Exxon Valdez Oil Spill
Restoration Project Annual Report

The Role of Zooplankton in the Prince William Sound Ecosystem

Restoration Project 96320-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.

Robert T. Cooney
Kenneth O. Coyle

Institute of Marine Science
University of Alaska Fairbanks
Fairbanks, Alaska 99775-7220

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Study History: Restoration Project 96320-H was continued in FY96 as part of the original integrated five-year Sound Ecosystem Assessment (SEA) program addressing injuries to pink salmon and herring populations in Prince William Sound initiated in April, 1994. Annual reports for this project have been submitted previously as part of single, integrated SEA program annual reports for FY94 and FY95. An invited paper (Cooney, R. T. and T. M. Willette. 1966. Factors influencing the marine survival of pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska) was presented at the Estuarine and Ocean Survival of Northeastern Pacific Salmon conference in Newport, Oregon, March 20-22, 1996. The paper was subsequently accepted for publication in the proceedings of the conference - a joint NOAA/NMFS and OSU Hatfield Marine Center report (in press). A second invited paper (Cooney, R. T. and R. D. Brodeur. 1966. Carrying capacity and North Pacific salmon production: stock enhancement implications) was presented at the 1996 William R. and Lenore Mote Symposium on Marine Stock Enhancement held at the Mote Marine Laboratory, Sarasota, Florida, November 21-23, 1996. A manuscript is being reviewed for the *Bulletin of Marine Science* which will publish selected papers from the symposium. A final report of project 230-H will be prepared for the Trustee Council as part of the formal close out of the program in FY99.

Abstract: Our work in 1996 demonstrates that in early May, 1996, populations of *Neocalanus* spp. in Prince William Sound and in the waters over the adjacent continental shelf were molting rapidly to stage V. Differences in community composition detected by cluster analysis defined two major macrozooplankton assemblages. One group was associated with water intruding the region from the adjacent continental shelf, while the other may have been a remnant population arising from local reproduction in the deep western and northwestern areas. *Neocalanus* and *Calanus* formed discrete layers in the upper 50 m of the water column at locations inside and outside Prince William Sound. At most locations, *N. plumchrus* and *flemingeri* stage V occurred shallower than *N. cristatus* stages III-V. *C. marshallae* distributions exhibited little preference for depth in the upper 50 m; layers being shallow at some locations and deep at others. We found no convincing evidence that plant stocks focus these calanoids into thin layers, although we were unable to test whether the grazers found food in unlimited quantities at all depths or actively sought out the depth of maximum photosynthesis. Layering behavior by *Calanus* and *Neocalanus* likely provides strata in the water column where filter or gulp feeding pelagic fishes can forage efficiently on zooplankton.

Key Words: *Calanus*, *Exxon Valdez* oil spill, layers, Macrozooplankton, *Neocalanus*, Prince William Sound.

Project Data: Zooplankton abundance and biomass information is part of the SEA data base

(Project 96320-J Information Services and Modeling)

Citation:

Cooney, R.T., and K.O. Coyle. 1997. The role of zooplankton in the Prince William Sound ecosystem, Exxon Valdez Restoration Project Annual Report (Restoration Project 96320-H), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska.

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Appendix 1. Vertical and horizontal distributions of macrozooplankton in Prince William Sound, Alaska, with emphasis on large calanoida (manuscript prepared for review by the *Journal of Plankton Research*).

Executive Summary

Previous 320-H studies of the role of zooplankton in Prince William Sound under the overall Sound Ecosystem Assessment (SEA) program have focused on describing seasonal and interannual variations in species composition and abundance, principally to support juvenile pink salmon growth and predation studies (320-E), but also to aid the broadscale numerical modeling of plankton fields in the region (320-J and 320-R). Work in FY96 focused attention on questions of *in situ* abundance and biomass, particularly the degree to which some macrozooplankters are capable of forming dense, near-surface layers that might prove to be efficient zones for the transfer of energy to higher trophic levels like adult walleye pollock. This collaborative work (high-frequency acoustics and optical plankton counting) was pursued on a joint cruise in early May aboard the University of Alaska vessel R/V *Alpha Helix*. Investigators from the University of Alaska and the Prince William Sound Science Center studied the layering phenomenon at a time when juvenile pink salmon were leaving natal streams and hatcheries for near-shore nursery areas, and populations of large calanoids were expected to be reaching seasonal biomass peaks.

This annual report presents results obtained by fishing a 1-m2 multiple opening-closing net environmental sensing system (MOCNESS) in the upper 50 m at locations inside and outside Prince William Sound. An appended draft manuscript describes patterns in broadscale horizontal and smallscale vertical distributions of selected macrozooplankters in the region. The work documents calanoid layers at many, but not all locations, zooplankton community affinities between the Sound and intruding water masses, and provides information about relationships between copepod layers or swarms and the vertical distribution of phytoplankton and mixing regimes in the water column. Results for other work in FY96 that were not met specifically by the field study in May are reported in the body of the report.

Introduction

The SEA program in Prince William Sound has undertaken an ecosystem approach to understanding the factors influencing pink salmon and herring production in the region. Study focus is on the early life stages of both species when most literature suggests that cohort strength is established. Juvenile pink salmon use Prince William Sound as a coastal nursery from late March through September before departing for oceanic feeding areas. In contrast, juvenile herring are resident in the Sound for 2+ years before recruiting to adult spawning populations. The juveniles of both species are dependent on zooplankton for food.

Previous studies of zooplankton in the subarctic Pacific Ocean demonstrate marked seasonality in upper-layer abundance and biomass (see Cooney, 1987 for a review). In coastal and nearshore waters, animal plankton populations respond to an early spring bloom of phytoplankton to build their populations. Cooney (1986) and Incze et al. (1997) provide evidence of the influence of ocean source populations on near-shore and coastal zooplankton assemblages. Oceanic stocks of large calanoid copepods invade the shelf each spring as part of the onshore transport of water in

the northern Gulf of Alaska. These populations are believed to provide food for fishes, birds and marine mammals.

SEA studies of the role of zooplankton in Prince William Sound strive to understand how the species composition, distribution, abundance and biomass of this group influences the survival of juvenile pink salmon and herring rearing in Prince William Sound. SEA investigators hypothesize that while zooplankton serves as critical forage for rapidly growing immature stages, it may also serve as a predation refuge for juveniles whose losses to larger fishes, birds and mammals is probably related to the kinds and amounts of alternate prey. A clear match between the timing of the wild pink salmon fry outmigration from natal areas into nearshore marine waters with the timing and magnitude of the developing calanoid bloom observed in the Sound by a hatchery plankton watch program is probably not coincidental. We believe this relationship results from evolutionary pressure to match fry with appropriate food and quite possible shelter from predation from large fish like adult pollock that can also derive energy from plankton. Observations in 1995 at the peak of the salmon outmigration indicated that most adult pollock were consuming large quantities of maturing calanoid copepods at that time. SEA surmises that to be efficient, forage populations must occur in dense, near-surface layers providing efficient filter or gulp-feeding. Most of the field work in FY96 was designed to investigate this notion.

Objectives

The following objectives were stated in the approved FY96 DPD:

1. Measure collaboratively with other SEA components horizontal and vertical distributions of zooplankton in support of large and small-scale mapping activities, and determine the degree to which layers of zooplankton occur in Prince William Sound during the peak of the large calanoid bloom and juvenile salmon outmigration from natal streams and hatcheries.
2. Describe the time series of abundance and biomass for PWSAC plankton watches conducted at the AFK and WN hatcheries.
3. Work collaboratively with the three SEA modeling subgroups to make zooplankton data available for model construction and hypothesis testing.
4. Contribute information to investigators studying the somatic energy content of juvenile herring.

Methods

Methods used to pursue the documentation (or not) of calanoid copepod layers in Prince William Sound are described in the method section of the attached appendix 1. Samples from the plankton watches at the AFK and WN hatcheries were obtained by hatchery personnel fishing 1/2-m nets vertically by hand in the upper 20 m of the water column weekly from mid March through June. After settled volumes were determined by the hatchery, samples were saved and

later processed in the Principal Investigator's laboratory.

Data were interpreted and made available to other collaborators in SEA via the SEA data base and by use of the SEA information network. In some cases, data exchange and application was facilitated by the Fall 1996 SEA workshop in Seward.

Results

Appendix 1 has been prepared for publication and describes the results of the MOCNESS survey work in Prince William Sound in early May, 1996. These results will join those collected by investigators sampling with high-frequency acoustic and optical plankton techniques to describe the structural properties of near-surface plankton layering and its implications for food web transfers to higher level consumers that also prey on juvenile pink salmon and herring. This broader, collaborative synthesis paper will probably be submitted in FY97.

Settled volume data for the AFK and WN hatcheries in southern and northern Prince William Sound respectively were examined for relationship with the Bakun upwelling index. However, the monthly index for May at location 60N 146W is missing from the time series, so I am unable to add the FY96 data to the regressions for AFK and WN hatcheries. Average settled volume at AFK in 1996 was somewhat lower (1.79 ml m-3) than the most recent high in 1995 (1.96 ml m-3). Samples are still being analyzed for species composition, abundance and biomass. These results will be reported in the FY97 annual report, and an attempt will be made to recover the May, 1996 upwelling observations from NOAA.

The principal investigator worked closely with project 320-R to assist with creating and testing a dynamic plankton 1-D model for Prince William Sound (see report of 320-R in this volume). The collaboration included providing data and data interpretation, and assisting with the preparation of a manuscript for publication that describes the preliminary results.

Information on the caloric content of several common zooplankters was made available to investigators studying and modeling the somatic energy content of juvenile herring. Previous work by Harris (1985) provided a starting point for initial evaluations of the energy input contributed by calanoid copepods, amphipods, pteropods and other dominant taxa. Data on zooplankton abundance and biomass continues to be posted in the SEA data base for use by all SEA (and other) investigators.

Discussion

Our field work continues to refine the role that zooplankton serves as a structuring element in food-webs influencing the survival of juvenile pink salmon and herring in Prince William Sound, Alaska. The suspicion that layering by large calanoids may be a common springtime phenomenon in the region was generally confirmed. Our preliminary results also add support to the idea that the northwestern and western parts of the Sound may be oceanographically isolated

from other regions, at least in the spring and early summer. Cluster analyses on both abundance and biomass involving 30-40 major species and taxonomic categories demonstrated strong coherence between locations inside and outside the Sound. These observations further refine our view of lake (isolated) and river (intrusion) portions of the Sound, and challenge further work to understand the role that these biological and physical affinities play in influencing juvenile pink salmon and herring survival. The possibility that *Neocalanus* in the western and northwestern region may originate from local stocks will be evaluated when the isotope samples collected on the cruise become available. This new information will further assist in the validation of ocean state and plankton models.

Conclusions

The results of work completed in FY96 strengthen our collective understanding of the role that zooplankton plays in food-webs influencing the survival of juvenile pink salmon and herring in Prince William Sound. Our views on relationships between populations inside and outside the Sound have been enhanced. A case for partial isolation of some regions, and coherence between others with intruding shelf waters builds on the idea that the region is partitioned in ways that might also be apparent at higher trophic levels. As the result of the *Alpha Helix* cruise, we now know that zooplankters, principally the late stages of the *Neocalanus* and *Calanus* can occur in narrow layers at a time pink salmon are emerging from natal areas into coastal nurseries. Within-layer densities exceeding 1000 individuals m-3 at some locations probably provide efficient feeding opportunities for a variety of consumers, some capable of also feeding on fry. This information is critical to the process of modeling prey switching driven by the bioenergetics demands of predators and prey, and is finding immediate use in this regard.

