Chapter 9

Plankton and Nekton Acoustics

Exxon Valdez Oil Spill
Restoration Project Final Report

Nekton-Plankton Acoustics

Restoration Project 98320N
Final Report

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July 2002

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Study History: The small runs of Prince William Sound pink salmon in 1992 and 1993, and the collapse of the herring population in 1993, prompted the *Exxon Valdez* Oil Spill Trustee Council to initiate the ecosystem-level studies to improve existing predictive tools. In 1993, the Sound Ecosystem Assessment (SEA) science plan was developed using the GLOBEC program as a guide. Funding of research began in the spring of 1994. The Nekton-Plankton Acoustics project (98320N) (SEAFISH) evaluated applications of acoustic measurement technology to collect information on fish and macrozooplankton distribution and abundance. Beginning in 1994, four annual reports were produced as part of the consolidated SEA report. Appended to this report are citations to three journal articles resulting from this project that have been published in the peer-reviewed literature.

Abstract: The major contribution of the Nekton-Plankton Acoustics project was to develop accurate estimation procedures for animal abundance and distribution information. These data were used for testing of the river-lake and prey-switching hypotheses and the development of predictive numerical models. The results include estimates of nekton predators and macrozooplankton prey along the outmigration corridor for the pink salmon in the spring and fall and winter density and distribution of the juvenile and adult herring and pollock populations. Other products include: stock assessments of adult pollock biomass in Feb-Mar 1995 and 1997 (37 and 36 thousand mt) and adult herring biomass in Sep 1993, Oct-Nov 1994, April 1995, Oct-Nov 1995, Mar-April 1996, and April 1997 (20, 13, 13, 24, 23, 40 thousand mt, respectively).

Key Words: *Clupea harengus, Exxon Valdez* oil spill, hydroacoustics, macrozooplankton assessment, *Oncorhynchus gorbuscha*, Pacific herring, pink salmon, population trends, salmon fry predators, stock assessment, *Theraga chalcogramma*, walleye pollock.

Citation:

Thomas, G.L., J. Kirsch, G. Steinhart, and N. Peters. 2002. Nekton-plankton acoustics project (SEAFISH) of the Sound Ecosystem Assessment Program, *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98320N), Prince William Sound Science Center, Cordova, Alaska.

Chapter 9: 98320N

Citations to published articles

Kirsch, J., G.L. Thomas, and R.T. Cooney. 2000. Acoustic estimates of zooplankton distributions in Prince William Sound, spring 1996. *Fisheries Research* 47:245-260.

Stokesbury, K.D.E., J. Kirsch, E.D. Brown, G.L. Thomas, and B.L. Norcross. 2000. Spatial distributions of Pacific herring, Clupea pallasi, and walleye pollock, Theragra chalcogramma, in Prince William Sound, Alaska. *Fishery Bulletin* 98(2):400-409.

Stokesbury, K.D.E., J. Kirsch, E.V. Patrick, and B.L. Norcross. 2002. Natural mortality estimates of juvenile Pacific herring (Clupea pallasi) in Prince William Sound, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 59(3):416-423.

1999 Final Report

Sound Ecosystem Assessment (SEA), Nekton-Plankton Acoustics - Project 94-99320N

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Summary

Background

The small runs of Prince William Sound (PWS) pink salmon in 1992 and 1993, and the collapse of the herring population in 1993, prompted the people in the region to ask the EVOS Trustee Council to support more fundamental fisheries research. About the same time, a National Science Foundation group of scientists working on the Ocean Ecosystem Dynamics Program (GLOBEC) concluded that our inability to predict changes in marine fish populations prevented us from separating natural and anthropogenic impacts (Cullen 1991). Acknowledging this situation, the EVOS Trustee Council funded the PWS Science Center (Science Center) in Cordova, Alaska to host development of the Sound Ecosystem Assessment (SEA) science plan. The SEA planning group included researchers and managers from several universities and agencies, local fishermen, Alaska Natives and concerned citizens. Scientists at the Science Center introduced the GLOBEC program as a guide in the SEA plan development. After strong endorsement by peer review, the EVOS Trustee Council announced a their intention to fund a 25 million dollar, five-year ecosystem program based upon the plan. Funding of SEA research began in the spring of 1994.

