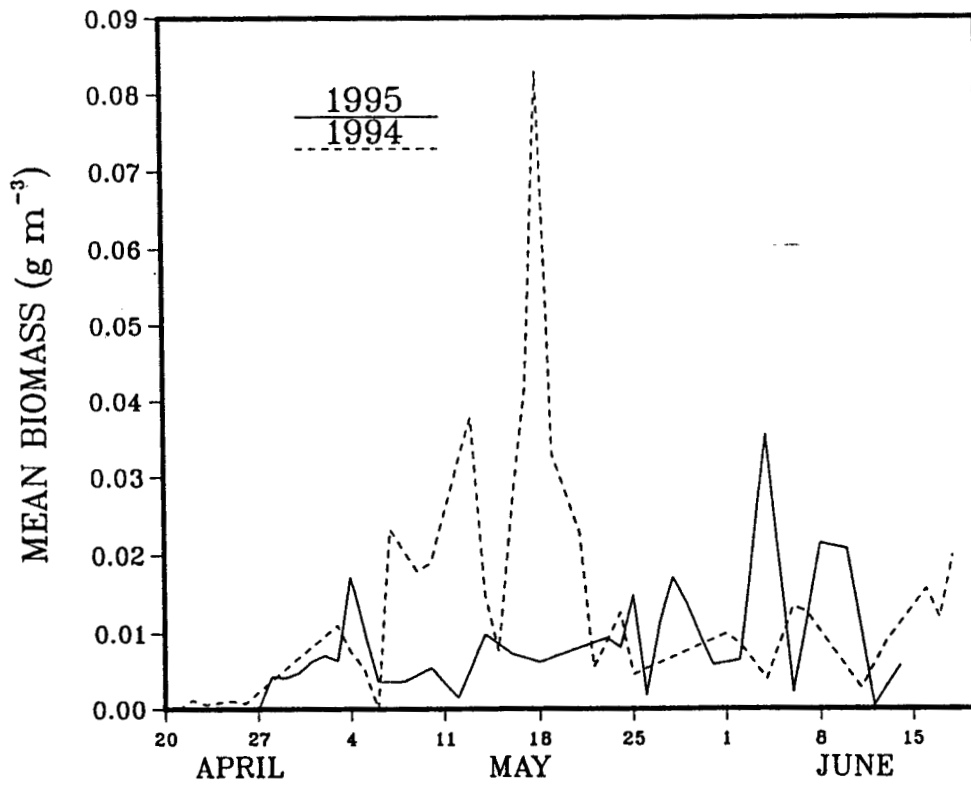


Figure 16. Variability in euphausiids (composite of *Thysanoessa* and *Euphausia*) during the spring in 1994 and 1995.