Acknowledgments

Literature Cited

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Appendix 1

Draft

(For Submission to the Journal of Plankton Research)

Vertical and Horizontal Distributions of Macrozooplankton
in Prince William Sound, Alaska, with Emphasis on Large Calanoida

R. Ted Cooney, Kenneth O. Coyle and Elizabeth Stockmar

Institute of Marine Science
University of Alaska Fairbanks
Fairbanks, Alaska 99775

Abstract

Macrozooplankton populations in Prince William Sound were dominated by juvenile euphausiids and calanoid copepods in early May, 1996. Much of the abundance and biomass was associated with the large, older copepodite stages of *Neocalanus plumchrus* and *N. flemingeri*. Horizontal plankton distributions reflected affinities with Gulf of Alaska source populations except for collections in Knight Island Passage and the waters in the northwestern corner of the region which clustered as a separate group. These differences are probably related to water mass characteristics (temperature and salinity), and perhaps population remnants from local reproduction isolated in the deep northern and western areas of the Sound.

At many locations where *N. plumchrus* and *flemingeri* stage V dominated the abundance and biomass, these species occurred in well-defined layers 5 to 25 m in vertical extent. Within-layer densities exceeding 1000 individuals/m3 and 2-3 g/m3 (wet weight) demonstrate locally abundant forage resources for pelagic fishes and other consumers. Unlike the oceanic Gulf of Alaska, the surface mixed layer was very shallow at most locations over the shelf and inside Prince William Sound. *Neocalanus plumchrus*, N. *flemingeri* almost always occurred above and/or in the near-surface pycnocline, while *N. cristatus* was restricted to deeper water in the upper 50 m. *Calanus marshallae* exhibited layering behavior as well, but no clear preference for deep or shallow was observed. Layers of maximum copepod density co-occurred with surface or

subsurface fluorescence peaks at only 32% of the locations in the region.

Introduction

Mackas, et al. (1993) described vertical habitat partitioning by large calanoids in the open subarctic Pacific Ocean. Their study demonstrated close correlation between upper-layer mixing regimes and depth preferences for *Neocalanus plumchrus*, *N. flemingeri*, *N. cristatus*, and *Eucalanus bungii*. Annually developing copepodites of the former two species were consistently found above or in the weak seasonal thermocline, while the latter were generally restricted to the water column below the seasonal thermocline. This separation was interpreted to reflect feeding preferences for protozoans in the spring and summer surface mixed layer by *N. plumchrus* and *flemingeri*, and detrital feeding on aggregates settling from the surface zone by *N. cristatus* and *E. bungii*.

Cooney (1986) documented the presence of *Neocalanus plumchrus*, *N. cristatus* and *Eucalanus bungii* over the shelf of the northern Gulf of Alaska south of Prince William Sound. These distributions were attributed to strong cross-shelf transport forced by down-welling favorable winds interacting with source populations in the epipelagic layer of the adjacent deep ocean. These interzonal copepods have previously been reported overwintering in Prince William Sound by Damkaer (1977). Coupled with a growing understanding of coastal flow patterns and the intrusion of shelf water into Prince William Sound (Neibauer et al., 1994), a mechanism exists to infuse the coastal zone of the northern Gulf of Alaska oceanically-derived copepods each year, some of which are apparently capable of reproducing in the deep waters of sounds and fjords. This seeding phenomenon has most recently been demonstrated for the waters of Shelikof Strait, a portion of the shelf environment west of Prince William Sound near Kodiak Island (Incze et al., 1997).

Our study was designed to investigate similarities in upper-layer spring-time macrozooplankton populations inside and outside Prince William Sound when the older copepodite stages of *Neocalanus* were expected in the surface waters (0-50 m). Historical records from the plankton watch program of a regional aquaculture corporation (Prince William Sound Aquaculture Corporation; Cordova, Alaska) demonstrate that a peak in settled plankton volume occurs in early to mid-May each year. These same records indicate that average spring-time (March-June) settled volumes have varied in the southern part of Prince William Sound by about a factor of 5 since 1981. It is unclear to what extent year-to-year variability is the result of differences in local production or seeding/flushing from, or to the adjacent Gulf of Alaska. Because about 10 percent of the Sound is deeper than 400 m, deep overwintering habitat is available to accommodate *a Neocalanus* diapause and reproduction as described by Fulton (1973) for the Strait of Georgia.

Additionally, observations of adult pollock (*Theragra chalcogramma*) feeding behavior in late April and early May in Prince William Sound demonstrated selection for stage 4 and 5 *N. plumchrus* and *N. flemingeri* (Cooney, unpublished). This behavior raises questions about *in situ* concentrations required to sustain filter feeding by large pelagic fishes. We hypothesized that locally produced copepods and those intruding into the region with the coastal current could efficiently feed populations of adult pollock and other consumers if these plankters were

restricted in their vertical distribution to narrow zones in the surface water (layers or swarms). Optical plankton records from a previous survey in Prince William Sound hinted at layers, although those observations were not accompanied by zooplankton collections. Our work sought resolution of the calanoid layer question with nets capable of resolving discrete depth distributions in strata as narrow as 5 m.

Methods

Zooplankton sampling was conducted in and adjacent to Prince William Sound, Alaska, a deep fjord-type estuary located at the northern-most reaches of the Gulf of Alaska (Figure 1). The region is deep (to 750 m), is bounded on to the west, north, and east by the Chugach Mountains, and communicates with the adjacent Gulf of Alaska via the Alaska Coastal Current (ACC) entering through Hinchinbrook Entrance and Montague Strait. The region occupies nearly 9000 km2 and exhibits 3200 km of shoreline. The adjacent shelf of the northern Gulf of Alaska is a wind-forced downwelling system for 8 months of each year. Stabilization or weak upwelling can occur in the summer months. Deep water in the Sound is renewed each year during the time of relaxed downwelling, late summer and early fall.

A MOCNESS sampler was employed at 24 stations inside and outside PWS to collect macrozooplankton in the upper 50 m (Figure 1). Sampling was undertaken at the peak of the early spring zooplankton bloom, early to mid-May, and about two weeks after the seasonal maximum in phytoplankton stocks judged by a moored fluorometer in the central region of the Sound. The MOCNESS fished nine,1-m2 Nitex nets of 0.505-mm mesh. Net one was lowered open from the surface to a depth below 50 m with the vessel steaming at about 1.5 m sec-1. The remaining nets were then opened and closed on a slow oblique retrieval. Sampling intervals were standardized at 50-40 m, 40-30 m, 30-25 m, 25-20 m, 20-15 m, 15-10 m, 10-5 m, and 5-0 m. Collections were carefully rinsed from nets and preserved in 10% seawater formalin for later processing. Processing included identification and enumeration of plankters and the various copepodite stages of the large calanoids. Representatives of species were weighed in size categories to convert numbers to estimated wet weight (Coyle, et al., 1990).

A SeaBird 911 CTD and *in situ* fluorometer were lowered at the beginning or end of each MOCNESS station to describe upper-layer hydrography and mixing, and the vertical distribution of phytoplankton. The fluorometer was not calibrated so only relative fluorescence was obtained from each cast. This was believed sufficient to examine the possibility that copepod layers might be strongly associated with vertical patchiness in plant stocks.

Results

Community composition

A cluster analysis was performed to determine similarities in the horizontal distribution of species composition among all stations. For each MOCNESS station, the top 5 ranked taxonomic categories (numbers or biomass) were selected from each of the 8 nets, and the overall listing of taxa used to differentiate between stations. Forty-three taxonomic categories contributed to the cluster analysis on abundance; 53 to clustering on biomass.

For abundance, the highest level of differentiation separated two groups that included 10 locations outside and from the central, northern and eastern regions of the Sound - Group 1, and 14 locations mostly in the northern and western part of the region - Group 2 (Figure 2). Only Station 15 in Group 2 clustered outside its geographic region (Figure 3). When biomass was used to cluster stations, the first level of differentiation separated two groups that were similar to those clustering on abundance. However, under the biomass ranking criteria three stations that previously clustered with Group 2 (Stations 6, 18 and 19), joined Group 1, while Station 9 shifted to the northwestern/western cluster (Figure 4). A t-test of differences between taxa and stages within groups for abundance and biomass demonstrated that for abundance, clustering was driven primarily by 8 different categories, while for biomass, the major differentiations were forced principally by only 2 categories (p<0.05; Table 1).

A ranking by numerical abundance within the major cluster groups was performed to describe the numerical dominants (Table 2). Group 1, the outer-shelf and central Sound assemblage was dominated by juvenile euphausiids (furcilia and calyptopis stages) and *Neocalanus flemingeri* stage V, while Group 2 was led by *N. plumchrus* and *N. flemingeri* stage V, with juvenile euphausiids playing a much lesser role. The top ten categories in Group 1 also contained the hydromedusan, *Aglantha digitale,* and the pterpod, *Limacina helicina.* These taxa were absent from the top ten ranking of Group 2.

Patterns of vertical distribution for large calanoids

Vertical profiles for the large calanoid species *Neocalanus plumchrus, N. flemingeri, N. cristatus*, and *Calanus marshallae* were examined for evidence of layering and association with the buoyancy frequency and fluorescence patterns in the upper 50 m at each location. We could only confidently distinguish between *N. flemingeri* and *N. plumchrus* at copepodite stage V, so restrict our accounts of those closely related copepods to that stage (Miller, 1988). A composite of *N.* spp. stage III and IV was examined separately. For *N. cristatus*, a composite of stages III-V is reported, and for *Calanus marshallae*, stages IV through adult were combined to search for patterns in vertical distribution. A distribution was considered "layered" in the upper 50 m when most of the abundance or biomass was restricted to 50% or less of the sampled domain.

Neocalanus flemingeri stage V ranked second in Group 1 and first in Group 2 by abundance, and *N. flemingeri* and *N. plumchrus* stage V ranked first and second respectively in both groups by biomass establishing their dominance throughout the region in early May, 1996. For outside waters and Prince William Sound Group 1, these species (stage V) co-occurred in 66% of the samples, while in Group 2 (western and northwestern stations and including station 15), co-occurrence was reduced to 37% of the samples. Also, in samples where they co-occurred, *N. plumchrus* was generally found at all depths in Group 1, but restricted to the upper portion of the sampling domain in Group 2, the exception being station 15 in which co-occurrence was present at all depths (Figure 5). The combined abundance and biomass of the stage Vs of these two species was greatest over the outer shelf near Middleton Island (station 9). Here, combined numbers and biomass exceeded 1500 individuals m-3 and 4 g m-3 respectively. For Group 1, 50% of the stations exhibited at least one depth for which the abundance of these combined species (stage V) exceeded 100 individuals m-3, while for group 2, 93 % of the stations exhibited at least one depth where the combined abundance exceeded 100 individuals m-

3. *Neocalanus plumchrus* and *N. flemingeri* stage V were found in dense layers at 50 % of the locations in Group 1, and 79% of the locations in Group 2 (Figure 6).

A composite of *Neocalanus plumchrus* and *N. flemingeri stages* III-IV exhibited vertical distributions similar to stage V. These copepodites occurred in dense layers at 50% of the locations in Group 1, and 79% of the locations in Group 2 (Table 3; Figure 7). Combined stages III and IV were more abundant than stage V at 4 locations (40%) in Group 1, but at only 1 location (7%) in Group 2. These stage differences suggest that the rate of development was more rapid in the western and northern regions of Prince William Sound, and that most IIIs and IVs had already molted to stage V across the region.