This report is part of the SEA program final report. The general goals of the SEA program were to improve the prediction of changes in the abundance of pink salmon and Pacific herring in Prince William Sound. The pink salmon survival study focused, but not exclusively, on hatchery fish since they represent over 90% of the juvenile salmon in the Sound during the spring. The herring survival studies focused on the first winter period for age 0 juveniles since the over-summer survival was not deemed tractable. Both fish stocks are assumed to be distinct to PWS and both were damaged by the 1989 oil spill and a part of the EVOS Trustee Council restoration program.

The SEA program was tasked to develop two predictive products. First, was an ecosystem-based, numerical model that predicts returning number of adult pink salmon spawners by indirectly estimating marine mortality of juvenile pink salmon in the spring. Second, was a population-energetics based, numerical model that predicts survival of juvenile herring over the winter. The development and operation of these numerical models requires accurate measurement technologies to assess the distribution, density and size of specific animal populations. The nekton-plankton acoustics project (94-99320-N) developed applications of acoustic measurement technology for this purpose.

Nekton-plankton acoustics project

We developed hydroacoustic applications to measure the distribution and abundance of pink salmon fry prey and predators (Steinhart et al 1999, Chapter 1; Kirsch et al. 1999, Chapter 2), and herring populations (Thomas et al. 1997, Chapter 3) in Prince William Sound. This information is a prerequisite for the development, verification and application of better tools to predict changes in the pink salmon and herring populations in the Sound. Improving the prediction of changes in pink salmon and herring populations was a primary goal of the Sound Ecosystem Assessment (SEA) program. Since these papers are undergoing peer review for publication in peer reviewed journals their citation requires prior contact and permission by the authors.

Unforeseen at the start of the SEA program was that walleye pollock dominated the pelagic fish assemblage of the Sound. Despite this, walleye pollock are not found as one of the ecosystem components of the EVOS restoration program (EVOS Trustee Council 1998). This is an oversight since they are the most dominant pelagic fish species in the Sound and elsewhere in the North Pacific they are being protected as a forage species to stimulate the recovery of depleted marine mammal and bird populations. This unexpected finding of the SEA program could have major implications on other aspects of the EVOS Restoration Program goals (Thomas et al. 1999, Chapter 4).

Pink salmon fry survival: Prey and predator assessment

After pink salmon fry are released from the hatcheries and the wild fry leave the streams, there is no way to directly measure their abundance until they return as adults the next year. In 1994, SEA investigators concluded that the development of anover-spring survival model for pink salmon fry was the first step in improving the prediction of adult salmon returns. The mechanisms of over-spring mortality was introduced in the two primary SEA hypotheses: river-lake and prey switching. The SEA modeling efforts have shown that numbers of the primary pelagic predator (adult walleye pollock) and primary macrozooplankton prey (*Neocalanus* spps.) along the spring outmigration route best explain the survival of fry released at the hatcheries. The temporal dynamics and contiguousness of the adult walleye pollock and *Neocalanus* copepod populations make hydroacoustics the appropriate choice of methods to use for assessing their densities.

Predator abundance

Two approaches were used to estimate the number of adult walleye pollock predators in the Sound ecosystem. First, we measured the adult walleye pollock along the fry outmigration path during the spring (Steinhart et al 1999). We used echocounting to estimate the relative abundance of adult walleye pollock because they were found as individual fish in the water column at this time of year. However, the near-surface distribution of the adult walleye pollock and their overlap with dense layers of zooplankton resulted in underestimating their densities using standard echo counting techniques. Do to this underestimation, all estimates of adult pollock in the spring are considered to be relative abundance. Second, to get a better understanding of the absolute abundance of adult pollock in the Sound we measured their biomass in the winter when the fish aggregated in relatively small areas prior to spawning (Thomas et al 1999). This was a less direct measure of fry predators since the portion of spawning adults that feed along the fry outmigration path is unknown. However, the midwater distribution of the fish at this time of year allowed for high precision estimates of biomass yielding the best assessment of absolute abundance, which is needed to understand the potential magnitude of predation.

