Chapter 4

The Role of Zooplankton

Exxon Valdez Oil Spill
Restoration Project Annual Report

Sound Ecosystem Assessment (SEA): The Role of Zooplankton
Restoration Project 97320-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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Study History: Project 320-H was established in FY 94 as a core study in the Sound Ecosystem Assessment (SEA) program. The intent of the work has been to demonstrate the role of macrozooplankton in processes supporting the production of pink salmon and herring in Prince William Sound. Zooplankton serves as food for many fish, bird and marine mammal stocks. SEA is investigating it's importance as forage for juvenile pink salmon and herring, and as alternative prey for consumers that also prey on juvenile pink salmon and herring in seasonally-varying complex food-webs. Previous annual reports of project 320-H appear in the SEA annual report series for 1994, 95, and 96. The project will complete a Final Report of all findings in FY 99. That report will include work completed in FY 98.

Abstract: Support for studies of the role of zooplankton in FY 97 emphasized the analysis of data collected in previous years, while diminishing the field activities. Zooplankton samples were only collected during a May oceanographic cruise, and from the AFK hatchery located on Evans Island. These activities reflect the shift in SEA tasks from field investigations to data analysis in the last two fully funded years. Observations from all locations and years were pooled by month to describe changing patterns in community composition and standing stock information needed to assess important linkages between forage supplies and growth and survival of juvenile pink salmon and herring. A manuscript describing patchiness in upper-layer calanoid populations was prepared and is now in review. This work addresses additional questions about patch-dependent feeding as input to models describing juvenile pink salmon survival as a function of predator prey switching. As part of a cooperative investigation of the target strengths of dominant macrozooplankters, project H is supplying information on the sizes of copepodite stages 4 and 5 *Neocalanus plumchrus* and *N. flemingeri*, juvenile euphausiids and pteropods to Dr. Kirsch (project N). Finally, the relationship between upwelling and south-Sound zooplankton stocks in April and May was updated. The regression has explained less variability over the SEA years than previously. The reasons for this change are being investigated.

Key Words: Zooplankton, macrozooplankton, SEA, *Neocalanus*, modeling

Project Data: Project H data resides in the SEA data base, and also in the Institute of Marine Science, University of Alaska Fairbanks, data base. All samples collected by the project have been processed in the laboratory and placed in these electronic archives.

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Executive Summary

Work in 1997 focused on four areas: 1) further descriptions of the layering and swarming behavior of large calanoids developing in the upper 50 m of Prince William Sound an in the adjacent coastal waters; 2) describing seasonal changes (numbers and biomass) in upper-layer zooplankton communities; 3) examining the degree of overlap between zooplankton communities sampled in embayments and from the open Sound; and 4) updating the Lake/River statistical relationship. The results of these investigations are reported here.

Objectives

The following general objectives were approved in the FY 97 DPD:

1. Provide information on the vertical and horizontal distributions of selected zooplankters, their sizes, and descriptions of seasonal changes in the composition of macrozooplankton in the upper 50 m of Prince William Sound.

2. Work collaboratively with SEA modeling projects to provide data on the seasonal, horizontal, and vertical compression of biomass serving as patch-dependent forage opportunities for juvenile pink salmon, herring and other planktivores in Prince William Sound.

3. Assist other projects determine the degree to which the open-Sound zooplankton community influences the growth and survival of juvenile herring rearing in edge-zone nursery areas.

Methods

Field collections of zooplankton follow procedures established in 1995 for the conduct of oceanographic cruises operating under SEA funding. A *Bering Explorer* cruise in May, and a collection from the AFK hatchery on Evan's Island provided the only samples taken in FY 97. Samples were processed in the UAF plankton laboratory and the results posted in IMS and SEA data bases.

Results

Vertical Patchiness. Collections obtained using a MOCNESS sampler in May, 1996 were analyzed to further evaluate the degree to which late stage *Neocalanus*, *Calanus* and *Eucalanus* exhibit tendencies to form distinct layers in Prince William Sound and over the adjacent shelf (Appendix I). There was considerable variability over the region, but the vertical patterns previously reported (SEA96) were reaffirmed. Locations sampled in Knight Island Passage and in the northwestern portion of the Sound consistently exhibited high average layer values of abundance and biomass for a composite of a mixture of stage V *Neocalanus flemingeri* and *N. plumchrus*; 568 individuals m^{-3}, and 1.63 g m^{-3}. The highest value for this composite occurred in

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the surface waters at the edge of the continental shelf near Middleton Island (1286 individuals m^{-3}; 3.64 g m^{-3}), while the lowest densities were encountered in southwestern Montague Strait and in Unakwik Inlet (< 25 individual m^{-3}, and < 0.05 g m^{-3}). Stations in the central and eastern portions of Prince William Sound exhibited numbers and biomasses ranging between these highs and lows.

Seasonal Succession. Seasonal changes in the numbers and biomass of the dominant contributors to macrozooplankton populations in Prince William Sound were determined by averaging all shipboard and hatchery collections across the years 1994, 95, 96 and 97 by month. The top 15 taxanomic categories (number and biomass) were then examined for seasonal changes. There were no samples available for the months of January, August and November.

Numbers and biomass were very low in the cold, well-mixed upper 50 m in February (Table 1). Gastropod larvae (undetermined species) and stage 1 copepodites of the Calanidae (probably *Neocalanus*) were the most numerous taxa at about 10 m^{-3}. Because of their size and number, gastropod larvae and adult female *Metridia pacifica* (copepoda) dominated the biomass. The remainder of top 15 taxa were comprised of species and groups common to other seasons, but occurring in very dilute quantities in winter.

By March, Calanidae stages 1 and 2 were obvious (ranked 1 and 4 by abundance respectively) signaling the beginning of the production cycle for *Neocalanus* in the surface waters (Table 2). The biomass was dominated by the large calanoid *Metridia okhotensis* (adult females) and barnacle nauplii, the latter a member of the meroplankton and a somewhat surprising member of the open water community. *Pseudocalanus* spp. (copepoda) was present in the upper 15 ranked taxa by biomass and abundance. This small copepod will dominate the plankton numerically in the months that follow.

By April, high numbers of euphausiid eggs signal reproduction for several species (genus *Thysanoessa* and *Euphausia*) in Prince William Sound (Table 3). *Pseudocalanus* spp. and bryozoan larvae exhibited numbers in excess of 100 individuals m^{-3}. The biomass in April was dominated by the maturing copepodite stages of *Neocalanus plumchrus* and *N. flemingeri* (4 and 5) as these populations build toward seasonally high biomass in May. *Calanus marshallae* was also contributing to the biomass at this time.

In May, abundance values for some species and composites have exceeded 500 m^{-3} (Table 4). Numbers in the upper 50 m are dominated by *Pseudocalanus* spp. (several late stages), while stage 5 *Neocalanus plumchrus* and *N. flemingeri* dominate the biomass; > 100 mg m^{-3}. Some neritic copepods like *Acartia* spp., are beginning to appear in appreciable numbers as the upper layers freshen and warm.

The community composition has shifted to more neritic species by June (Table 5). *Pseudocalanus* spp. claims seasonal highs, but *Evadne* (Cladocera), *Acartia* spp. and *Oikopleura* (Larvacea) are also ranked in the upper 50 by abundance. Because of its high numbers,

Pseudocalanus also dominates the biomass in June, but the pteropod, *Limicina helicina* is a close second. *Neocalanus* falls precipitously in the rankings, as stage 5 copepodites leave the upper layers for overwintering depths. July is similar to June in the composition of the zooplankton community in the upper 50 m (Table 6). However, seasonally high numbers and biomass are beginning to decline.

In September (August missing) *Pseudocalanus* spp. and *Acartia* spp. continue to be the most abundant zooplankters, but most numbers have fallen below 100 individuals m^{-3} (Table 7). Biomass is led by *Pseudocalanus*, but different taxa like ctenophores and *Sagitta elegans* are prominent contributors. Later in October, *Pseudocalanus* spp. and *Metridia pacifica* rank high in numerical abundance and biomass (Table 8).

December completes the year (November missing) with *Pseudocalanus* again dominating the now greatly diminished numbers; < 25 individuals m^{-3}. The medium-sized subtropical copepod *Mesocalanus tenuicornis*, and *Euphausia pacific* and *Metridia* spp. stage V lead the biomass rankings (Table 9). The late fall and early winter community contains more jelly plankton, euphausiids and amphipods than were found in other seasons. Presumably, some of these contributors appear when more of the sampling is conducted after dark (short day-length in December).

Nearshore/Offshore Comparisons. Work conducted by the SEA Herring sub-group (see project T) reports that juveniles rearing in embayments derive a large percentage of their energy from plankters that seem to prefer a shallow, edge-zone habitat. When rankings by biomass are compared between the open water zooplankton community (upper 50 m) with that sampled at the herring study sites (upper 30 m), it is evident that the overlap in highly ranked species is generally less than 50% by site, location in the bay (inner, middle and outer) and season (Table 10). There appears to be no seasonal or within-bay patterns that emerge from this comparison. Overall, Whale Bay exhibited the highest overlap (49 % common species), while Simpson Bay showed the least (37%). A more comprehensive analysis will be needed to explain these differences.