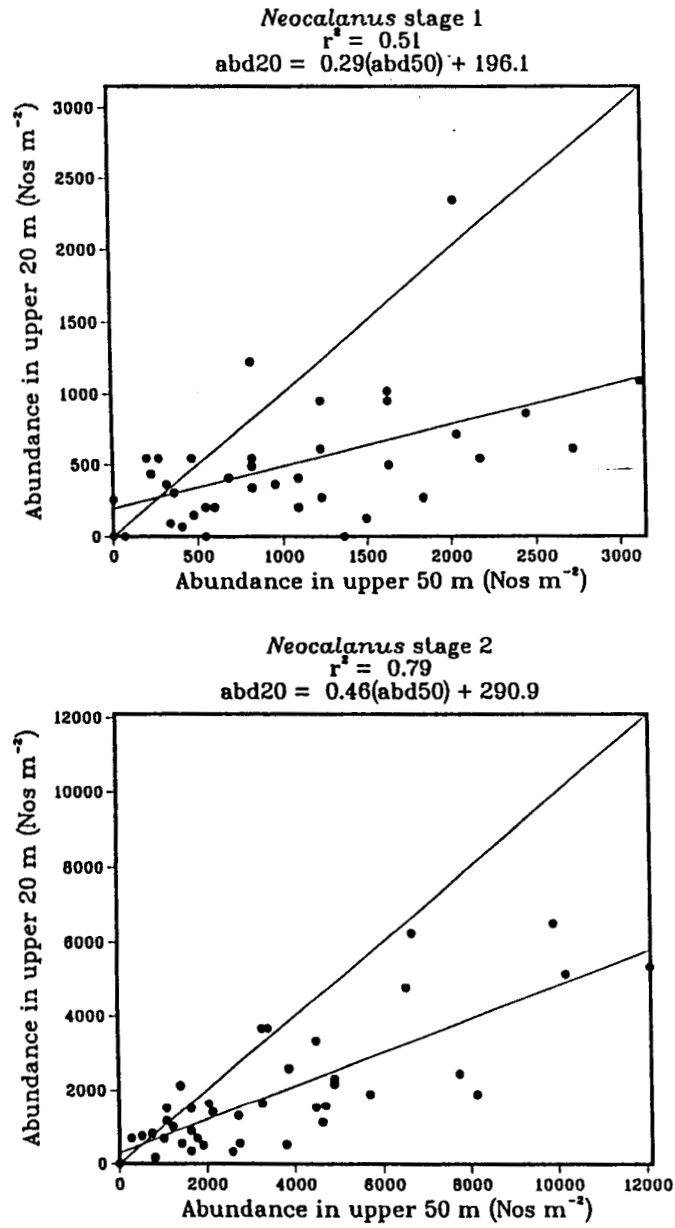


Figure 17. Regressions of 20 m abundance on 50 m abundance for CI (upper) and CII (lower) *Neocalanus* sampled in vertical tows in April and May, 1995.