The large copepod *Neocalanus cristatus* stages III-V was much less abundant at all locations than *N. plumchrus* and *flemingeri*; at only 3 of 24 locations did the concentration of *N. cristatus* exceed 10 m-3. However, even at diminished numbers, this copepod occurred in layers at 50% of the locations in Group 1 and 93% of the locations in Group 2 (Table 3). In Group 1, the distribution of *N. flemingeri* and *N. plumchrus* stage V overlapped with *N. cristatus* at 70% of the locations, whereas in Group 2, there were only 2 locations of overlap (14%). Generally, maximum densities of *N. cristatus* occurred deeper in the water column than did *N. plumchrus* and *N. flemingeri* (Figure 9).

Calanus marshallae, stages IV-adult exhibited a lesser capacity to form dense layers. For Group 1, only 30% of the locations were represented by layering compared to 71% of the locations in Group 2 (Table 3). *C. marshallae* demonstrated no clear pattern of depth distribution (Figure 10).

Vertical patterns of florescence and copepod distributions

Subsurface maxima were apparent at 6 of 10 locations in Group 1 and at all locations in Group 2 (Figure 11). Surface florescence maxima occurred at the shelf-break location 9, and in the ACC at Station 11. Stations 13 and 14 in Montague Strait exhibited generally homogeneous patterns of fluorescence with depth. For the copepod species and stages examined in this study, maximum densities were closely aligned with florescence maxima at 40 % of the locations in Group 1, but at only 25% of the locations in Group 2. Overall, copepod layers co-occurred with subsurface fluorescence maxima at less than 32% of the locations (Figure 12).

Fluorescence levels varied throughout the region. Four Group 1, 4 of 10 locations exhibited depths where the fluorescence exceeded 1.0 volt. In Group 2, only 3 of 14 locations had fluorescence peaks exceeding 1.0 volt. These results indicate the spring phytoplankton bloom was probably over, except over the outer continental shelf south of the Sound and at spotty locations inside the Sound.

Vertical patterns in buoyancy frequency

Buoyancy frequency measures the degree of mixing with depth in the water column. Maxima correspond within regions of reduced vertical mixing. At most stations in this study, buoyancy frequency was maximum in the upper 20 m in response to seasonal freshwater input and thermal stabilization. Only at Station 9 at the self-break was there a well-defined subsurface maximum in buoyancy frequency at about 20 m (Figure 13). There was no consistent relationship between copepod distributions and the buoyancy frequency at any location. Since

Neocalanus cristatus generally occurred deeper in the water column than the other species and stages, it was most often (but not always) found below the near-surface maximum in buoyancy frequency.

Patterns in watercolumn temperature and salinity

Stations 9 and 10 at the edge and over the continental shelf were warm (8 C) and saline (>32 ppt). Station 11 in the ACC was also warm, but much less saline at the surface (30.5 ppt). In contrast, locations clustering with Group 2 (excluding Station 15) tended to be colder and less saline (6-7 C, ranging up to 30 ppt). The remaining locations in central and northern Prince William Sound were intermediate between these endpoints suggesting that a mixing process between intruding shelf and interior Sound waters was probably responsible for the observed gradients (Figure 14).

Discussion

We found that some macrozooplankton collections in Prince William Sound demonstrated statistical affinities with locations outside the region, while others grouped with an assemblage located primarily in Knight Island Passage and the northwestern part of the Sound. We have no explanation why one location (station 15) north of Hinchinbrook Entrance clustered with the other assemblage. We interpret the physical separation of these two groups as signaling strong continuity between northern, central, eastern and southern portions of Sound and waters intruding from the adjacent Gulf of Alaska, but isolation from this intrusion at locations in the west and northwest regions. Measured and modeled flow fields in the spring in Prince William Sound exhibit inflow at Hinchinbrook Entrance and outflow through Montague Strait (Neibauer et al., 1994; Mooers and Wang, submitted). This flow is generally believed to move northward and westward through the Sound. Our results seem to indicate the biological and physical influences of this flow are not as strongly demonstrated in the western and northern parts of the Sound as they are in other regions. Shelf waters intruding the Sound are generally warmer and more saline than those inside the region. As the intruding watermass spreads through the Sound, it cools and becomes less saline before exiting at Montague Strait. The western and northern waters in Knight Island Passage and in the northwestern regions appear more dominated by local processes; glacial meltwater probably forms a stable freshwater lens at the surface in much of that region.

Damkaer (1977) reported *Neocalanus* spp. in diapause in the deep waters of Prince William Sound in October. This is not surprising since Fulton (1973) described overwintering populations of *Calanus (Neocalanus) plumchrus* in the Strait of Georgia at depths of about 400 m. Prince William Sound is deeper than 400 m in the northern and western regions so should accommodate local reproduction, but only in these areas. Copepodites originating from deep-water stocks would presumably occur most abundantly in or near the location where spawning occurs. Because of this, we believe that some major portion, or all of the late stage *Neocalanus* spp. in Group 2 are remnants from local deep-water spawning in that region and exist there because of physical isolation from intruding shelf and ocean sources in the late winter and spring. If this is so, interannual variability in standing stocks of *Neocalanus* spp. at other locations in the Sound must be associated with year-to-year differences in source stocks over the shelf and/or

differences in rates of seeding or flushing associated with late winter and spring intrusions of shelf water. Conversely, year-to-year variations in western and northwestern *Neocalanus* spp. stocks are probably related more to the reproductive success of adults spawning in the deep northwestern and western regions of Prince William Sound.

Prior to our study, limited information on adult pollock feeding ecology and some preliminary optical plankton counting observations (Prince William Sound Science Center; Cordova, Alaska) suggested that some zooplankton populations were probably occurring in layers or swarms in the upper 50 m in sufficient densities to support filter or gulp-feeding by large pelagic fishes and possibly other consumers. The ability to feed on plankton has been reported for pollock but not in the context of available food fields. Our results in May, 1996, demonstrate convincingly that layering by late-stage copepodites of *Neocalanus plumchrus* and *N. flemingeri* was occurring at within-layer densities up to 1000 individuals m-3 and 2-3 g m-3. The much larger *N. cristatus* also demonstrated layering behavior, but densities rarely exceeded 10 individuals m-3. A closely related large calanoid, *Calanus marshallae*, was abundant and formed layers as well. However, this medium-sized species exhibited no clear preference for deep or shallow parts of the upper 50 m, while *N. plumchrus* and *flemingeri* generally preferred the upper 30 m and *N. cristatus* was quite consistently found deeper. These patterns in *Neocalanus* vertical distribution generally agree with the findings of Mackas et al., (1993).

At most locations where physical stratification was apparent, there was a well-defined subsurface maximum in fluorescence. However maxima in copepod densities or biomass occurred in the subsurface peak in fluorescence at less than half the locations. *Neocalanus* spp. stage V should have been elaborating wax esters at this time (Miller, 1993), so might reasonably have been expected to co-occur with peaks food. In the absence of strong evidence that maxima in phytoplankton were focusing the vertical distributions of these large grazers, we conclude that either food was not limiting growth at most depths in the upper 50 m, or the copepods were targeting regions of high plant productivity, not standing stock. Unfortunately, our observations do not permit distinguishing between these possibilities.

In summary, our study demonstrates that in early May, 1996, populations of *Neocalanus* spp. in Prince William Sound and in the waters over the adjacent continental shelf were molting rapidly to stage V. Differences in community composition detected by cluster analysis defined two major macrozooplankton assemblages. One group was associated with water presumably intruding the region from the adjacent continental shelf, while the other could have been a remnant assemblage arising from local reproduction in the deep western and northwestern areas. *Neocalanus* and *Calanus* formed discrete layers in the upper 50 m of the water column at many locations inside and outside Prince William Sound. At most, *N. plumchrus* and *flemingeri* stage V occurred shallower than *N. cristatus* stages III-V. *C. marshallae* distributions exhibited little preference for depth in the upper 50 m, layers being shallow at some locations and deep at others. We found no convincing evidence that plant stocks focus these calanoids into thin layers, although we are unable to determine whether the grazers found food in unlimited quantities at all depths or actively sought out the depth of maximum photosynthesis. Layering behavior by *Calanus* and *Neocalanus* likely provides strata in the water column where filter or gulp feeding pelagic fishes can feed efficiently on plankton. This possibility is being pursued by other studies at this time.

Acknowledgements

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Table 1. Significant statistical differences between groups clustering on number or biomass

Taxonomic Category	Group 1	Group 2	Probability
Clustering on number	Indiv. m-3*	Indiv. m-3*	P
Neocalanus flemingeri V	9.7	35.1	0.007
N. plumchrus V	3.8	9.5	0.031
Calanus marshallae adult	1.5	2.7	0.015
Euphausiid eggs	2.1	1	0.012
Euphausiid furcilia	13.2	4.5	0.046
Barnacle nauplii	4	1.6	0.007
Aglantha digitale	5.9	1.7	0.002
Limacina helicina	4.7	2.1	0.037
Clustering on biomass	g m-3*	g m-3*	P
Neocalanus spp. IV	0.019	0.038	0.038
Calanus marshallae IV	0.007	0.004	0.037

* = geometric mean

Table 2. Ranking taxa by abundance in groups identified by cluster analysis

Group I - Outside and central Sound	Group II - western and northwestern Sound
1 Euphausiid furcilia	1 *Neocalanus flemingeri* stage V
2 *Neocalanus flemingeri* stage V	2 *Neocalanus* spp. stage IV
3 *Neocalanus* spp. stage IV	3 *Neocalanus plumchrus* V
4 Euphausiid calyptopis	4 *Pseudocalanus* spp. V
5 *Aglantha digitale*	5 *Pseudocalanus* spp. adult female
6 *Pseudocalanus* spp. adult female	6 *Neocalanus* spp. stage III
7 *Calanus marshallae* stage IV	7 *Calanus marshallae* stage III
8 *Calanus marshallae* stage III	8 Euphausiid furcilia
9 *Limacina helicina*	9 *Calanus marshallae* stage IV
10 *Pseudocalanus* spp. stage V	10 Euphausiid calyptopis