The Lake/River Problem. One of the most puzzling problems that project H has been investigating is the process that manifests as the Lake/River phenomenon. In 1993 when the SEA program was developed, a strong statistical correlation was observed between spring-time zooplankton stocks measured at the AFK hatchery and the April/May upwelling index computed for a location on the shelf just east of Prince William Sound. Spring-time settled volumes tended to be much higher at AFK during years when the upwelling index was most positive, and lower when the index was negative. SEA interpreted this relationship to capture relative rates at with locally reproducing zooplankton stocks were flushed from the region each year by the wind-forced coastal flow . When the onwelling was strongest (most negative upwelling indices), more of the Sound would become involved by the intruding coastal flow (river-like) presumably removing larger amounts of upper layer plankton than when the flushing rates were low (more positive upwelling indices). Under less intense flushing (lake-like) stocks were consistently

higher at the south Sound index station.

Since April, 1994, the r^2 value for the Lake/River relationship has fallen from approximately 0.80 to less than 0.60 (Figure 1). Apparently, the relationship has been compromised by data acquired during the SEA sampling period, 1994-97. While it is not clear what has happened, the regression predicted that 1997 would be a very high (lake-like) zooplankton year. Those numbers failed to materialize. In fact, 1989 was the last time that zooplankton populations were extraordinarily high in the Sound. The lack of a strong zooplankton year has precluded directly evaluating the conditions that cause this to happen. Our synthesis work will involve experimental studies with the SEA biophysical model and I have hopes that we may be able to explain, or partially explain the Lake/River phenomenon using this approach.

Discussion

The subarctic pelagic ecosystem is characterized by intense seasonality and the compression of plankton biomass into short busts of production and accumulation near the ocean surface. A continuing study of patch-dependent foraging opportunities arising from predictable zooplankton patchiness focuses much of the sea modeling efforts. We are now aware that discrete layers of large calanoids (*Neocalanus, Calanus* and *Eucalanus* spp.) develop in the upper 50 m of Prince William Sound each spring as part of the one-year life cycles of these animals. These layers are visited by adult pollock recharging their post-spawning energy reserves, and probably by other consumers in the system as well. Our sampling, and observations by the PWSAC hatchery plankton watch program consistently demonstrate high stocks of *Neocalanus* spp. in the northwestern corner of the Sound. It now seems likely that a large percentage of these stocks arise from local deepwater reproduction beginning in February. The predictability of this forage resource is probably responsible for attracting adult pollock into the northern reaches of Knight Island Passage, and around the Perry Island, Lone Island and Port Wells areas during the spring.

A general seasonal picture of upper-layer zooplankton stocks is emerging as the result of SEA collections. February and March represent times of minimal numbers and biomass. However, even at this time, the "seeds" of the coming zooplankton production cycle are in place. April is a time of euphausiid spawning, with huge numbers of eggs occurring in the upper 50 m. April also sees the beginning of *Pseudocalanus* production, and seasonal highs in the numbers of *Neocalanus*. April is also the time of the phytoplankton bloom (see project G report) marking the end of the overwintering period for juvenile herring. Finally, the wild salmon out-migration from natal stream begins in April, with juveniles schooling in nearshore nursery areas. By May, *Neocalanus* has progressed to stage V and dominates the upper-layer animal plankton biomass. Pteropods and larvaceans appear in May, and *Pseudocalanus* populations expand. By June and July, most of the larger calanoids have left the upper water column for overwintering depths and are replaced by pteropods, larvaceans, cladocerns, and seasonal highs in *Pseudocalanus* and *Acartia*. This is the time that surface waters reach seasonal thermal highs and contintue to become diluted by runoff. By September and October, the water column is about as fresh as it will become. Plankton stocks are falling rapidly, but are still dominated numerically by

Pseudocalanus, although a variety of other taxa now contribute. A fall phytoplankton bloom with implications for fall feeding juvenile herring may occur from September - November (see report of project G, T). By December, upper-layer stocks of zooplankton have declined to near-seasonal lows. *Pseudocalanus* and *Mesocalanus* dominate, but abundance falls below 25 individuals m^{-3} and a few mg m^{-3}. The winter hiatus has returned. This is the time that juvenile herring are presumably fasting in their nearshore refuges.

Comparisons between the community composition described by rankings of biomass in inshore and offshore zooplankton stocks indicate the nearshore regions are dominated by different species at all locations and seasons. An overlap in the rankings of less than 50% may be partially accounted for by the presence of the planktonic stages of intertidal and shallow sub-tidal invertebrates in the shallow environments. This possibility is being studied (see project T).

The Lake/River relationship continues unresolved. Since the beginning of SEA the statistical correlation between the strength of the upwelling index computed from observed sea-surface pressure and spring-time stocks of zooplankton at AFK has been going down. The implications of this change remain obscure. However, a recent publication by Hayward (1997) discusses regime shifts in the Pacific ocean and may prove useful in determining whether major changes have occurred in the subarctic environment since the oil spill in 1989. Also, an interesting mechanism explaining differences in salmon production between Alaska and Washington waters has been articulated by Gargett (1997). The mechanism involves different and opposite responses to atmospheric forcing and the deepening of the nutricline in these two regions. Her analysis indicates that when production is stimulated in a region by increased nutrient input (bottom-up forcing), the overall production cycle is favored and salmon production increases. SEA has investigated the latter phenomenon (increased consumer production) and has documented why the survivals of salmon should increase under these conditions.

Conclusions

Project H continues to make progress toward understanding and describing the upper-layer net zooplankton community and its role in Prince William Sound. Work completed in 1997 included a detailed description of season changes and layering phenomena by many of the larger calanoid species and consideration of onshore/offshore distributions. These results provide information about seasonally varying forage resources that many of the other consumers in the system track and utilize. The information is being shared with other components of SEA, particularly the juvenile salmon work (project E) and the numerical modeling (projects R, J and T).

Acknowledgments

References

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Table 1.

ZOOPLANKTON SPECIES COMPOSITION OPEN SOUND STATIONS -February			
ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Gastropod larvae	12.6	Gastropod larvae	0.0022
Calanidae I	9.4	*Metridia pacifica* AF	0.0014
Pseudocalanus spp. AF	8.3	*Pseudocalanus* spp. AF	0.0009
Oithona spp. copepodites	4.8	*Thysanoessa longipes*	0.0005
Pseudocalanus spp. V	4.4	*Pseudocalanus* spp. V	0.0004
Bivalve larvae	3.6	*Calanus marshallae* V	0.0003
Oithona similis AF	2.7	Calanidae I	0.0003
Acartia longiremis AF	2.0	*Metridia okhotensis* AF	0.0003
Metridia pacifica AF	1.7	*Metridia* spp. V	0.0002
Bryozoan larvae	1.5	Hydromedusae	0.0002
Microcalanus sp.	1.4	*Acartia longiremis* AF	0.0001
Pseudocalanus spp. IV	1.4	*Limacina helicina* juv	0.0001
Podon sp.	1.3	Barnacle nauplii	0.0001
Pseudocalanus spp. AM	0.9	*Aglantha digitale*	0.0001
Limacina helicina juv	0.8	*Oikopleura* sp.	0.0001

Table 2.

ZOOPLANKTON SPECIES COMPOSITION OPEN SOUND STATIONS -March			
ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Calanidae I	56.1	*Metridia okhotensis* AF	0.0139
Barnacle nauplii	31.8	Barnacle nauplii	0.0060
Bryzoan larvae	25.1	*Calanus marshallae* AF	0.0024
Calanidae II	23.0	*Pseudocalanus spp.* AF	0.0023
Pseudocalanus spp. AF	22.2	Calanidae I	0.0018
Euphausiid eggs	21.7	Calanidae II	0.0016
Pseudocalanus spp. V	11.7	*Metridia pacifica* AF	0.0013
Mertidia okhotensis AF	7.4	*Thysanoessa longipes*	0.0012
Oithona similis AF	7.0	*Thysanoessa spinifera*	0.0012
Oithona spp. copepodites	5.2	*Neocalanus* spp. III	0.0011
Oithona similis V	4.9	*Pseudocalanus* spp. V	0.0010
Neocalanus spp. III	4.9	*Sagitta elegans*	0.0009
Pseudocalanus spp. IV	4.1	*Parathemisto libellula*	0.0007
Pseudocalanus spp. AM	3.6	*Aglantha digitale*	0.0006
Euphausiid nauplii	3.4	*Thysanoessa inermis*	0.0006

Table 3.