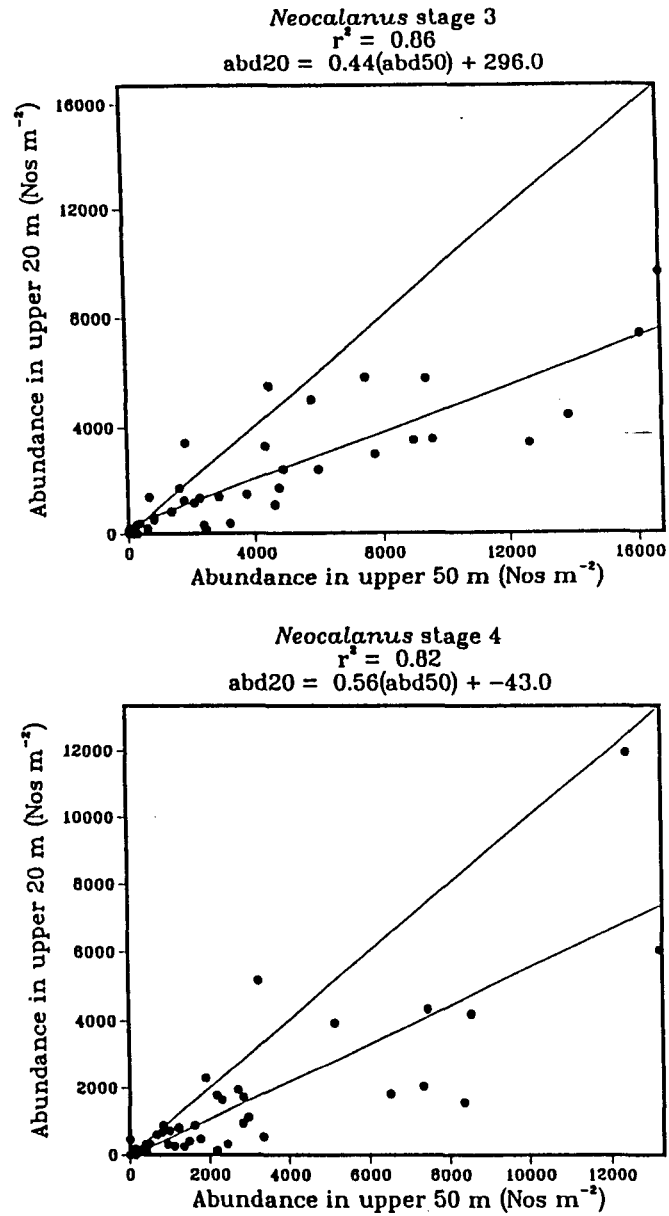


Figure 18. Regressions of 20 m abundance on 50 m abundance for CIII(upper) and CIV (lower) *Neocalanus* sampled in vertical tows in April and May, 1995.

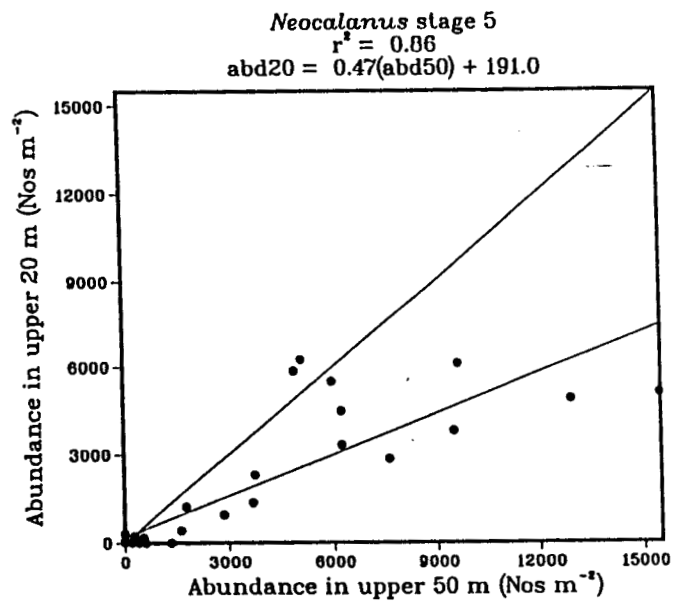


Figure 19. Regression of 20 m abundance on 50 m abundance for CV *Neocalanus* sampled in vertical tows in April and May, 1995.

Adult Pollock Stomachs

29 April-12 May, 1995; NW PWS

Stomach Content by Biomass

(Pollock subsample selected for full stomachs)

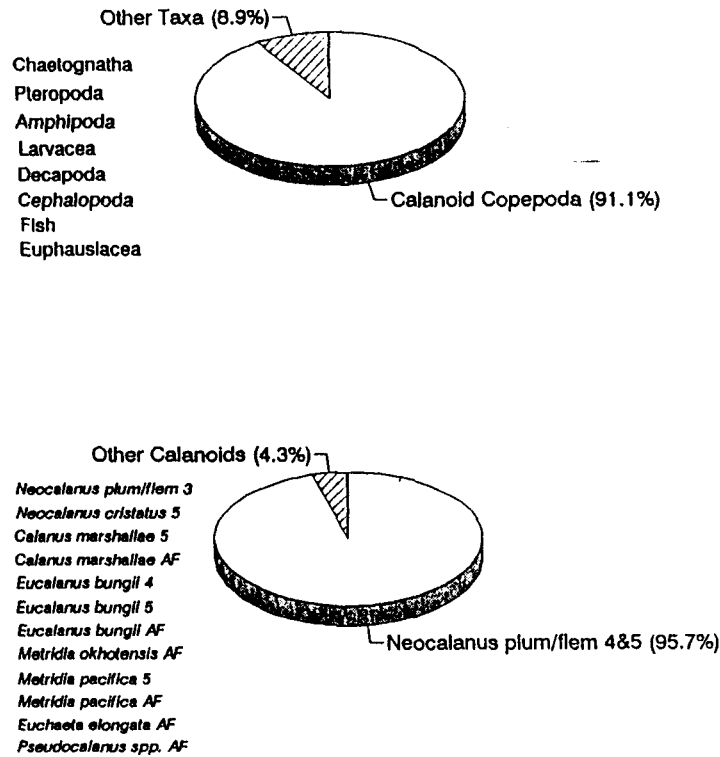


Figure 20. The diet composition by taxa (biomass) in stomachs of adult pollock sampled by midwater trawling in late April and May, 1995; F/V Alaska Beauty