Table 3. Tendencies for large calanoids to form layers in cluster groups 1 and 2

Taxonomic category	Group 1	Group 2	Overall
Layering by abundance	% locations	% locations	% locations
Neocalanus flemingeri and *N. plumchrus* stage V	50	79	67
N. spp. stages III-IV	50	79	67
N. cristatus stages III-IV	50	93	75
Calanus marshallae III-Adult	30	71	54
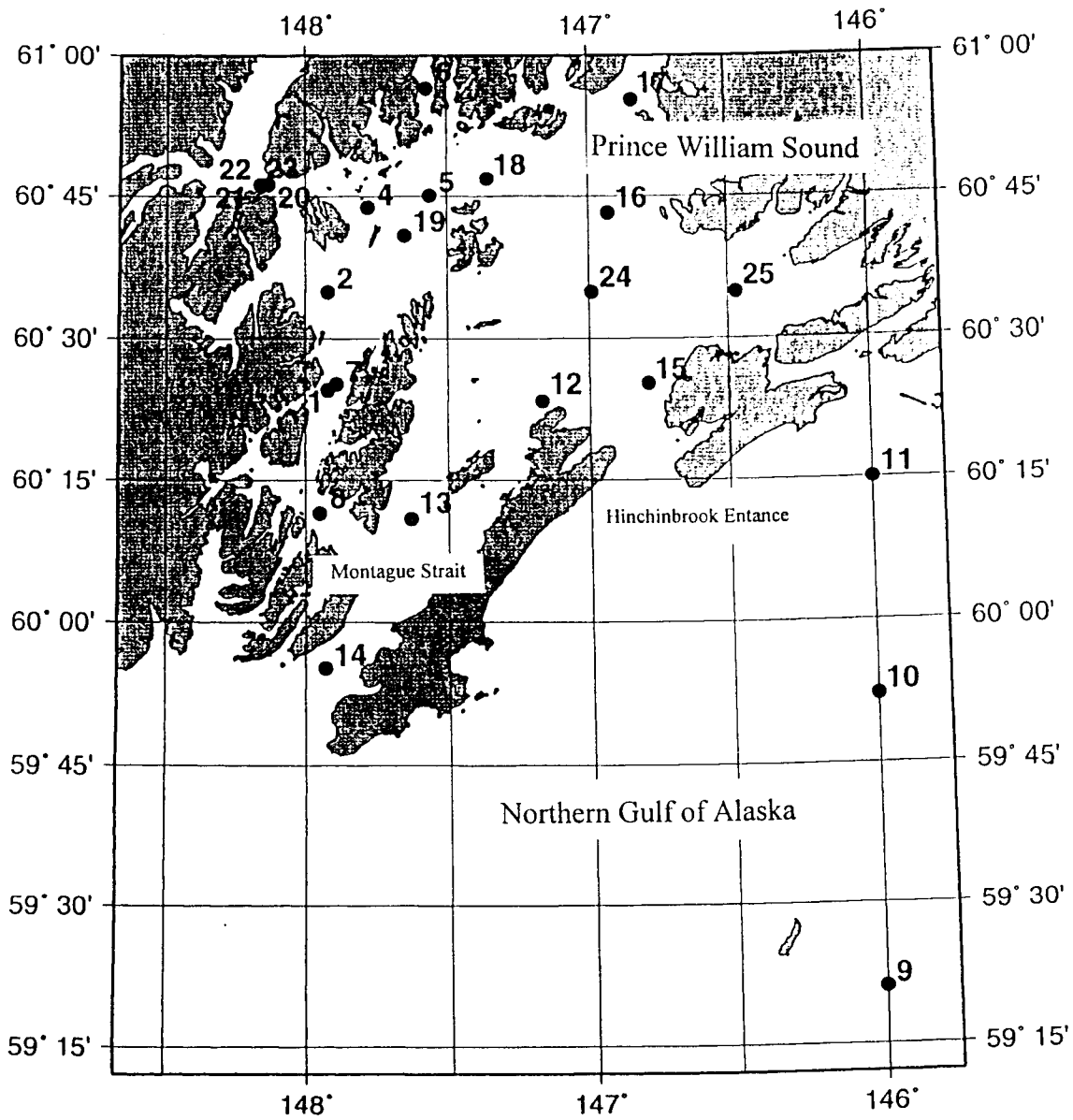
Figure 1. Prince William Sound, Alaska depicting geographic features and the location of MOCNESS stations occupied in May, 1996.