ZOOPLANKTON SPECIES COMPOSITION OPEN SOUND STATIONS - April			
ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Euphausiid eggs	232.7	*Neocalanus* spp. IV	0.0362
Pseudocalanus spp. V	121.9	*Neocalanus p/f* V	0.0343
Pseudocalanus spp. IV	120.7	*Metridia okhotensis* AF	0.0303
Bryozoan larvae	102.8	*Neocalanus* spp. III	0.0161
Pseudocalanus spp. III	100.6	Barnacle nauplii	0.0154
Barnacle nauplii	81.1	*Pseudocalanus* spp. V	0.0107
Neocalanus spp. III	72.7	*Calanus marshallae* AF	0.0095
Calanidae II	65.3	*Pseudocalanus* spp. AF	0.0064
Pseudocalanus spp. AF	62.7	*Pseudocalanus* spp. IV	0.0064
Oithona similis AF	56.9	*Sagitta elegans*	0.0057
Pseudocalanus spp. II	45.5	Euphausiid eggs	0.0049
Neocalanus spp. IV	43.7	Calanidae II	0.0046
Euphausiid nauplii	41.5	*Pseudocalanus* spp. III	0.0035
Calanidae I	35.4	Fish eggs	0.0028
Oithona spp. copepodites	28.7	*Metridia pacifica* AF	0.0028

Table 4.

ZOOPLANKTON SPECIES COMPOSITION OPEN SOUND STATIONS -May			
ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Pseudocalanus spp. V	537.6	*Neocalanus p/f* V	0.1305
Pseudocalanus spp. IV	393.6	*Pseudocalanus* spp. V	0.0745
Pseudocalanus spp. AF	259.3	*Pseudocalanus* spp. AF	0.0267
Pseudocalanus spp. III	171.9	*Neocalanus* spp. IV	0.0234
Bryozoan larvae	133.1	*Pseudocalanus* spp. IV	0.0209
Pseudocalanus spp. AM	123.5	Euphausiid calyptopis	0.0111
Acartia longiremis AM	103.6	*Metridia okhotensis* AF	0.0097
Acartia spp. V	100.4	*Calanus marshallae* V	0.0091
Acartia longiremis AF	98.1	*Calanus marshallae* IV	0.0081
Fritilaria sp.	92.5	*Acartia longiremis* AF	0.0072
Euphausiid nauplii	85.6	*Limacina helicina* juv	0.0069
Acartia spp. IV	80.1	*Oikopleura* sp.	0.0063
Oithona similis AF	73.4	*Neocalanus cristatus* V	0.0062
Euphausiid eggs	73.2	*Calanus marshallae* AF	0.0061
Euphausiid calyptopis	67.3	*Pseudocalanus* spp. III	0.0060

Table 5.

ZOOPLANKTON SPECIES COMPOSITION OPEN SOUND STATIONS -June			
ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Pseudocalanus spp. V	1179.9	*Pseudocalanus* spp. V	0.1032
Pseudocalanus spp. AF	799.7	*Pseudocalanus* spp. AF	0.0824
Pseudocalanus spp. IV	683.5	*Limacina helicina* juv	0.0680
Limacina helicina juv	393.2	*Limacina helicina*	0.0584
Pseudocalanus spp. III	302.7	*Pseudocalanus* spp. IV	0.0363
Pseudocalanus spp. AM	292.4	*Neocalanus p/f* V	0.0219
Evadne sp.	236.3	*Calanus marshallae* V	0.0215
Acartia longiremis AF	216.3	*Sagitta elegans*	0.0184
Acartia longiremis AM	185.0	*Aglantha digitale*	0.0182
Oithona similis AF	150.5	*Acartia longiremis* AF	0.0160
Acartia spp. V	125.1	*Aequorea sp.*	0.0141
Oikpleura sp.	71.2	*Pseudocalanus* spp. AM	0.0135
Acartia spp. IV	66.0	*Pseudocalanus* spp. III	0.0107
Oithona spp. copepodites	63.1	*Metridia* spp. V	0.0093
Bivalve larvae	53.6	*Oikopleura* sp.	0.0092

Table 6.

ZOOPLANKTON SPECIES COMPOSITION OPEN SOUND STATIONS -July			
ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Pseudocalanus spp. AF	837.2	*Pseudocalanus* spp.AF	0.0862
Pseudocalanus spp. V	523.3	*Pseudocalanus* spp. V	0.0458
Oithona similis AF	246.8	*Limacina helicina* juv	0.0360
Pseudocalanus spp. IV	219.1	*Limacina helicina*	0.0323
Limacina helicina juv	216.3	*Oikopleura* sp.	0.0270
Pseudocalanus spp. AM	187.1	*Pseudocalanus* spp. IV	0.0116
Pseudocalanus spp. III	112.1	*Phacellophora cantschatica*	0.0094
Euphausiid eggs	108.0	*Pseudocalanus* spp. AM	0.0087
Acartia longiremis AF	104.0	*Calanus marshallae* V	0.0078
Acartia spp. V	72.0	*Acartia longiremis* AF	0.0078
Oikopleura sp.	69.6	*Eirene indicans*	0.0070
Acartia spp. IV	69.2	*Sagitta elegans*	0.0061
Evadne sp.	65.0	Barnacle nauplii	0.0056
Limacina helicina	52.7	Ctenophora	0.0044
Acartia longiremis AM	52.5	*Pseudocalanus* spp. III	0.0040

Table 7.

ZOOPLANKTON SPECIES COMPOSITION
OPEN SOUND STATIONS -September

ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Pseudocalanus spp. AF	190.2	*Pseudocalanus spp.*AF	0.0196
Pseudocalanus spp. V	17.9	Ctenophora	0.0085
Pseudocalanus spp. AM	15.9	*Sagitta elegans*	0.0085
Acartia longiremis AF	13.8	*Metridia* spp. V	0.0051
Metridia spp. V	13.3	Siphonophora	0.0029
Oikopleura sp.	12.2	*Thysanoessa spinifera*	0.0024
Limacina helicina juv	10.2	*Melicertum campanula*	0.0021
Metridia spp. IV	9.8	*Calanus pacificus* V	0.0021
Metridia spp. III	8.6	*Euchaeta elongata* V	0.0019
Acartia longiremis AM	7.9	*Calanus marshallae* IV	0.0018
Calanus pacificus V	5.1	*Eirene indicans*	0.0016
Metridia pacifica AF	4.8	*Pseudocalanus* spp. V	0.0015
Calanus marshallae IV	4.5	*Limacina helicina* juv	0.0013
Euphausiid eggs	4.3	Euphausiid furcillia	0.0013
Calanus marshallae V	3.9	*Lar flavicirratus*	0.0013

Table 8.

ZOOPLANKTON SPECIES COMPOSITION
OPEN SOUND STATIONS -October

ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Pseudocalanus spp. AF	121.1	*Metridia pacifica* AF	0.0229
Metridia pacifica AF	29.1	*Pseudocalanus* spp. AF	0.0125
Acartia longiremis AF	22.3	*Oikopleura* sp.	0.0097
Oikopleura sp.	19.1	*Metridia* spp. V	0.0065
Metridia spp. V	17.1	Ctenophora	0.0058
Pseudocalanus spp. V	11.6	*Sagitta elegans*	0.0057
Acartia longiremis AM	7.4	*Aglantha digitale*	0.0026
Metridia spp. IV	6.7	Siphonophora	0.0025
Calanus marshallae III	6.2	*Parathemisto pacifica*	0.0024
Pseudocalanus spp. AM	5.9	*Thysanoessa raschii*	0.0022
Metridia spp. III	5.2	*Thysanoessa longipes*	0.0020
Calanus marshallae IV	4.1	*Gaetanus intermedius* V	0.0020
Oithona spinirostrus AF	3.8	*Calanus marshallae* III	0.0019
Acartia spp. V	3.0	*Calanus marshallae* V	0.0018
Calanidae II	2.4	*Calanus marshallae* IV	0.0017

Table 9.