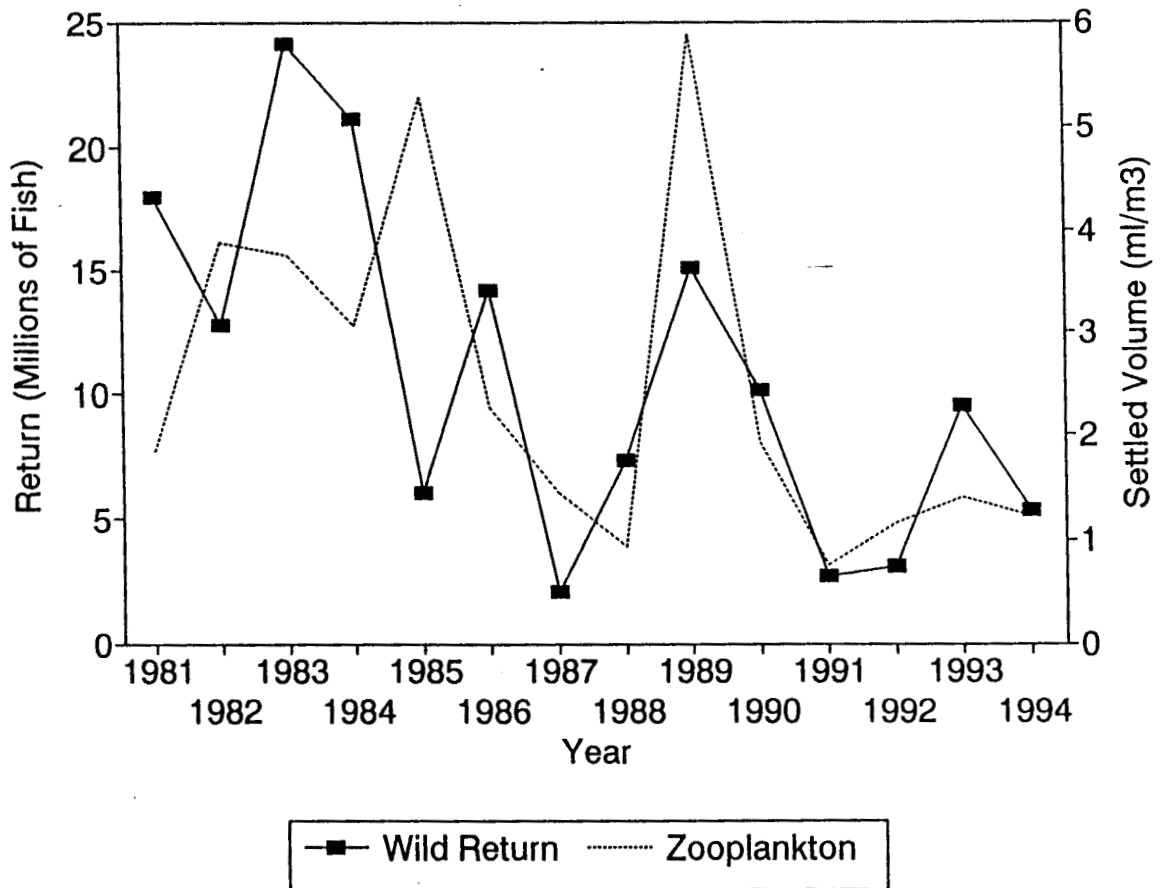


Figure 21. A time-series for zooplankton (AFK) and adult wild pink salmon returns in Prince William Sound.