Clustering on Abundance
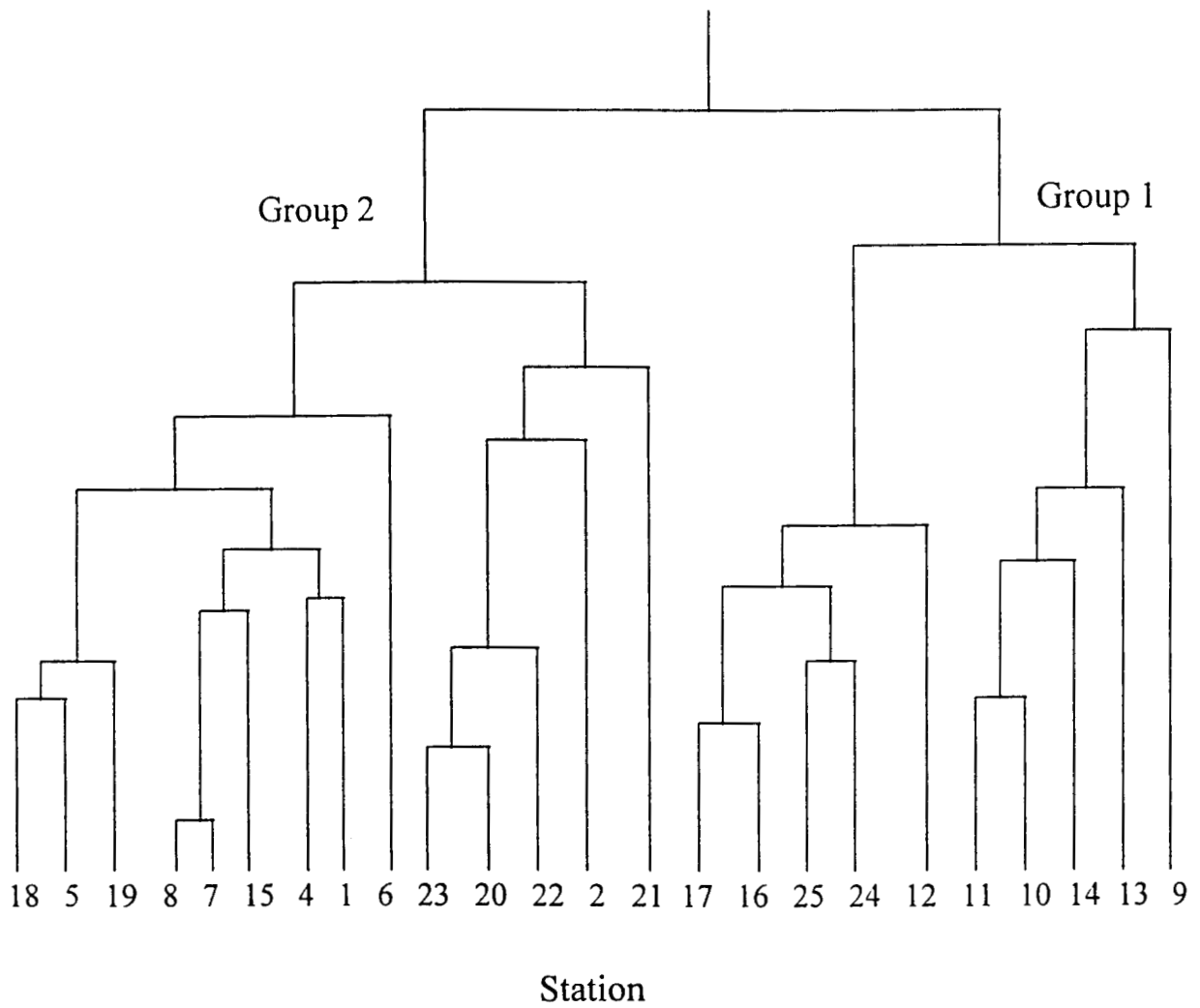
Figure 2. Results of clustering station locations by zooplankton abundance for samples collected in May, 1996
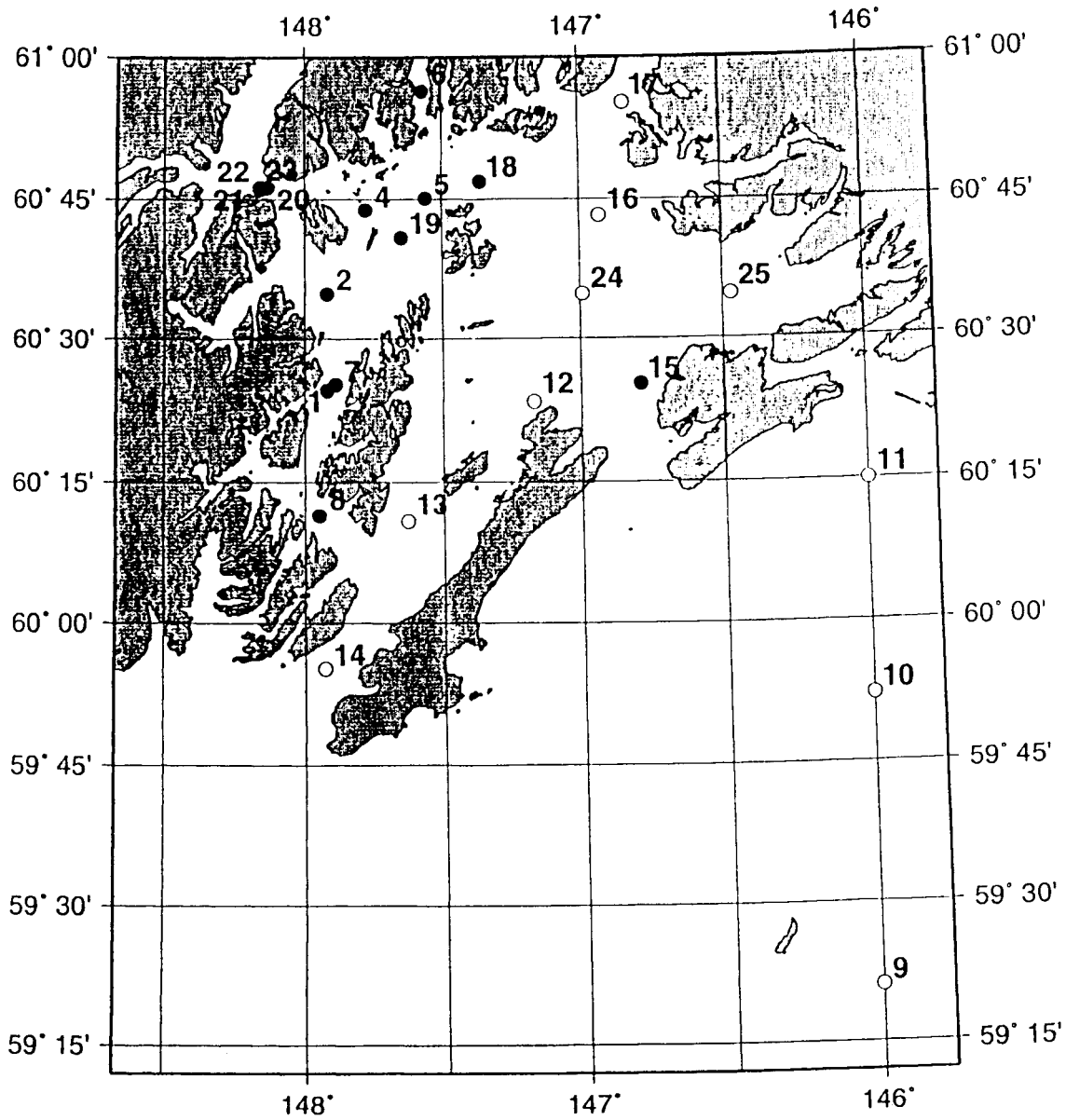
Figure 3. The locations of stations clustering by abundance in Group 1 (open circles) and Group 2 (closed circles).
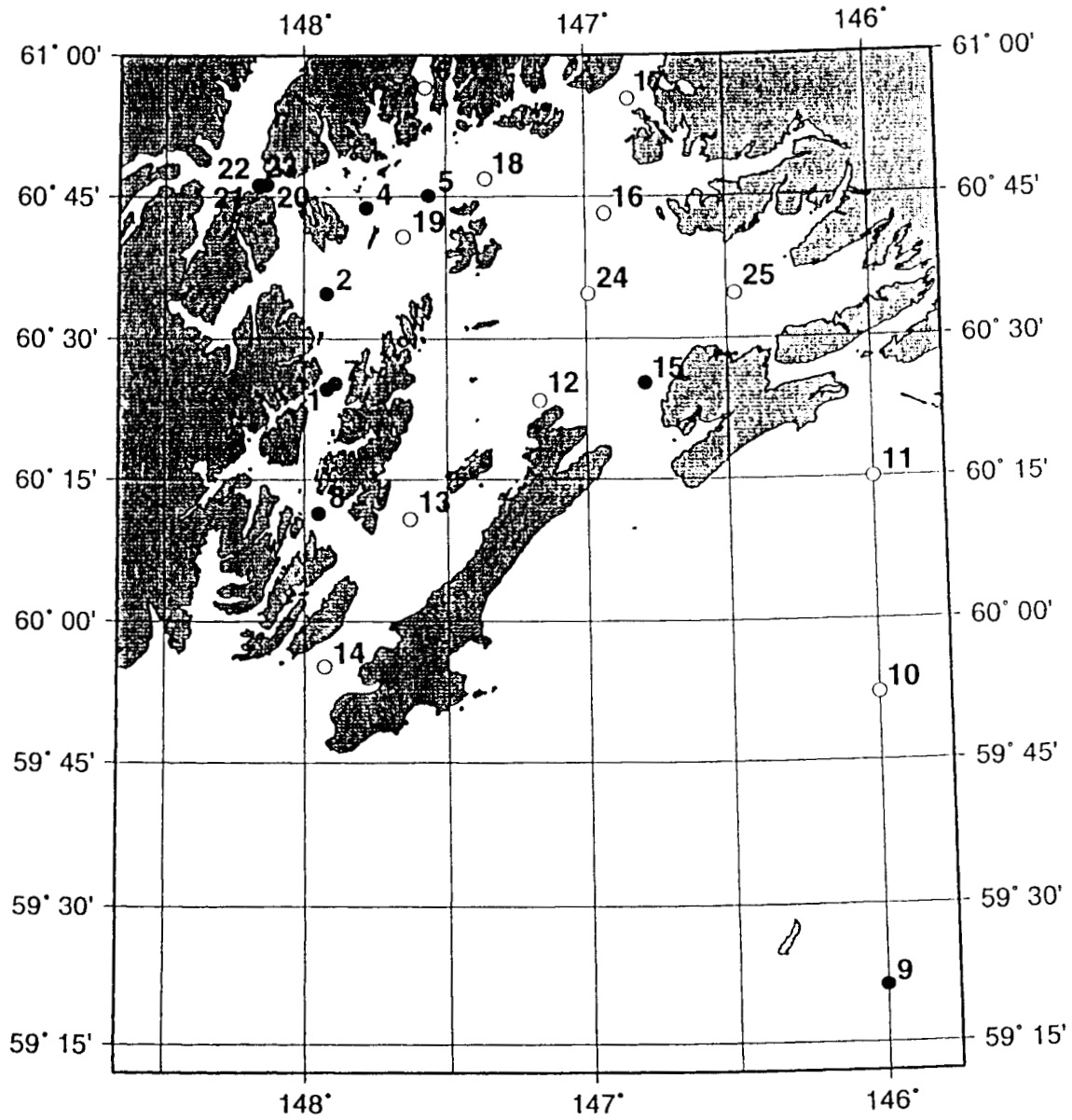
Figure 4. The location of stations clustering by biomass in Group 1 (open circles) and Group 2 (closed circles).
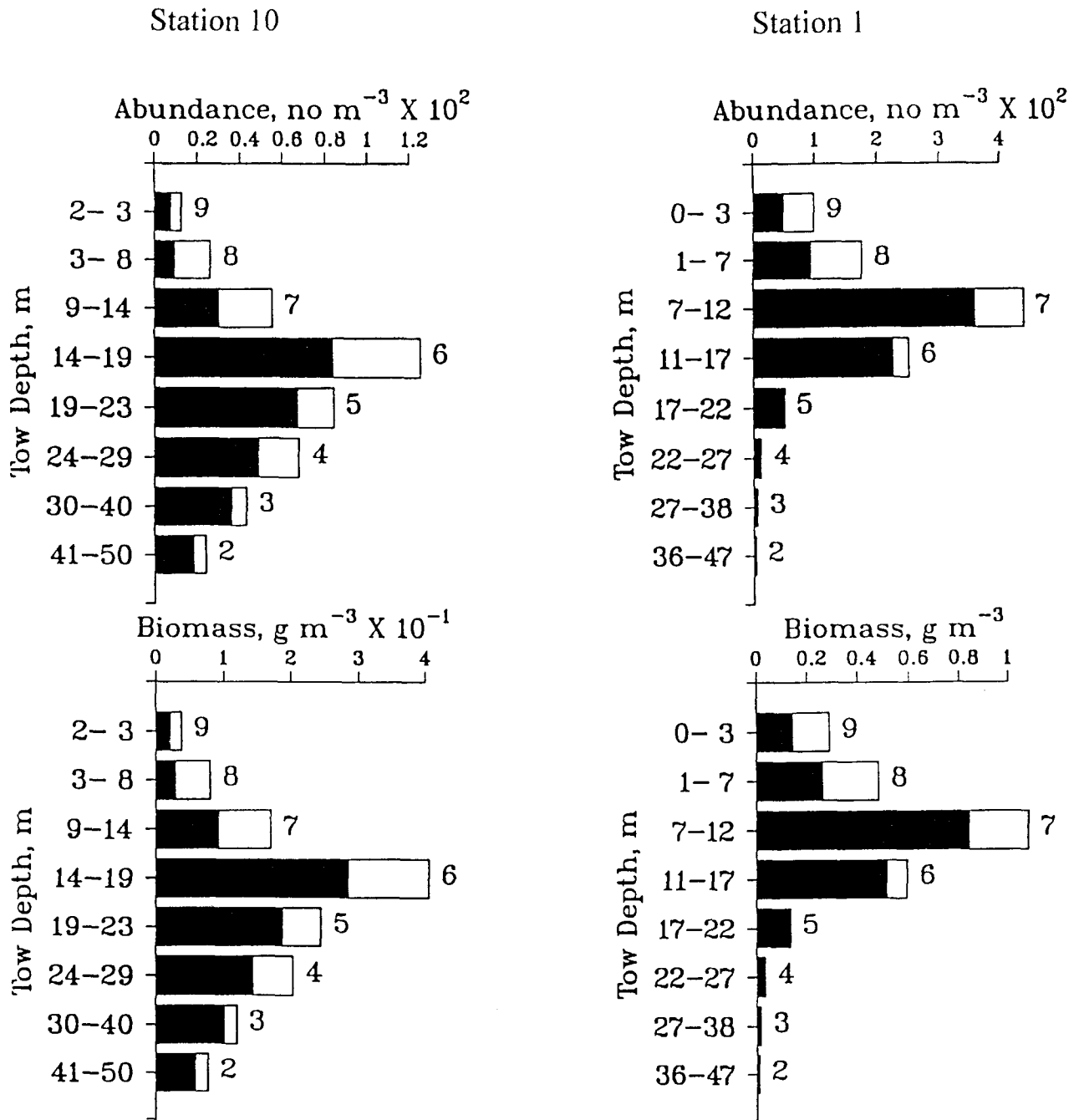
Figure 5. Co-occurrence of *Neocalanus flemingeri* and *N. plumchrus* stage V at Station 10 (Group 1) and Station 1 (Group 2). Open bars are *N. plumchrus*.
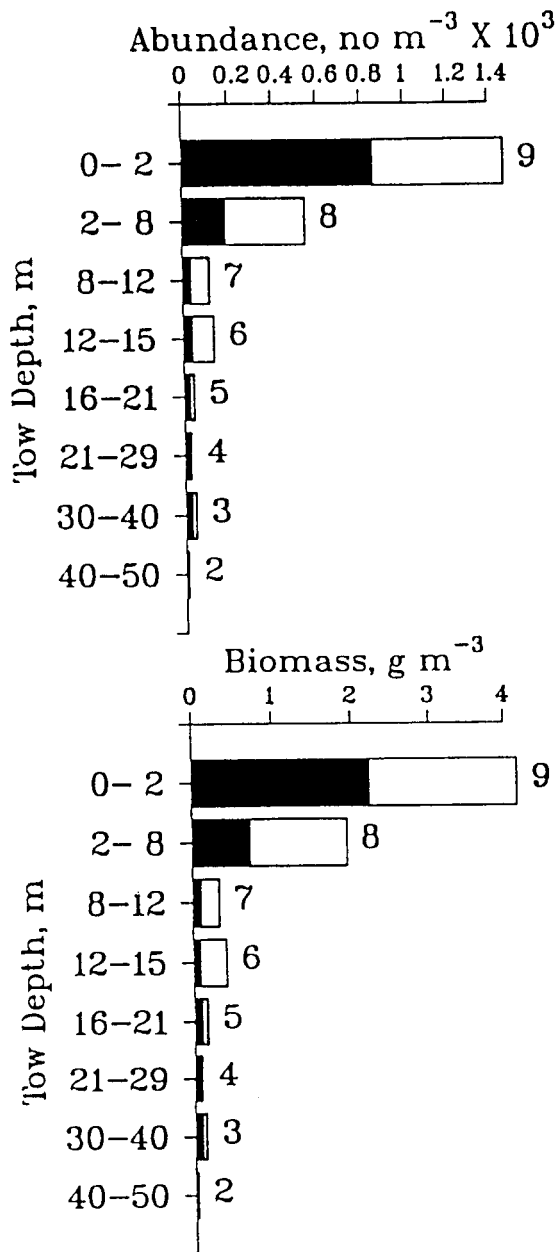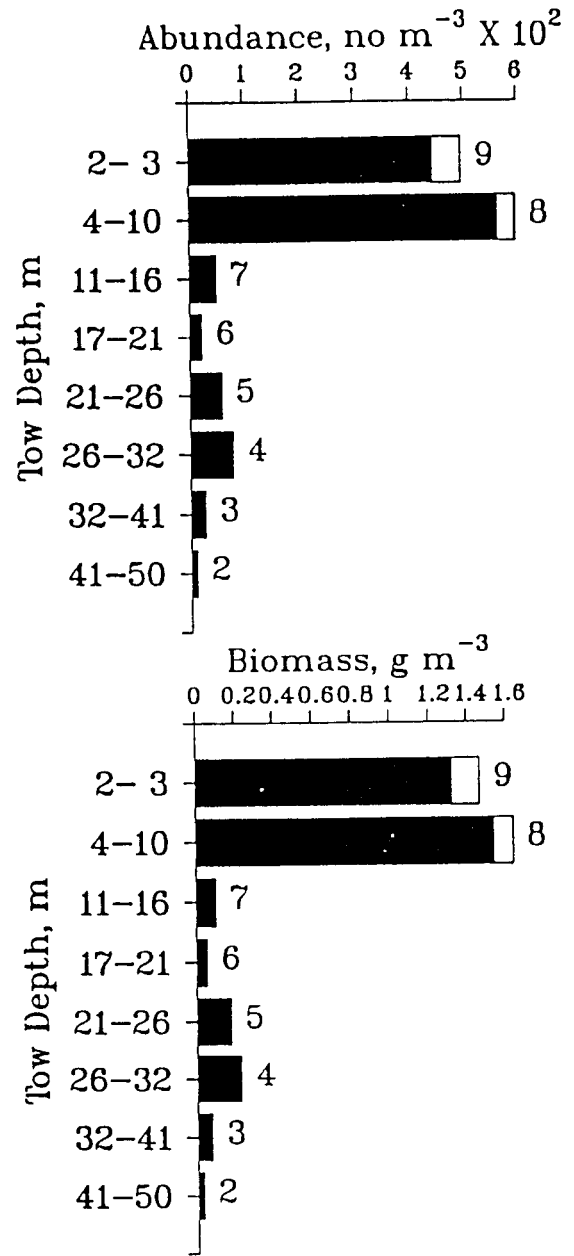
Figure 6. Examples of *Neocalanus flemingeri* and *N. plumchrus* stage V layering in Group 1 (Station 9) and Group 2 (Station 8).
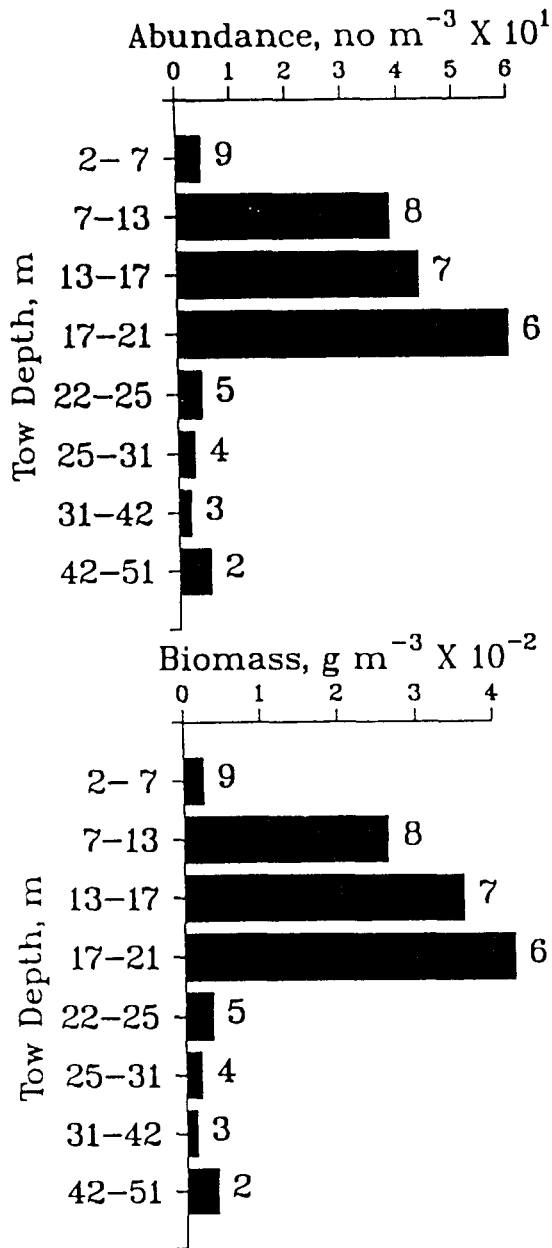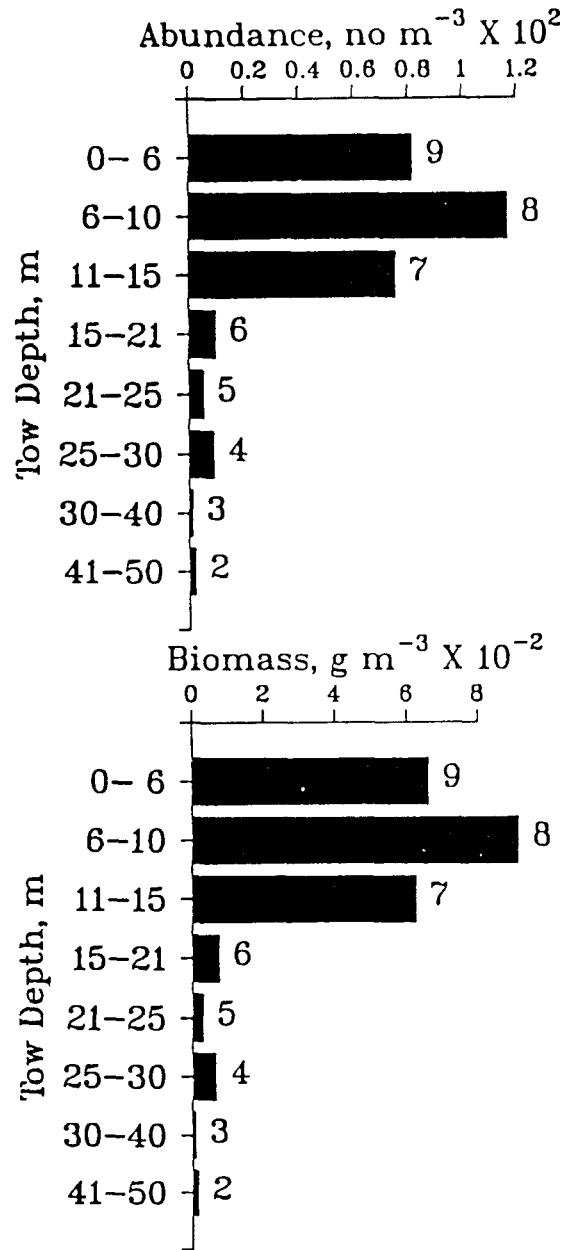
Figure 7. Examples of *Neocalanus* spp. stages III-IV layering in Group 1 (Station 16) and Group 2 (Station 18).
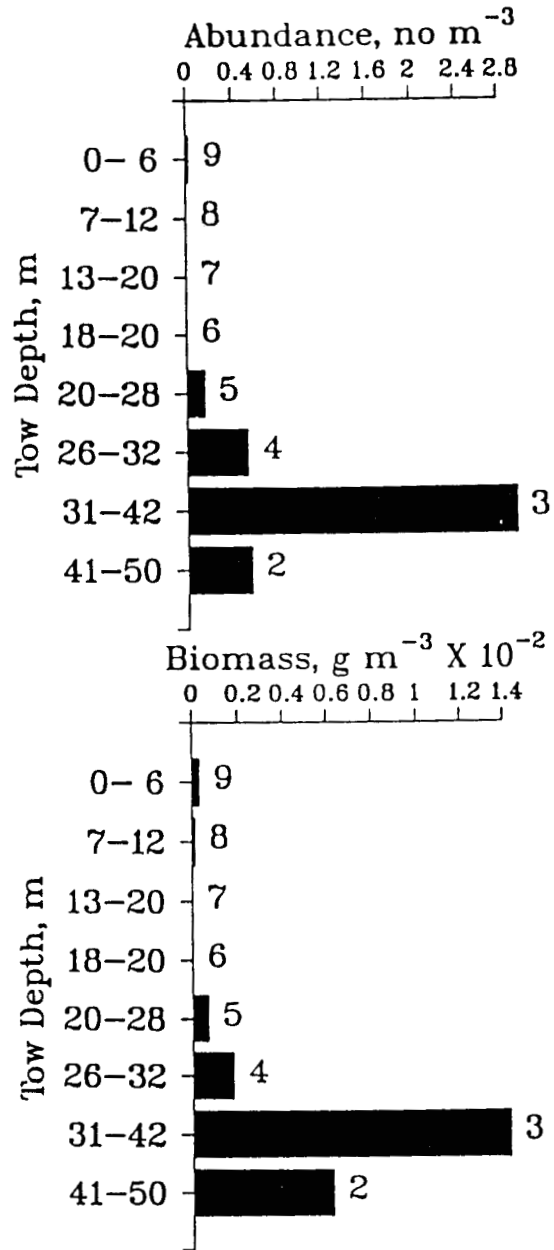
Station 24