ZOOPLANKTON SPECIES COMPOSITION OPEN SOUND STATIONS -December			
ABUNDANCE (No./m3)		BIOMASS (g/m3)	
Pseudocalanus spp. AF	24.8	*Mesocalanus tenuicornis*	0.0118
Mesocalanus tenuicornis	18.1	*Euphausia pacifica*	0.0094
Metridia spp. V	15.8	*Metridia* spp. V	0.0060
Metridia spp. IV	11.2	*Thysanoessa inermis*	0.0046
Pseudocalanus spp. V	5.3	*Cyphocaris challengeri*	0.0043
Metridia spp. III	5.2	*Metridia pacifica* AF	0.0035
Aglantha digitale	4.8	*Sagitta elegans*	0.0031
Metridia pacifica AF	4.4	*Pseudocalanus* spp. AF	0.0026
Oithona spinirostris AF	2.9	*Parathemisto libellula*	0.0018
Limacina helicina juv	2.7	*Thysanoessa raschii*	0.0016
Acartia longiremis AF	2.1	*Dimophyes arctica*	0.0013
Pseudocalanus spp. IV	1.9	*Aglantha digitale*	0.0012
Limacina helicina	1.8	*Metridia* spp. IV	0.0012
Gastropod larvae	1.3	*Limacina helicina*	0.0011
Sagitta elegans	1.3	*Aegina rosea*	0.0011

Table 10.

| Number of the top 15 ranked open-water zooplankters (biomass) also occurring in the top 15 ranked zooplankters (biomass) from the SEA Herring study bays			
Month	*Inner Bay*	*Middle Bay*	*Outer Bay*
Eaglek Bay (6.0)*			
February	Missing	Missing	Missing
May	5	4	5
July	7	9	7
October	5	7	5
Simpson Bay (5.5)			
February	5	7	6
May	5	5	5
July	7	8	7
October	2	4	Missing
Whale Bay (7.4)			
February	8	9	8
May	Missing	7	7
July	6	8	9
October	8	7	4
Zaikof Bay (6.3)			
February	8	7	5
May	6	5	5
July	7	7	9
October	5	5	7
* = Average of all comparisons within a site			

April/May Zooplankton on April/May UW Index
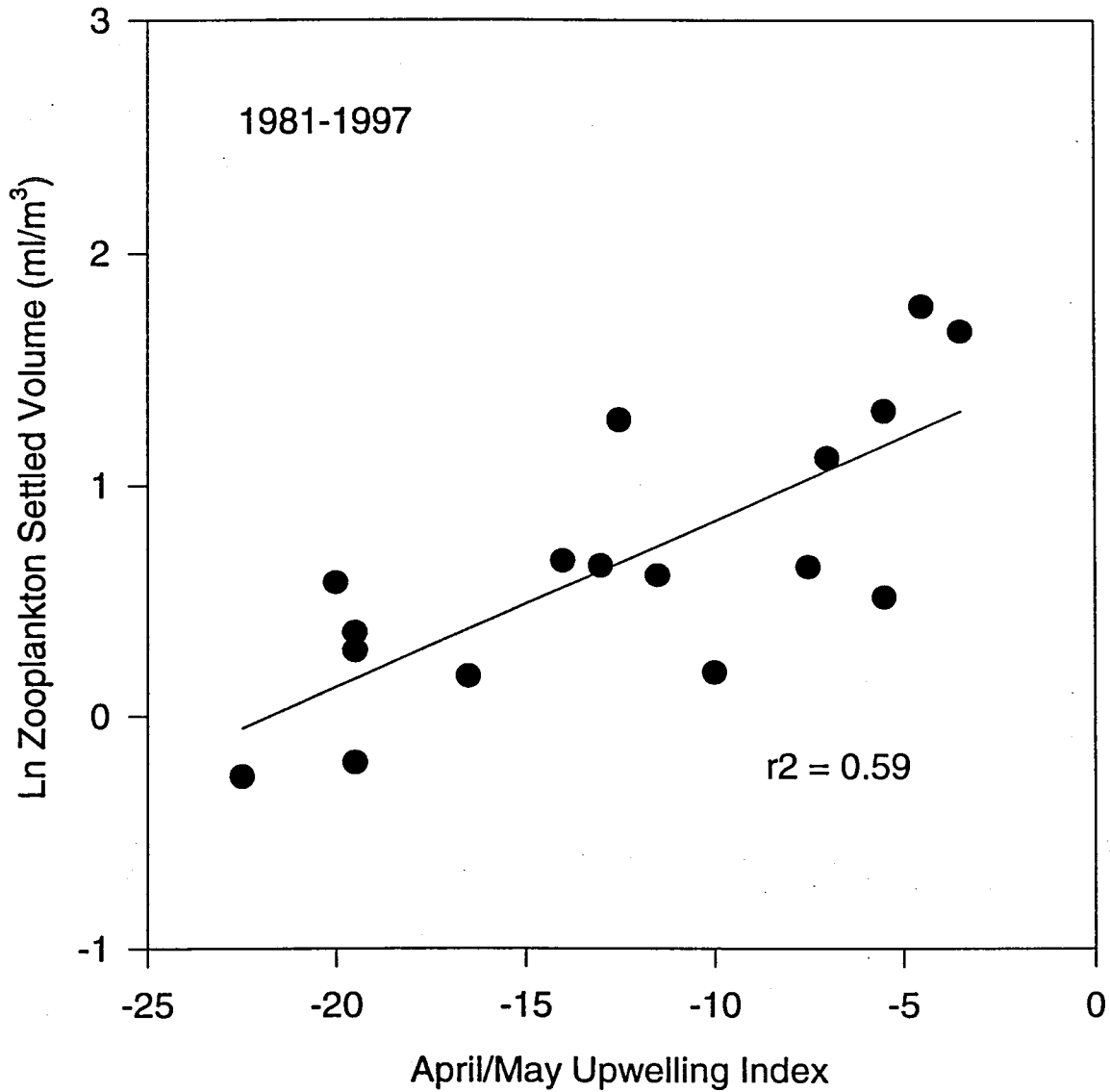
Figure 1. The relationship between zooplankton settled volumes measured at the AFK Hatchery and the upwelling index calculated for a location on the shelf south and east of Prince William Sound, Alaska; 1981-97.

Project 320-H

Appendix 1 (attachment)

Vertical Patchiness in Populations of Large Calanoida in Coastal Waters of
the Northern Gulf of Alaska in Spring

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Abstract

A suite of large copepods, representing the mid to late copepodite stages of *Neocalanus*, *Eucalanus* and *Calanus* were frequently encountered in distinct strata in the upper 50 m of Prince William Sound and adjacent coastal waters in early May, 1996. *Neocalanus flemingeri* and *N. plumchrus* stage V contributed a large proportion of the numbers and were the largest component of the biomass of zooplankton in these layers. *Neocalanus cristatus*, *Eucalanus bungii*, and *Calanus marshallae* were also present but in lesser proportions. None of these species and stages demonstrated consistent relationships with vertical patterns in either fluorescence or upper-layer mixing. However, there was a tendency for *N. flemingeri* and *N. plumchrus* to occur closer to the surface than *N. cristatus* or *E. bungii* at most locations.

The maximum combined abundance for copepodite stage V of *N. plumchrus* and *N. flemingeri* (similar in size and weight) at the 24 sampling sites averaged 377.1 individuals m^{-3}, and ranged from 0.4 to 1286.2 individuals m^{-3}. Locations in Knight Island Passage, near Perry Island, south of Esther Island, and at the shelf break near Middleton Island hosted the highest concentrations of these stages. Locations in southwestern Montague Strait and in southern Unakwik Inlet registered the lowest numbers of these large calanoids.

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 seasonal mixing zones and depth preferences for *Neocalanus plumchrus*, *N. flemingeri*, *N. cristatus*, and *Eucalanus bungii* in the spring and summer. Annually developing copepodites of the former two species were consistently found above or in a weak thermocline, while the latter usually occurred in or below the thermal structuring. This vertical separation was interpreted to reflect: 1) different responses to turbulence; and 2) feeding preferences for protozoans in the spring and early summer surface mixed layer by *N. plumchrus* and *N. 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 on-shelf transport of surface water forced by down-welling favorable winds interacting with source populations in the epipelagic layer of the adjacent deep ocean. Coupled with a growing understanding of coastal flow patterns and the seasonal intrusion of shelf water into Prince William Sound (Neibauer et al., 1994), we now know a mechanism exists to infuse the coastal zone of the northern Gulf of Alaska and Prince William Sound with oceanically-derived copepods each year. 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 manuscript describes vertical patchiness in populations of *Neocalanus*, *Eucalanus* and *Calanus* in and near Prince William Sound, Alaska, in May, 1996. The purpose of the work was to investigate the extent to which large calanoids in the Sound and over the adjacent shelf occur in dense, near-surface layers during the time when pink and chum salmon fry emigrate from natal streams into coastal shallows, and when fry predators like juvenile and adult walleye pollock and adult herring are recharging their seasonally depleted energy reserves. Large calanoid copepods comprise a substantial portion of the diet of pollock and herring in the spring (Cooney and Willette, 1997), and it is believed that during years of exceptional copepod biomass, fishes like adult walleye pollock feed primarily on zooplankton and less on alternative forage like

salmon fry and other small fishes. For this mechanism to function energetically, we reasoned that pollock and other planktivores must encounter high-density copepod swarms or layers in the surface waters of the region. Our study in May, 1996, sought evidence for vertical structuring in populations of large calanoida and other zooplankters in Prince William Sound and over the nearby continental shelf.