We believe these two acoustic assessment approaches have different strengths that when combined offer the best overall description of the adult walleye pollock population that the pink salmon fry must face each year on their outmigration. Thus, hydroacoustic surveys of adult walleye pollock in the spring and winter provide the predator density information needed to use the over-spring fry survival model to estimate adult pink salmon returns the following year. If the future EVOS monitoring program is to use the SEA fry survival model to predict adult pink salmon returns, acoustic surveys of predator abundance will need to be incorporated into the monitoring program.

Prey assessment

The patchiness of macrozooplankton prey makes representative sampling of density with plankton nets improbable. Yet knowledge of prey abundance is a critical component of the fry survival mechanisms of river-lake and prey switching. To overcome this limitation, we used synoptic MOCNESS and hydroacoustic measurements to scale a Sound wide acoustics survey of macrozooplankton backscatter (Kirsch et al. 1999). Benfield et al. (1998) has had some success with replacing the costly MOCNESS sampling with a plankton video recorder to identify species and measure sizes of dominant macrozooplankton. If the future EVOS monitoring program is to use the SEA fry survival model to predict adult pink salmon returns, the spring survey of macrozooplankton densities will need to be incorporated into the monitoring program. Some efficiency can be accomplished by using a multi-frequency approach on the spring survey to synoptically assess both the predator and prey densities. In addition, these acoustic surveys of macrozooplankton may be desirable for the study of other planktivores in the Sound.

Pacific Herring: Assessment of over-winter and over-summer survival

The development of an overwinter survival model for juvenile herring survival was considered a tractable problem by SEA investigators in 1994 (as opposed to the estimation of over-summer survival). Two approaches were used to estimate the abundance of herring year-classes in the Sound. First, hydroacoustic surveys of the adult herring overwintering in the Sound were conducted in conjunction with Alaska Department of Fish and Game to estimate the recruitment of juveniles into the adult population. The acoustic biomass estimates were shown to be highly precise (Thomas et al. 1997). Second, hydroacoustic survey procedures were developed to directly estimate the age 0 and 1 herring abundance in the fall and spring. By conducting juvenile surveys, the time interval to verify model predictions was reduced from three years to every six months (by the number of age 0 fish surviving the first summer and subsequently the first winter). Shortening the interval of measurement to six months makes the development of an over-summer survival model for age 0 herring feasible.

Our acoustic surveys show that the adult herring population in Prince William Sound has undergone a second collapse (1992-93 and 1997-98) in biomass since the spill in 1989. These collapses are unique to the PWS herring population so in light of the possible immune system and genetic damage shown for other species the linkage to the 1989 oil spill cannot be dismissed. Also, with the herring's importance as a forage fish, knowledge of their abundance and distribution is critical to understanding the recovery of many piscivorus species of marine birds and mammals. Thus, herring monitoring is a likely candidate for the future EVOS monitoring program. Since the fall and spring acoustic survey methods we developed yield precise estimates of the distribution and abundance of the adult and juvenile herring, they are important candidates for inclusion with the EVOS monitoring program. Once verified, the application of the SEA over-winter survival model may replace the need for spring surveys of the juveniles but the fall-juvenile and spring-adult surveys will remain critical to understanding the annual changes in the herring population that can have pronounced impacts on the productivity of birds and mammals in the Sound.

Walleye pollock: The Sound's "waist-taxon"

Pollock were shown to be the super-dominant, waist-taxon in the Bering Sea trophic structure (Livingston et al. 1997). Thomas et al. (1999) describes pollock as the super-dominant, waist-taxon of the Sound's trophic structure. We hypothesize that herring may compete with pollock for the waist-taxon position in the trophic structure during more stormy weather regimes. In any event, knowledge waist-taxon abundance, where they occur, is a prerequisite to understanding the fate of lower trophic level production and the productivity and diversity of higher trophic levels (birds and mammals). Thus, incorporation of acoustic surveys of pollock and herring are a prerequisite for the EVOS monitoring program if one goal is to track changes in damaged fish, bird and mammal populations so that recovery can be assumed.