Abundance, no m^{-3}

0   0.2 0.4 0.6 0.8 1   1.2 1.4 1.6

Tow Depth, m	
1– 6	9
6–11	8
11–15	7
16–21	6
21–25	5
25–30	4
31–41	3
41–50	2

Biomass, g m^{-3} X 10^{-3}

0   1   2   3   4

Tow Depth, m	
1– 6	9
6–11	8
11–15	7
16–21	6
21–25	5
25–30	4
31–41	3
41–50	2

Station 4

Abundance, no m^{-3}

0   0.4 0.8 1.2 1.6 2   2.4 2.8

Tow Depth, m	
0– 6	9
7–12	8
13–20	7
18–20	6
20–28	5
26–32	4
31–42	3
41–50	2

Biomass, g m^{-3} X 10^{-2}

0   0.2 0.4 0.6 0.8 1   1.2 1.4

Tow Depth, m	
0– 6	9
7–12	8
13–20	7
18–20	6
20–28	5
26–32	4
31–42	3
41–50	2
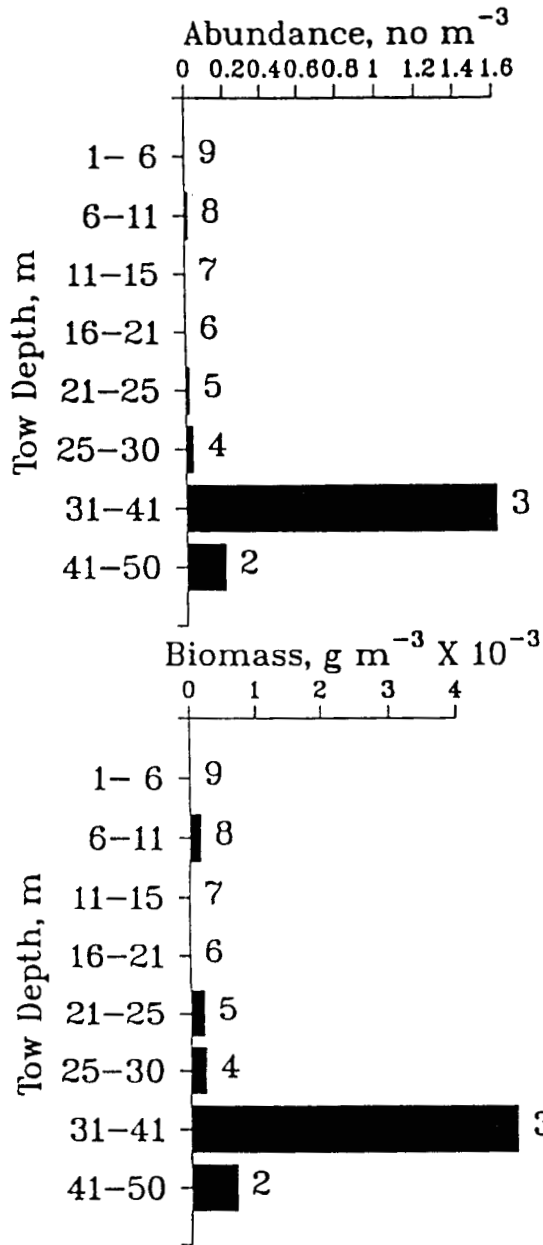
Figure 8. Examples of *Neocalanus cristatus* stages III-V layering in Group 1 (Station 24) and Group 1 (Station 4).