Methods

The R/V *Alpha Helix* supported our plankton work in and adjacent to Prince William Sound, Alaska, a large coastal fjord-type estuary located at the northern-most reaches of the Gulf of Alaska. The Sound is deep (to 750 m), is bounded 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. Prince William Sound occupies nearly 9000 km^2 with 3200 km of shoreline (Grant and Higgens, 1910). The adjacent shelf of the northern Gulf of Alaska is a wind-forced downwelling system for approximately 8 months of each year (Neibauer et al., 1994). Stabilization or weak upwelling can occur in the summer months. Deep water is renewed each year during the time of relaxed downwelling, late summer and early fall (Schmidt, 1977).

A MOCNESS sampler was employed at 25 stations inside and outside PWS to collect macrozooplankton in the upper 50 m (Figure 1; station 3 aborted). Sampling was conducted at the peak of the spring zooplankton bloom, early to mid-May, and about two weeks after the maximum in phytoplankton stocks judged by a real-time reporting moored fluorometer in the central region of the Sound. The MOCNESS fished nine,1-m^2 Nitex nets of 0.505-mm mesh. Net one (1) was lowered open as a drogue 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 during 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. Each net filtered at least 100 m3 of water. Collections were carefully rinsed from nets and preserved in 10% seawater formalin. Laboratory processing included identification and enumeration of plankters and the various copepodite stages of the large calanoids. Representative copepodite stages were weighed in size categories

to convert numbers to estimated wet weights (Coyle, et al., 1990). Only copepodite stages II and above were considered in our evaluation of these collections.

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 measurement was believed sufficient to examine the possibility that copepod layers might be strongly associated with vertical patchiness in seasonally declining pelagic plant stocks. Buoyancy frequency was calculated from CTD observations at each location.

Results

Composition of the Near-Surface Net Zooplankton Community

Catches were averaged across all nets and stations to rank taxonomic categories by abundance and biomass (Table 1). The top fifteen categories ranked by average numerical abundance (no. m^{-3}) contained 11 representatives of the Copepoda distributed among six species. Copepodite stage V *Neocalanus flemingeri* and *N. plumchrus* ranked first and fifth respectively. For average biomass (mg m^{-3}), the Copopoda accounted for 9 of 15 categories; *N. flemingeri* and *N. plumchrus* stage V ranked first and second. Other large calanoid categories ranked in the top 15 by abundance and biomass included a composite of *N. flemingeri* and *N. plumchrus* stage IV, *N. cristatus* stage V, *Eucalanus bungii* stages II, III and IV, *Metridia* spp. stage V, *M. okhotensis* adult female, *Calanus marshallae* stages II, IV and adult female, and *Pseudocalanus* spp., stage V.

Non-copepods ranked in the upper 15 taxa by abundance and biomass, included a composite of euphausiid furcillia and calyptopis stages representing the genera *Euphausia* and *Thysanoessa*, the pteropod *Limacina helicina*, the small medusa, *Aglantha digitale*, the chaetognath *Sagitta elegans*, and zoea of unidentified Pandalidae. In all, 152 taxonomic categories were sorted from the MOCNESS samples in May.

Patterns of Vertical Distribution

Vertical profiles of the large calanoid species *Neocalanus plumchrus, N. flemingeri, N. cristatus, Eucalanus bungii* and *Calanus marshallae* were examined for evidence of layering and association with buoyancy frequency and fluorescence patterns in the upper 50 m at each sampling location. We could only confidently distinguish between *N. flemingeri* and *N. plumchrus* at copepodite stage V, so restrict our accounts of these closely related copepods (Miller, 1988) to that stage. A composite of *N.* spp. stage III and IV was examined separately. For *N. cristatus*, a composite of stages II-V is reported, for *Eucalanus bungii*, all stages were combined, and for *Calanus marshallae*, stages IV through adult were composited 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 plumchrus and *N. flemingeri* stage V copepodites were found in layers at 15 of 23 locations (Table 2). Maximum numbers and biomass (combined stage V; 1286.2 individuals per m3 and 3.63 g per m3) occurred at location 9 near the edge of the continental shelf south of Prince William Sound (Figure 1). While *N. flemingeri* was the dominant of the pair at most locations and depths, *N. plumchrus* was equally abundant in a few collections, particularly those in the upper 25 m and from the more southerly sampling locations (Figure 2). There were no locations where *N. plumchrus* was absent from collections.

The composite of *Neocalanus* spp. (unidentified *N. plumchrus* and *flemingeri*) copepodite stages III-IV were layered at 13 of 23 sampling locations (Table 2). There were only four locations where these stages deviated substantially from the vertical patterns of the older stage V, but copepodite stages III-IV were less abundant than stage V at all but four locations. At no depths or locations did these combined stages exceeded 500 individuals m^{-3} (Figure 3).

Copepodites of *Neocalanus cristatus* exhibited layering behavior at 16 of the 21 locations (Table 2). At all but three locations, levels of abundance were consistently less than 10 m^{-3}, or an order of magnitude below densities observed for *N. plumchrus* and *flemingeri*. Where it occurred, *N. cristatus* maximum abundance was generally restricted to water depths below 20 m (Figure 4).

Eucalanus bungii (all copepodites) occurred as layered populations at 16 of 21 locations

(Table 2). Combined densities were less than 10 m^{-3} at all but six locations. *Eucalanus bungii* also occurred most abundantly below the upper 20 m (Figure 5).

Mid to late stage copepodites of *Calanus marshallae* demonstrated diminished layering behavior relative to the other species, exhibiting strata at only 12 of 22 locations (Table 2). Densities of *C. marshallae* did not exceed 100 m^{-3} at any location or depth. This species tended to layer shallower rather than deeper in the upper 50 m (Figure 6).

Spatial Variability in Copepod Layer Densities

Not all locations within Prince William Sound or over the nearby shelf reflected the same densities of large calanoids in near-surface layers. For the dominant species and stage, *Neocalanus flemingeri* and *N. plumchrus* stage V, numbers and biomass were consistently high at locations sampled in Knight Island Passage, near Esther Island, and around Perry and Lone Islands; 569 individuals m-3 and 1.63 g m-3 (Table 3). These densities were only exceeded by samples taken at the single shelf edge station near Middleton Island (location 9). In comparison, samples from Unakwik Inlet (location 6), from over the continental shelf (locations 10 and 11) and from the southwestern portions of Montague Strait exhibited the lowest layering numbers and biomass. Locations for the eastern and central portions of Sound fell between theses highs and lows. An examination of the hydrographic records from these areas suggested that the water was less stratified in Hinchinbrook Entrance, southern Montague Strait, and over the continental shelf outside the Sound.

Vertical Patchiness in Relation to Patterns in Fluorescence

Profiles of fluorescence in the upper 50 m exhibited subsurface maxima at 20 of 23 locations. At some locations, these maxima were well-defined, narrow regions of the water column; at others the maxima were broad and less-well defined (Figure 7). Stage V *Neocalanus plumchrus* and *N. flemingeri* occurred most abundantly at depths corresponding to the fluorescence maximum at about half the sampling locations (Table 4). At the remainder of the locations, stage V was dispersed above, below, or showed no depth preference relative to fluorescence maxima.

Neocalanus spp. stages III-IV occurred in maximum densities corresponding with fluorescence maxima at 9 of 23 locations (Table 4). At other locations, these same stages were found above, below or demonstrated no relationship to peaks in fluorescence.

Neocalanus cristatus stages III-V were most abundant at subsurface fluorescence maxima at 6 of 21 locations. *Eucalanus bungii* maximum densities corresponded to subsurface fluorescence peaks at 7 of 21 locations, and *Calanus marshallae* stages IV-Adult at only 5 or 22 locations. At other times these species and stages occurred most abundantly above or below maxima, or exhibited no apparent correspondence with fluorescence patterns.

Vertical Patchiness in Relation to Patterns of Upper-Layer Mixing

April and May are typically months of increasing meltwater input to Prince William Sound (Simmons, 1996). Because of the volumes involved, water column stability is established primarily by salinity. During this cruise, there were only 6 locations at which an upper mixed layer was detectable by buoyancy frequency; station 9 at the shelf break is the best example (Figure 8). The remaining surface mixed zones were compressed in the upper 5-m or less. This circumstance eliminated appreciable upper mixed-layer habitats at most sites. Only at station 9 did *Neocalanus plumchrus* and *N. flemingeri* stage V have space to occur abundantly in the upper mixed regime. At the remainder of the sampling sites, most *Neocalanus*, *Calanus* and *Eucalanus* occurred in and below the shallow upper mixed zone.

Discussion

Our survey of near-surface populations of large calanoid copepods in Prince William Sound and the nearby Gulf of Alaska demonstrated that *Neocalanus*, *Calanus* and *Eucalanus* can occur in well-defined strata in the upper 50 m during spring. The numerical dominants in our collections, *Neocalanus flemingeri* and *N. plumchrus* stage V, contributed substantially to the overall upper-layer biomass of macroplankton retained by a 0.505-mm mesh in early May. Fewer numbers of a composite of *N. flemingeri* and *N. plumchrus* copepodite stages III-IV suggest that the seasonal shift in population structure from stage IV to stage V was well underway at the time of our cruise.