Chapter 1 – Steinhart et al. 1999

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Co-occurring patches of walleye pollock (*Theragra chalcogramma*) and zooplankton in Prince William Sound, Alaska, USA.

by

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ABSTRACT

We conducted two acoustic surveys of Prince William Sound (PWS) in the spring of 1995. The primary goal of these surveys was to observe the spring zooplankton bloom and the distribution of post-spawning walleye pollock (*Theragra chalcogramma*), one of the dominant fish species in the Sound. In this paper, we examine the spatial distributions of pollock and zooplankton in April and May, 1995. Zooplankton biomass varied from 0.1-1.7 g/m3 from the net tows, while acoustic estimates of zooplankton biomass varied by three orders of magnitude (1000 x). We observed near surface (0-50 m) patches of zooplankton from 100 m to 5000 m long. In April, these patches were composed of 85% calanoid (72% *Neocalanus spp.*) copepods by weight. By May, calanoid copepods accounted for only 55% (24% *Neocalanus spp.*) of the biomass, but pteropod denisty doubled (from 0.7 to 2.2 g/m^3). Acoustic data showed post-spawning walleye pollock abundance was highest near the surface (0-50 m), and was positively correlated with zooplankton biomass (r^2=0.42 in April, and r^2=0.31 in May). Post-spawning walleye pollock were feeding heavily on the plankton found in the patches: copepods in April and pteropods in May. Early-spring feeding on zooplankton by adult walleye pollock is not fully understood, but collaborates with other pollock studies in the Bering Sea, and could be an important factor affecting the production of pollock in PWS.

INTRODUCTION

Walleye pollock (*Theragra chalcogramma*) are one of the most abundant fish in Prince William Sound (Thomas et al. 1997). Acoustic surveys in Prince William Sound (PWS) have estimated the pre-spawning biomass of pollock at over 100,000 tonnes (Alaska Department of Fish and Game [ADF&G], Cordova, Alaska, unpublished data). Pollock are important to the marine ecosystems of Alaska, both as predators (Dwyer et al. 1987; Bailey 1989) and while juveniles, as prey (Smith 1981; Hatch and Sanger 1992; Springer 1992). Although earlier studies have looked at behavior, distribution and abundance of adult pollock in the Gulf of Alaska (GOA) and the Bering Sea from summer through winter (Traynor 1986; Brodeur and Wilson 1996), little is known about the spring distribution and behavior of post-spawning pollock in PWS. With such a large adult pollock population in PWS, their dual role as both a predator and a competitor could be important to the recruitment of other economically important fishes in Prince William Sound (Walters et al. 1986; Cooney 1993); such as, Pacific herring (*Clupea pallasi*) and pink salmon (*Oncorhynchus gorbuscha*).

The match-mismatch hypothesis (Cushing 1972; Cushing 1982) has suggested that much of the variability in recruitment success of marine fish is due to the time of fish hatching and how it coincides with the plankton production cycle: a bottom-up hypothesis. In contrast, predation by a dominant fish can also explain survival of other fish and lower trophic levels: a top-down hypothesis (Carpenter et al. 1995). These two hypotheses are not entirely separate: direct and indirect effects of each process can lead to the same results. For example, during a year where the fish hatch is not timed with the zooplankton bloom, or during a poor production year, there will be less food for growth and survival of young fish (a direct bottom-up effect of low zooplankton abundance). Optimal foraging theory suggests that with reduced zooplankton abundance, predators of zooplankton may switch their diet (Werner and Mittelbach 1981), and may include more juvenile fish (Willette et al., MS submitted). During a year of low production or mismatched larval fish hatch, not only is their less food for young fish, but they may experience high rates of mortality from predators (an indirect bottom-up effect, or a direct top-down effect).