Station 4
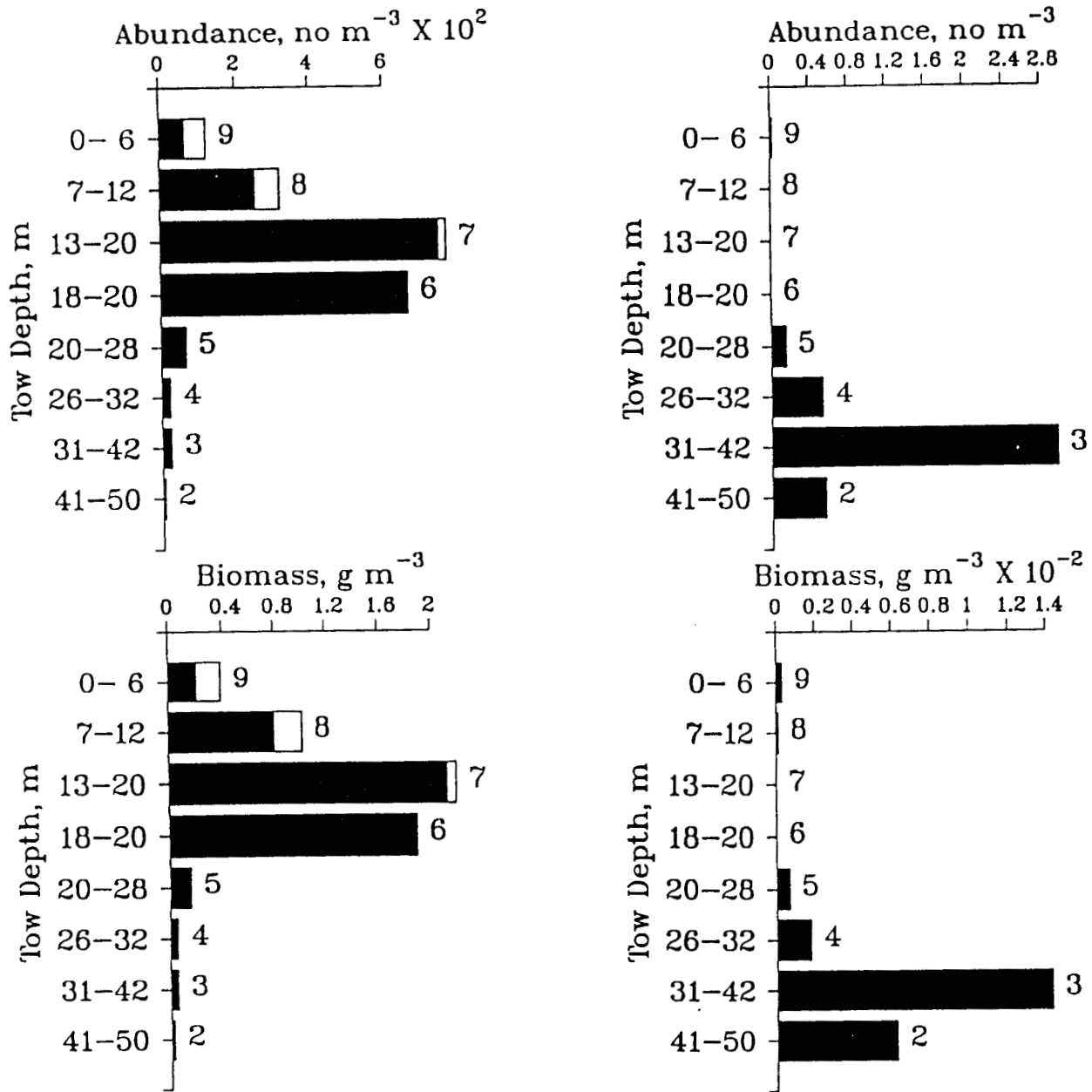
Figure 9. Comparing the vertical distributions of *Neocalanus flemingeri* and *N. plumchrus* stage V with *N. cristatus* stages III-V at Station 4.
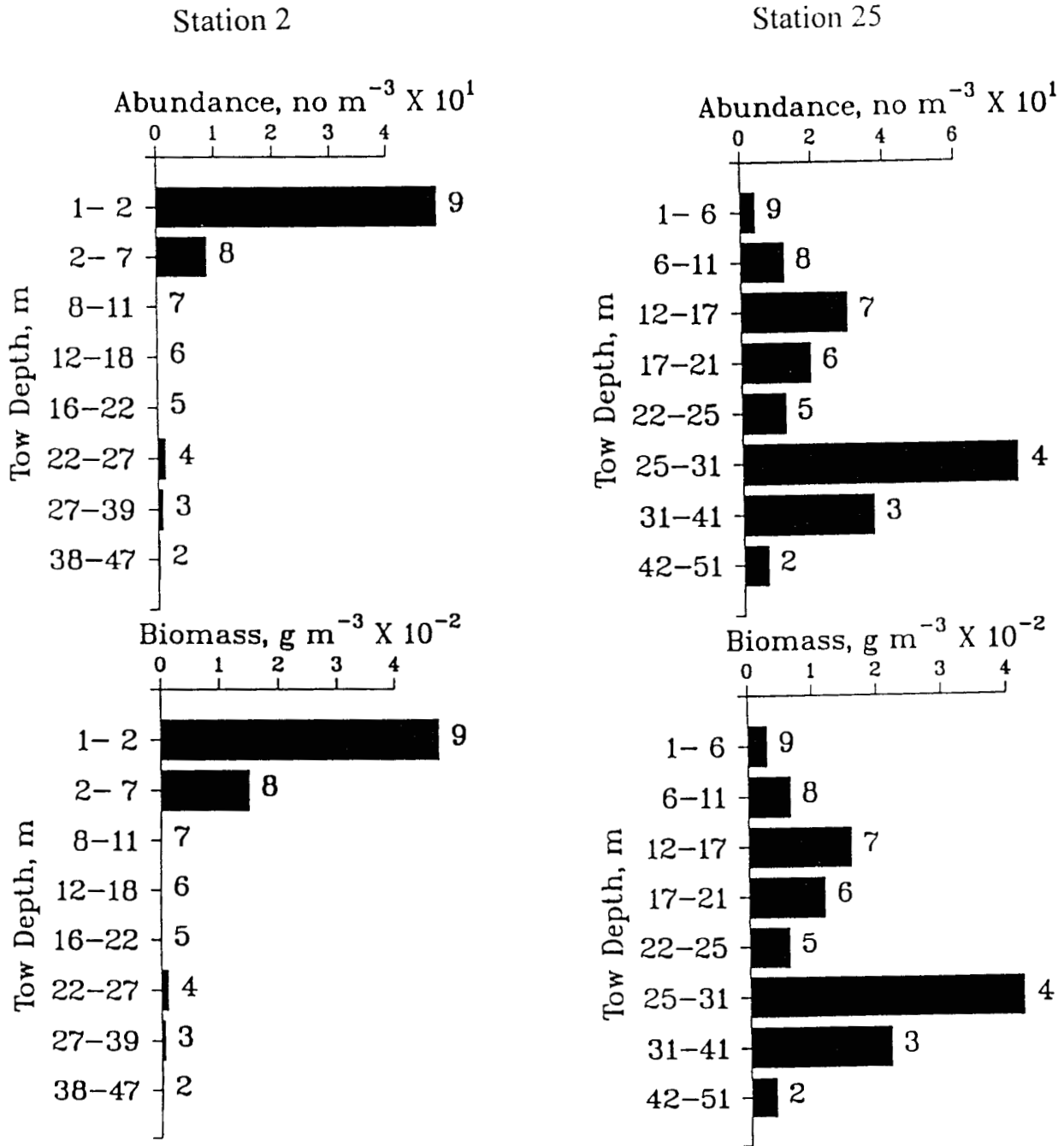
Station 2

Station 25

Abundance, no m^{-3} X 10^{1}

Abundance, no m^{-3} X 10^{1}

Biomass, g m^{-3} X 10^{-2}

Biomass, g m^{-3} X 10^{-2}

Figure 10. Comparing the depth of layering for *Calanus marshallae* stages IV-Adult at Stations 2 and 25.
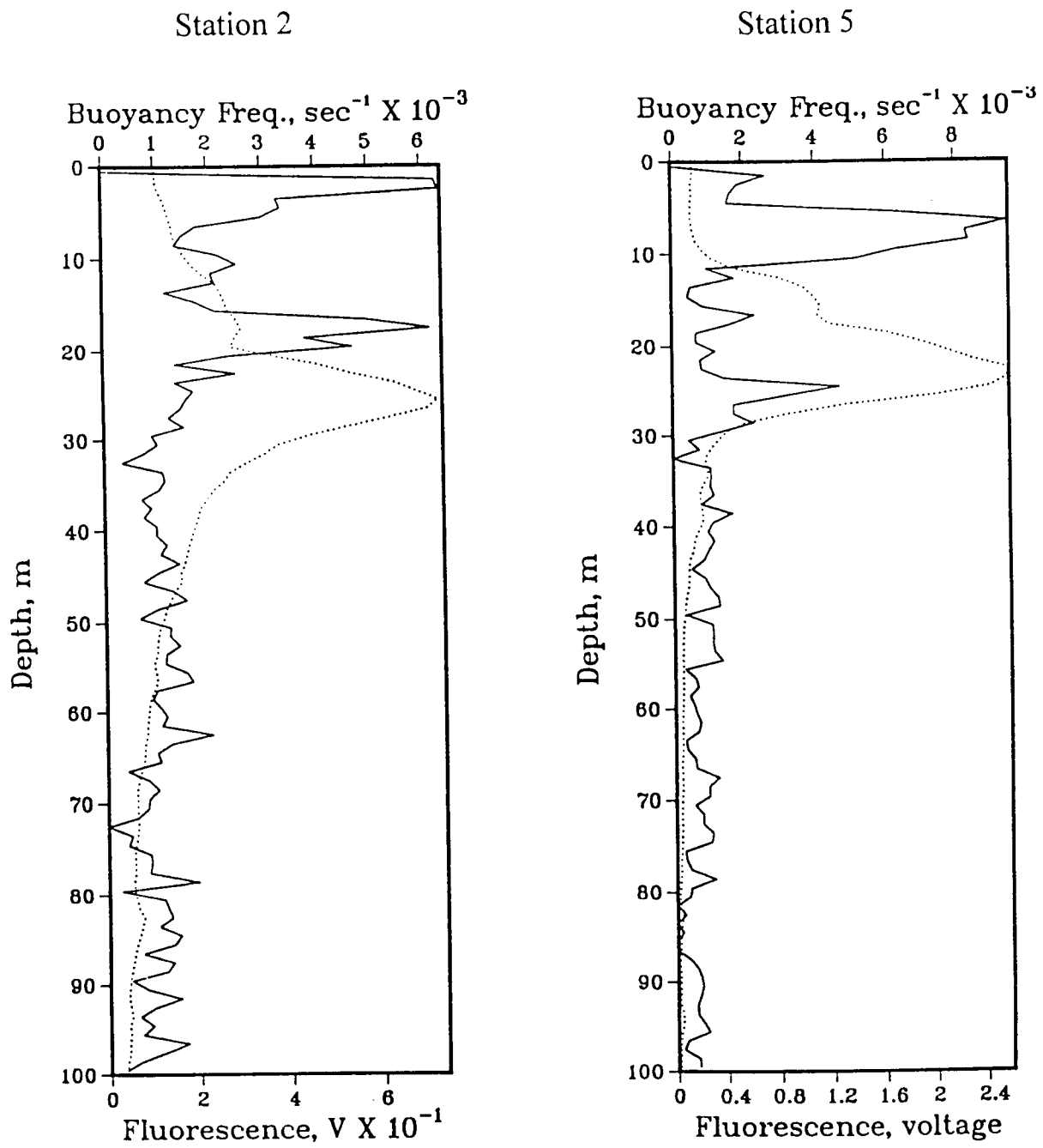
Station 2   Station 5