Vertical patterns in population structure of *Neocalanus* and *Eucalanus* were similar to those described for open ocean populations (Mackas, et al., 1993). In most cases, *N. flemingeri* and *N. plumchrus* occurred shallower than *N. cristatus* and *E. bungii*. However, unlike the oceanic subarctic ecosystem, these distributions did not appear to be partitioned by surface mixing zones. At the time of our cruise, increasing freshwater input and seasonal surface warming, coupled with exceptionally calm conditions, resulted in pronounced upper layer stability and the absence of a clearly defined surface mixed layer at all but one location. Only at the shelf edge south of Prince William Sound was there a pronounced near-surface mixed layer, and that was only 10-15 m deep. At this location, *N. plumchrus* and *flemingeri* stage V copepodites occurred most abundantly in the surface mixed zone as previously described by others for the open subarctic oceanic environment (Mackas, et al., 1993).

We had predicted that under diminishing phytoplankton production following the peak of the spring bloom, subsurface plant maxima might be responsible for focusing the older developmental stages of *N. flemingeri* and *N. plumchrus* into distinct strata . However, a general lack of coherence between observed fluorescence maxima and copepod distributions indicate this was probably not the case. *N. flemingeri* and *N. plumchrus* stage V occurred above, in and below subsurface plant maxima at roughly similar frequencies. We did not calibrate the *in-situ* fluorometer, so are unable to determine if these large grazers were able to obtain suitable rations in residual plant stocks above or below subsurface maxima. The general lack of convergence around chlorophyll maxima suggests that food was probably non-limiting at most depths in the upper 50 m.

Our observations confirmed the suspicion that near-surface layers or swarms of large copepods are features of the coastal zooplankton communities in the northern Gulf of Alaska in the spring. Because of their densities, these layers probably provide predictable, energetically-optimal forage resources for large pelagic fishes like adult and juvenile pollock and herring, some of which have been found feeding almost exclusively on *Neocalanus* spp. Since the largest, oldest copepodite stages are strictly transient members of the upper layers, these concentrated forage resources are likely only available for a few critical weeks each year. Our observations further demonstrate that the layers of *Calanus*, *Neocalanus* and *Eucalanus* were not

uniform in numbers and biomass within the region. Shallow or constricted areas subjected to high tidal mixing were less likely to host layers than locations over deeper, more stratified water. This observation suggests the ability of these large copepods to swarm in narrow vertical strata can be compromised at some locations by tidal energy or current shears.

Acknowledgments

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Table 1. Ranking of macrozooplankton by numerical abundance and biomass		
Taxanomic Category	Ranking by Abundance	Ranking by Biomass
Neocalanus flemingeri CV	1	1
Euphausiid furcilia	2	5
Neocalanus spp. CIV	3	3
Pseudocalanus spp. CV	4	
Neocalanus plumchrus CV	5	2
Euphausiid calyptopis	6	14
Eucalanus bungii CIII	7	11
Pseudocalanus spp. AF	8	
Eucalanus bungii CII	9	
Calanus marshallae CIII	10	
Neocalanus spp. CIII	11	
Calanus marshallae CIV	12	12
Limacina helicina	13	9
Aglantha digitale	14	6
Metridia spp. CV	15	
Neocalanus cristatus CV		4
Sagitta elegans		7
Metridia okhotensis		8
Calanus marshallae AF		10
Pandalidae zoea		13
Eucalanus bungii CIV		15

Table 2. The freqency of calanoid layering in the surface waters of Prince William Sound in May		
Taxonomic Category	Layered	Not Layered
Neocalanus plumchrus/flemingeri CV	15	8
N. spp. CIII-IV	15	8
N. cristatus Stages CIII-V	16	5
Eucalanus bungii CII-V	16	5
Calanus marshallae CIV-Adult	12	8

Table 3. Maximum numbers and biomass of a composite of *Neocalanus flemingeri* and *N. plumchrus* stage V at locations in Prince William Sound and over the adjacent shelf		
Stations and locations	Abundance (No. m^{-3})	Biomass (g m^{-3})
Stations 1-8 (excluding Station 6 in Unakwik Inlet) and 19-23 in Knight Island Passage and northwestern Prince William Sound		
Average	567.9	1.629
Station 9 at the shelf break		
	1286.2	3.643
Stations 10 and 11 over the shelf south of Prince William Sound		
Average	95.6	0.286
Stations 13 and 14 in lower Montague Strait		
Average	11.6	0.034
Stations 12, 15-18 and 24-25 in eastern and central Prince William Sound		
Average	183.0	0.531
Station 6 in Unakwik Inlet		
	21.9	0.045

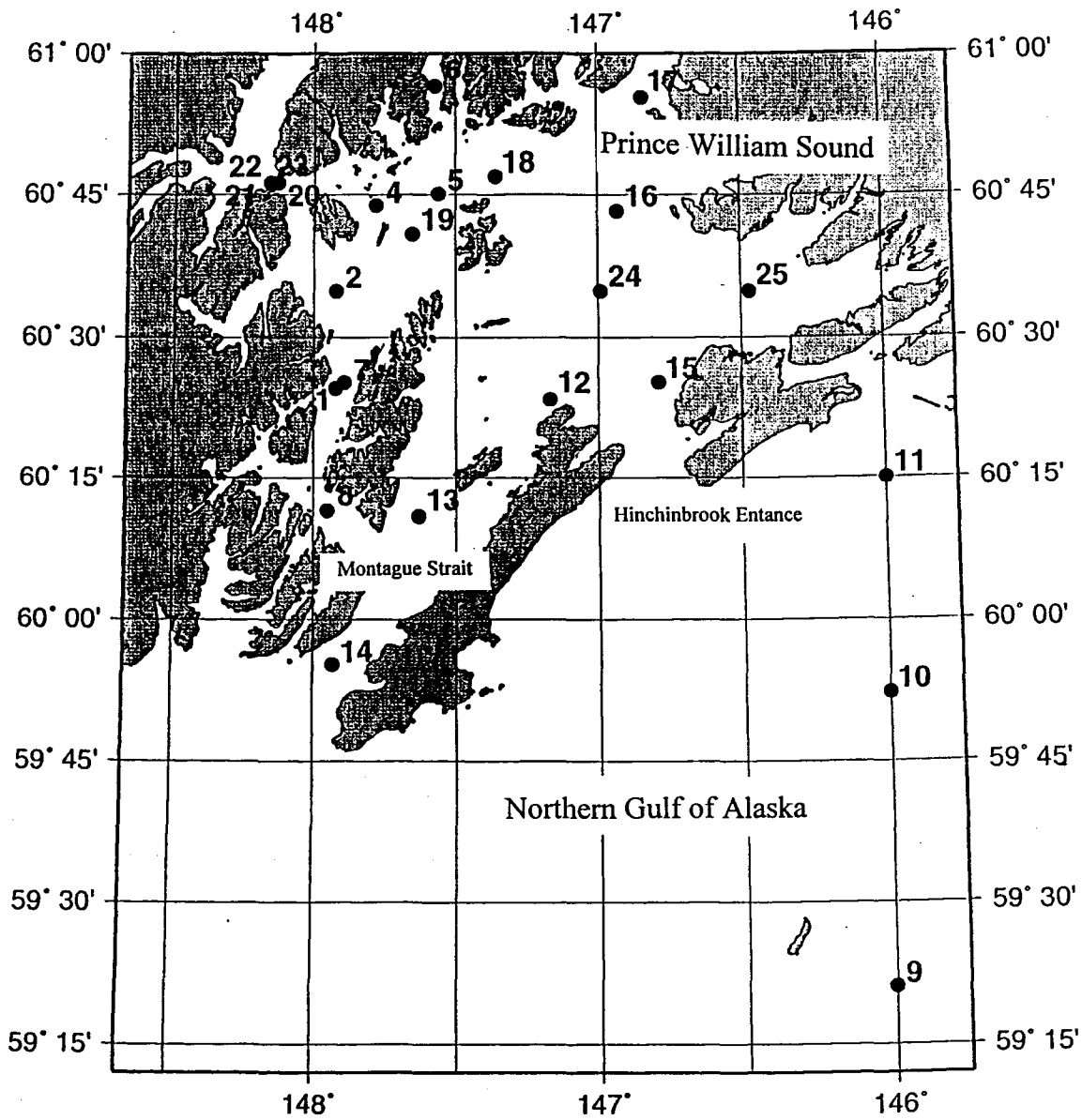| Table 4. Correspondence between the patterns of water column fluoresence and large calanoid depths of maximum abundance		
Taxonomic Category	In Fluoresence Peak	Outside the Fluoresence Peak
Neocalanus plumchrus/flemingeri CV	10	13
N. spp. CIII-IV	7	16
N. cristatus CIII-V	6	15
Eucalanus bungii CII-V	7	14
Calanus marshallae CIV-Adult	6	15