After the 1989 *Exxon Valdez* oil spill, stocks of Pacific herring and pink salmon in PWS have had variable recruitment success. The low returns of hatchery-released pink salmon in 1992 and 1993 are hypothesized to be the result of poor survival during their outmigration from PWS (Willette 1996). Both bottom-up and top-down mechanisms are suspected, and adult pollock, being one of the most abundant pelagic fish in PWS, is one of the most likely candidates for causing the decline. Walleye pollock have been shown to be both a predator of pink salmon fry, and a competitor for zooplankton in PWS (Willette et al., MS submitted). The outmigration of pink salmon fry starts in mid-April with a large hatchery releases which continue through the month of May. The smolts migrate through PWS for approximately 2 months (ADF&G, unpublished data). During this outmigration, competition with pollock for zooplankton may result in lower salmon survival. Furthermore, low plankton biomass may cause the pollock to consume more salmon smolts, compounding salmon mortality (Willette et al., MS submitted). In the Bering Sea, pollock switched their diet to include more fish during periods of low zooplankton abundance (Dwyer et al. 1987; Bailey 1989).

Although the PWS hatcheries attempt to match the pink salmon releases with the spring zooplankton bloom, changes in climatic conditions can effect the success of this strategy. The formation of stable layers or patches of plankton can be important for the survival of young fishes (Lasker 1975, Leggett 1986). If the smolts are released at a time when plankton abundance is low, or when storms prevent the formation of zooplankton patches, the effects of competition and predation by pollock may be accentuated. Therefore, understanding the distribution of adult pollock and zooplankton patches is important to understanding the survival of pink salmon, and other fishes in PWS.

Our objective was to describe the spatial distribution of pollock and zooplankton in Prince William Sound during the spring of 1995. Specifically, we looked at the spatial and temporal overlap of post-spawning adult walleye pollock and the suite of calanoid copepod species that comprise much of the spring zooplankton bloom (*Calanus* spp., *Neocalanus* spp., and *Pseudocalanus* spp.). We hypothesized that walleye pollock and zooplankton would be found in co-occurring patches during the spring. Describing the extent of this co-occurence is a fist step in developing a better understanding of predator/prey interactions in PWS.

MATERIALS AND METHODS

Prince William Sound is located at the northern edge of the Gulf of Alaska (Fig. 1). This large fjord/estuary covers an area of approximately 8800 km^2, and has about 3200 km of shoreline (Grant and Higgins 1910). Coastal rainforests, high mountains, and glaciers border the shoreline of PWS. The area is exposed to seasonally intense storms moving in from the Gulf of Alaska, resulting in 5-7 m of annual rainfall.

In 1995, two broadscale surveys of PWS were conducted during 27 April to 1 May, and 23-27 May (Fig. 1). Fish and zooplankton were measured with hydroacoustics and the acoustic targets were verified with vertical plankton tows and mid-trawl hauls. All sampling was conducted during daylight hours.

Acoustic data were collected using a BioSonics 101-120 kHz 6°/15° dual-beam echosounder. The transducer was mounted on a tow-body which was towed alongside the boat at a depth of 2 m at an approximate speed of 2 m/s. The parameters of the acoustic system were: source level = 225.023 dB; receiver gain = -159.282 dB; transducer directivity = 0.0010718; pulse width = 0.4 ms. We set the noise threshold to 0.04 V, and the range to 250 m for these cruises. The acoustic system was calibrated before each cruise using a tungsten-carbide ball, of known target strength, suspended within the beam of the transducer (Foote and MacLennan 1982). The data were processed in real-time using BioSonics ESP software on a 486 computer and were geo-referenced and time-coded using data from a Magellan DLX-10 GPS receiver. Echo integration, dual-beam target strength (TS), and GPS data were stored on the computer hard disk, and backed up on a tape drive. Raw acoustic signals were stored on Digital Audio Tape and printed on paper echograms.