Figure 11. Examples of subsurface fluorescence maxima (dotted line) at Stations 2 and 5.
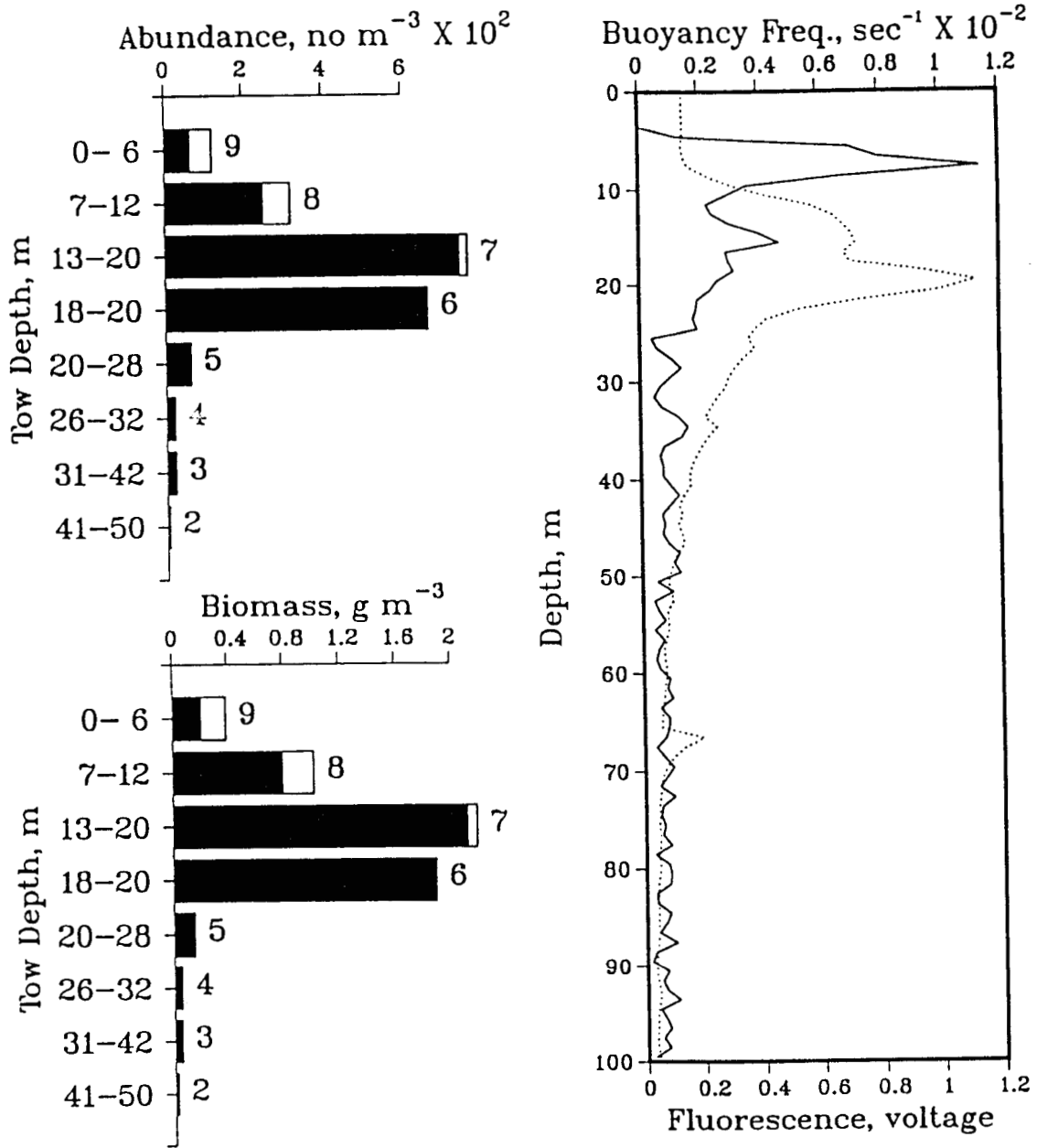
Figure 12. Example of a location where *Neocalanus flemingeri* and *N. plumchrus* stage V co-occurred with a fluorescence maximum (Stations 4).
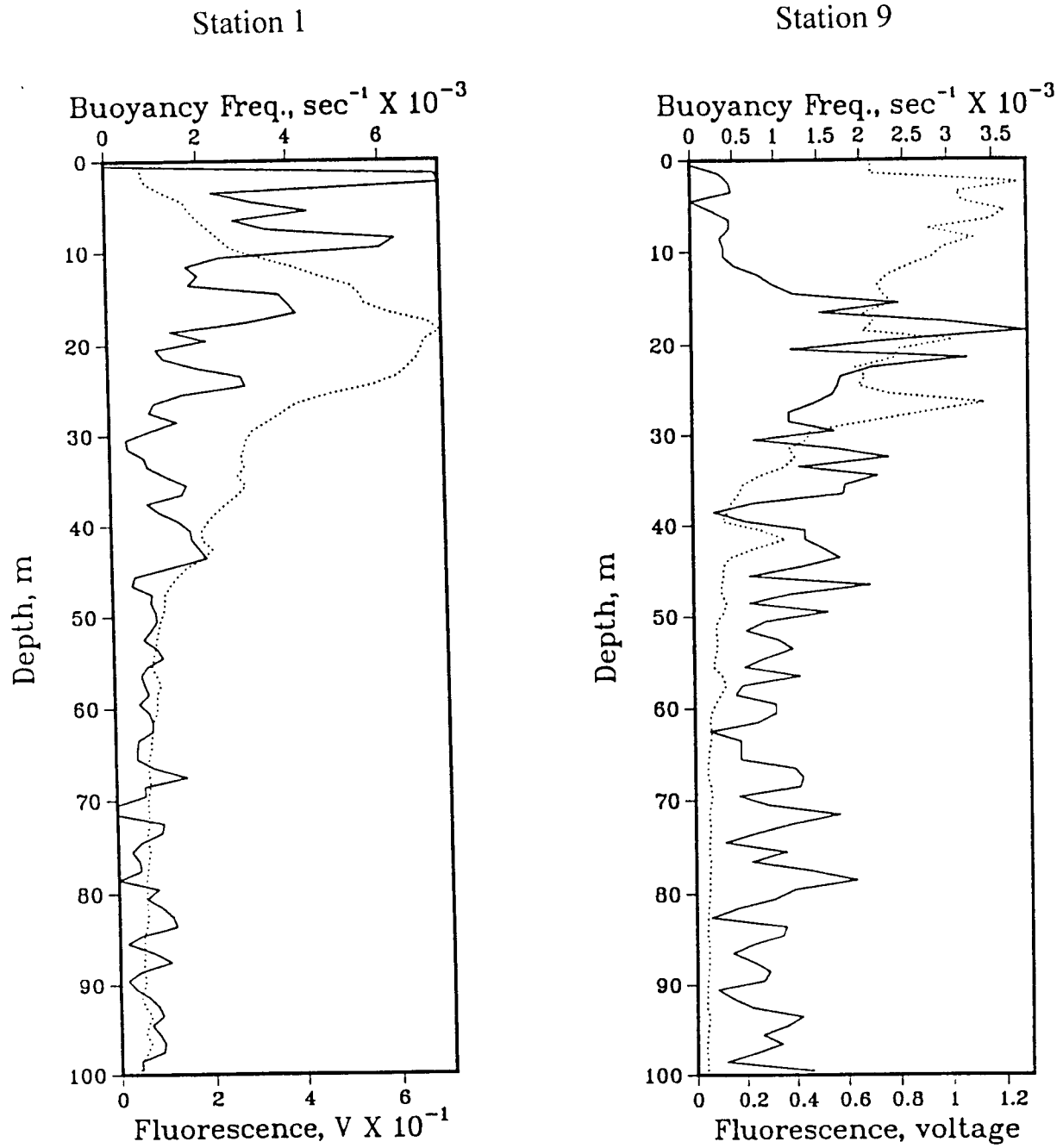
Figure 13. Examples of buoyancy frequency distributions (solid line) with depth illustrating maxima near the surface (Station 1) and below the surface (Station 9).
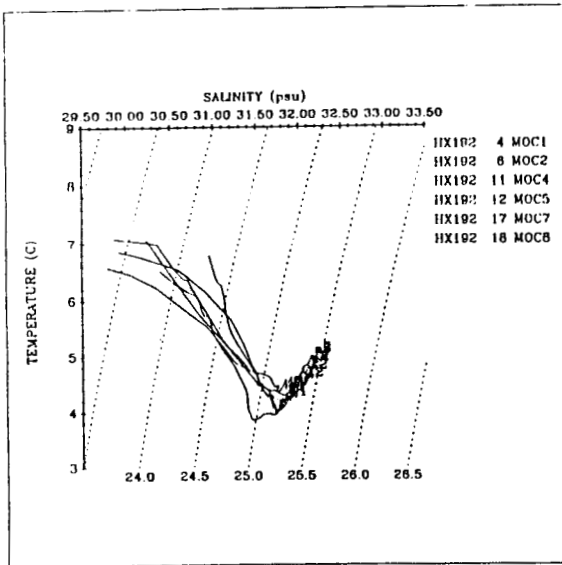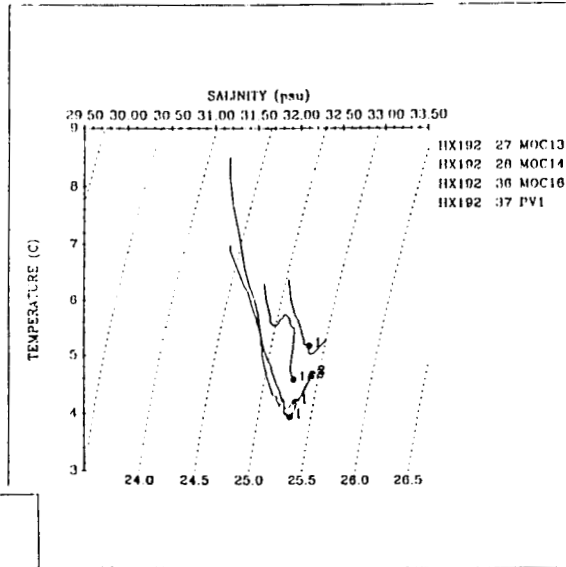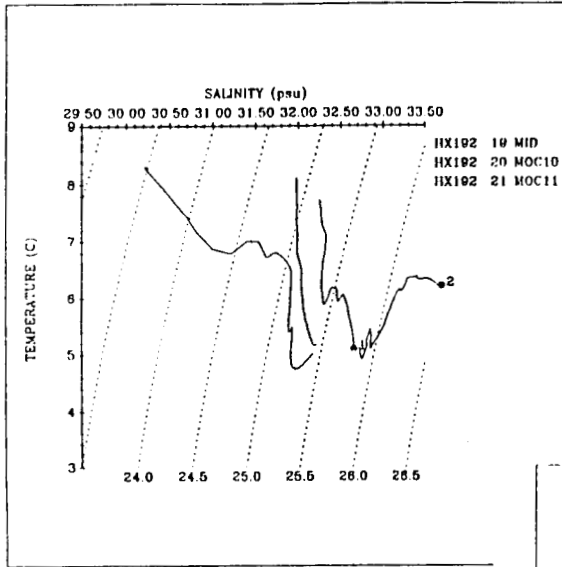
Figure 14. Temperature and salinity plots for locations in Group 1 outside the Sound (top panel), for Group 1 inside the Sound (middle panel) and Group 2 (lower panel).