Figure 1. Prince William Sound, Alaska depicting geographic features and the location of MOCNESS stations occupied in May, 1996.
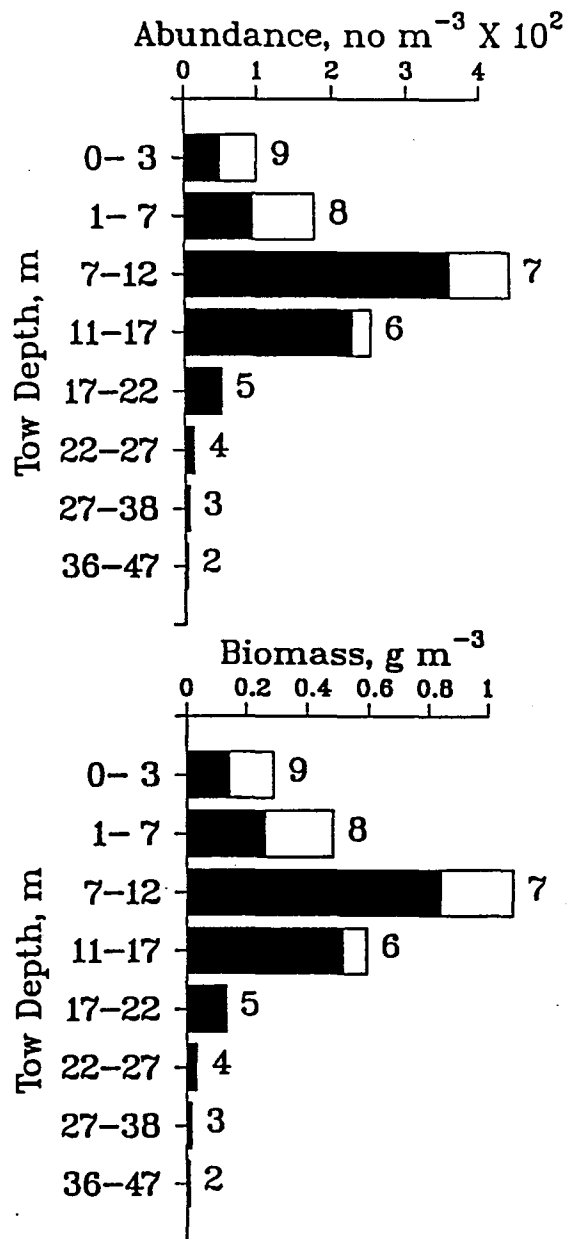
Tow No: 1: Neocalanus plumchrus/flemingeri V

Abundance, no m^{-3} X 10^2

| | 0 | 1 | 2 | 3 | 4 |

0– 3 — 9
1– 7 — 8
7–12 — 7
11–17 — 6
17–22 — 5
22–27 — 4
27–38 — 3
36–47 — 2

Tow Depth, m

Biomass, g m^{-3}

| | 0 | 0.2 | 0.4 | 0.6 | 0.8 | 1 |

0– 3 — 9
1– 7 — 8
7–12 — 7
11–17 — 6
17–22 — 5
22–27 — 4
27–38 — 3
36–47 — 2

Tow Depth, m

Figure 2. Vertical distributions of *Neocalanus plumchrus* (open) and *N. flemingeri* stage V (closed) demonstrating the former occurs more abundantly in the shallower depths.

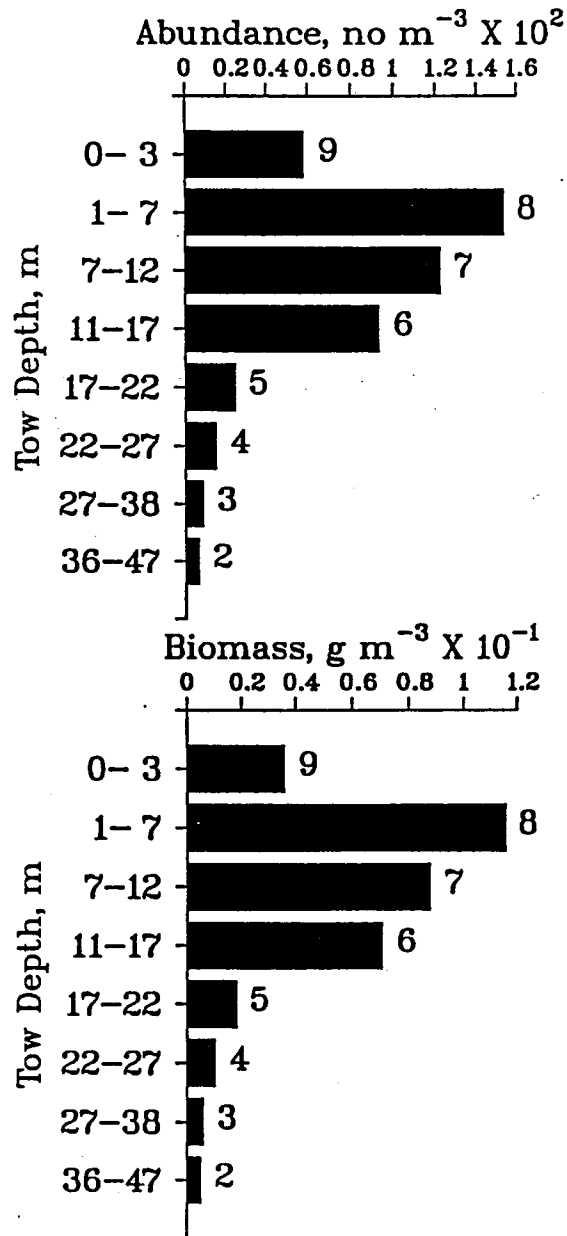## Tow No: 1: Neocalanus spp. III & IV

Abundance, no m^{-3} X 10^{2}

0   0.2 0.4 0.6 0.8 1   1.2 1.4 1.6

Tow Depth, m

Depth	
0– 3	9
1– 7	8
7–12	7
11–17	6
17–22	5
22–27	4
27–38	3
36–47	2

Biomass, g m^{-3} X 10^{-1}

0   0.2 0.4 0.6 0.8 1   1.2

Tow Depth, m

Depth	
0– 3	9
1– 7	8
7–12	7
11–17	6
17–22	5
22–27	4
27–38	3
36–47	2

Figure 3. Vertical distributions of a composite of *Neocalanus plumchrus* and *N. flemingeri* stages III and IV.
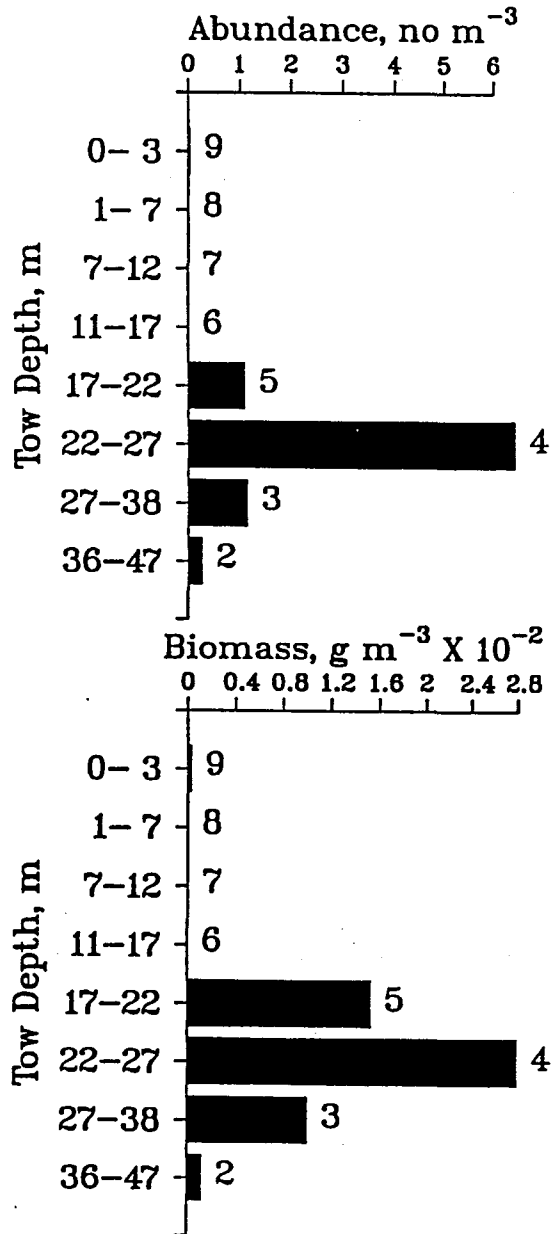
Tow No: 1: Neocalanus cristatus III, IV, V

Figure 4. Vertical distributions of *Neocalanus cristatus* stages III-V.
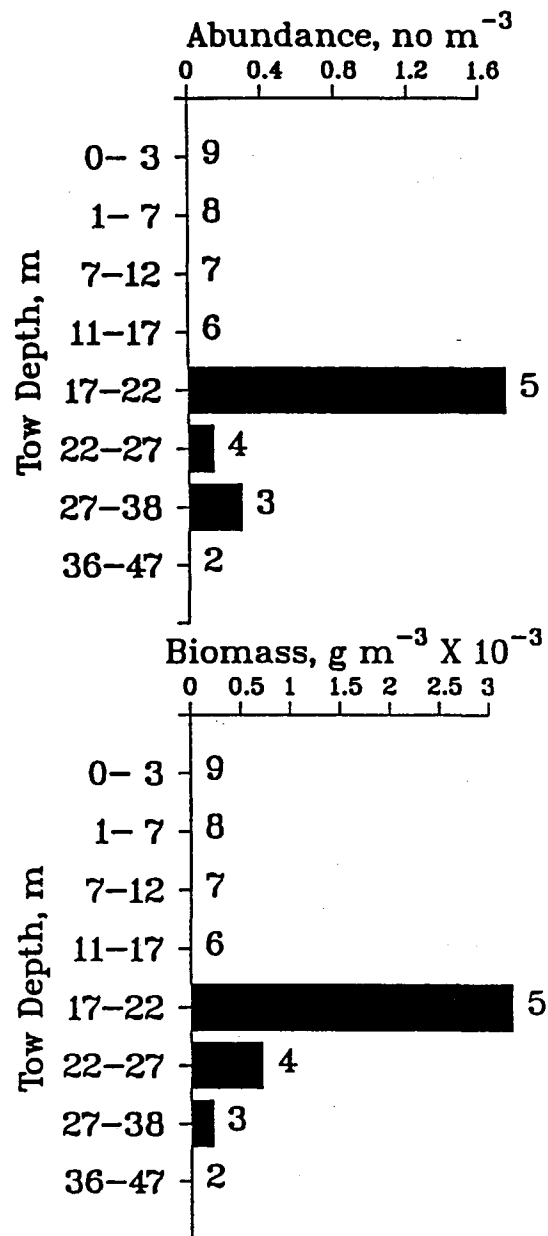
Tow No: 1: Eucalanus bungii all stages

Abundance, no m^{-3}

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

Figure 5. Vertical distributions of all copepodite stages of *Eucalanus bungii*.

Tow No: 2: Calanus marshallae adults, IV, V

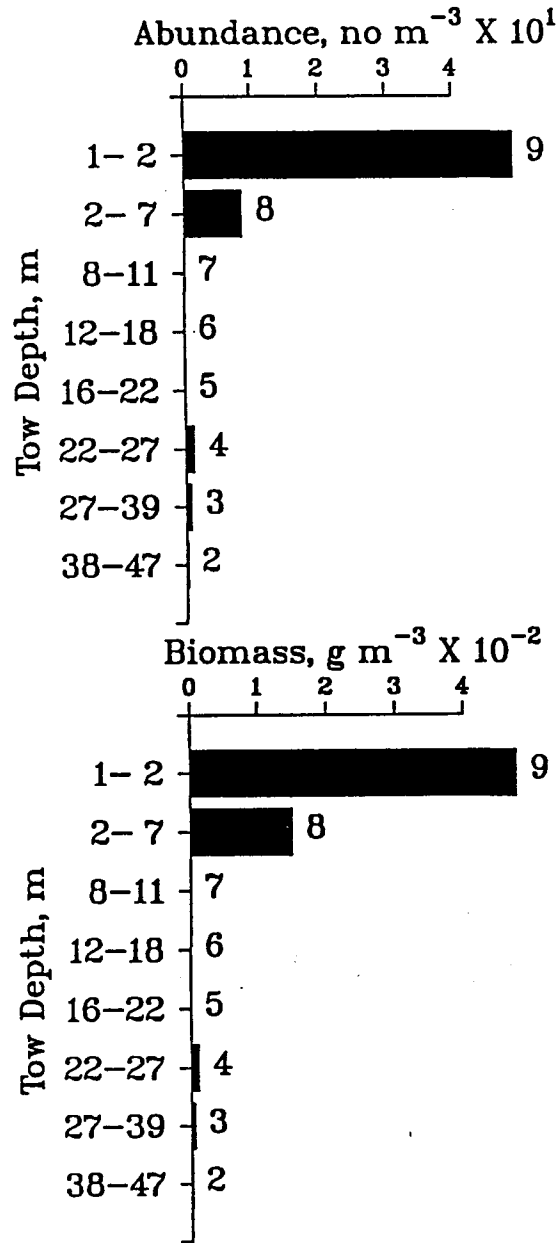Abundance, no m^{-3} X 10^1

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

Figure 6. Vertical distribution of a composite of *Calanus marshallae* stages IV-adult.
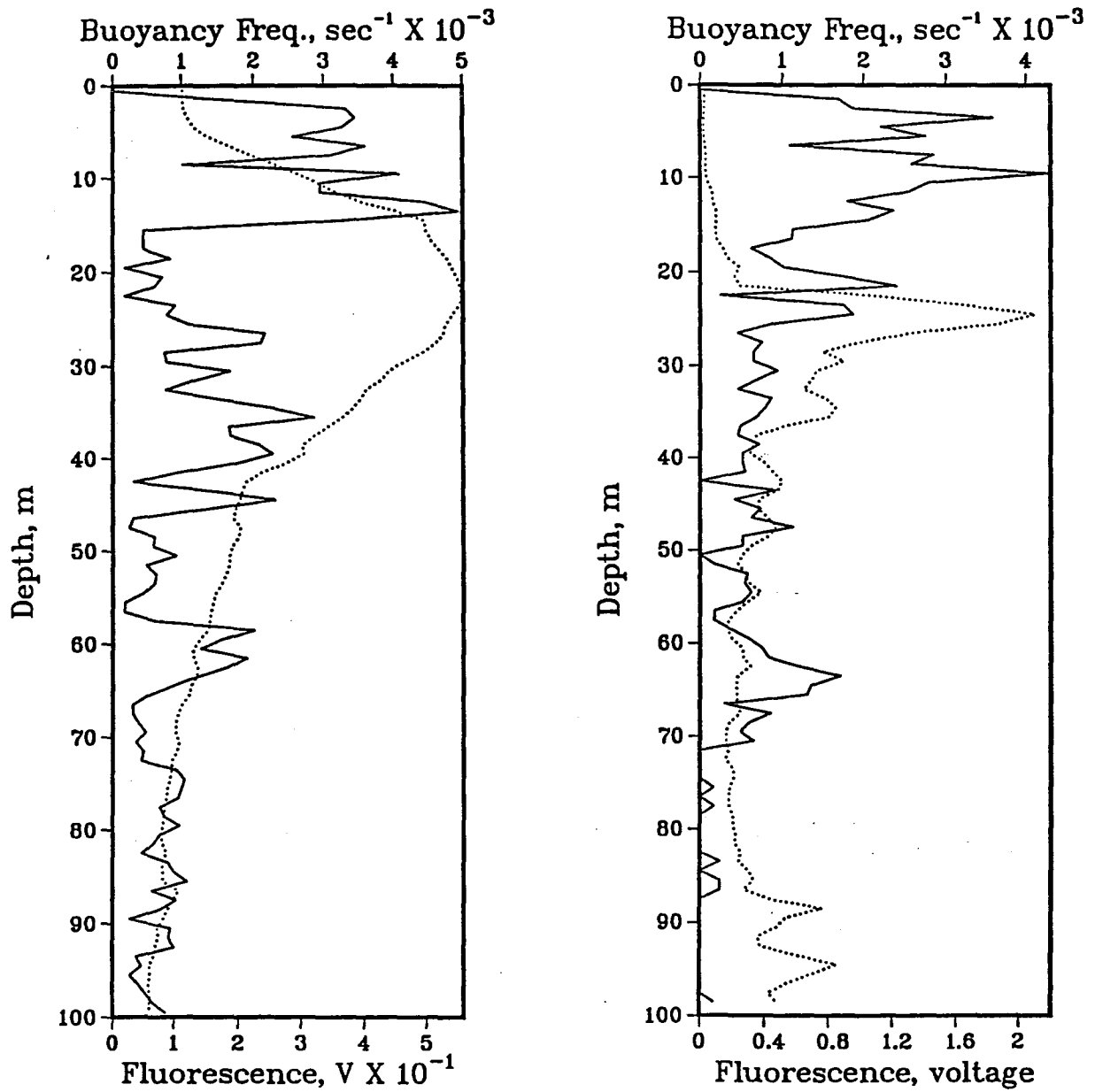
Figure 7. Examples of broad (left) and narrow (right) sub-surface fluorescence maxima (dotted distributions. The solid line depicts the buoyance frequency at these two locations.

Chapter 5

Biophysical Modeling and Remote Sensing