Once the cruise was completed, the acoustic files were transferred to UNIX workstations for data reduction and analyses. Initial processing of acoustic information was done with in-house software written to apply the acoustic calibrations and to correct euphausiids (-93.8 dB), and pteropods (-89.2 dB). The target strengths of these zooplankton were estimated from mean lengths and widths taken throughout PWS, and from estimates of the reflection coefficient, R (see Kirsch et al., MS submitted, for complete details). We did not include all plankton species in this analysis because many of the plankton caught in the zooplankton nets were either too small to be seen with our 120 kHz transducer, or had low densities, so they would have a Sv that was negligible compared to that of the primary species.

Zooplankton were sampled with vertical net tows using a 0.5 m ring net with 333 μm mesh (18 tows in April, 10 tows in May). The net was towed vertically through the top 50 m. Most hauls were done at the beginning or end of the acoustic transects, but some net hauls were pulled through distinct patches of plankton. The samples were preserved in a formalin solution. In the lab, the zooplankton were enumerated, measured, and identified to species. The mean length of each species was used to calculate the mean weight, and then multiplied by the number of individuals in the sample to yield biomass estimates.

Once the acoustic data arrays for pollock-sized targets and zooplankton were generated, we analyzed the data to look for spatial overlap between the two distributions. First, we generated maps of zooplankton patches and pollock densities. We visually identified zooplankton layers or patches using the electronic echograms and measured the length of the patch, which we call the chord length. Given our ping rate, boat speed, and echo-integration report size (32 pings), the smallest patch that could be identified was approximately 50 m in chord length. We assumed the patches were round, and that the chord length was a suitable estimate of the diameter. Since the assumption that zooplankton patches are round is flawed, we only used this data to generate images of zooplankton and pollock distributions. We then used the acoustic estimates of pollock and macro-zooplankton density to calculate regressions between pollock density in different depth ranges (0-50 m, 0-100 m, and 0-150 m) and macro-zooplankton density (top 50 m) at several different horizontal spatial scales (cell sizes: 50 m to 10,000 m long).

RESULTS

The spring zooplankton community in Prince William Sound was comprised of several species, but was dominated by calanoid copepods: 89% in April and 72% in May (by weight). Total zooplankton biomass in the top 50 m declined by approximately 50% from April to May, mostly due to a decline in the number of *Neocalanus spp.* (Fig. 2). Vertical plankton net hauls found a significant decline in mean zooplankton biomass from 0.54 g/m^3 in April to 0.28 g/m^3 in May (heteroscedastic t-test for unequal variances, df=22, t=2.45, p=0.011). During April, *Neocalanus spp.* made up 72% of the total zooplankton biomass, but by May, *Neocalanus spp.* accounted for only 24%. The acoustic data showed a significant decline in mean macro-zooplankton density (*Neocalanus spp.*, euphausiids, and pteropods) from 420 plankton/m^3 in April, to 260 plankton/m^3 in May (heteroscedastic t-test for unequal variances, df=27, t=9.73, $p<<0.05$).

Not only were zooplankton most abundant during the April cruise, they were also more patchy. Zooplankton biomass estimates from net hauls ranged from 0.15-1.7 g/m^3 ($s^2=0.18$, n=18) in April, and 0.14-0.54 g/m^3 ($s^2=0.02$, n=10) in May. The variance in zooplankton biomass from the nets was significantly higher for the April than the May cruise ($F_{(17,9)}$=11.61, p= 0.0004), suggesting more patchiness in the plankton distribution in April. The variance in acoustic estimates of macro-zooplankton in cells 50 m deep by 50 m long was twice as high during April (s^2=2.5 e^{12}) than during May (s^2=1.1 e^{12}). This was a statistically significant decrease, but the significance may be an artifact of the huge sample sizes of acoustic data sets (April n= 3963, May n=3890 cells).

Many patchy layers of zooplankton were seen with the hydroacoustic system (Fig. 3). In general, there were more zooplankton patches identified on the electronic echograms from the April cruise (n=37) than from the may cruise May (n=21). Zooplankton patches averaged 1,700 m chord length in April (range: 150-5,000 m), and 3,200 m in May (range: 300-7,000 m). Although we did not design these surveys to compare density between or within zooplankton patches, zooplankton biomass estimates from net tows varied up to an order of magnitude (0.15-1.7 g/m^3). The hydroacoustic data, which have a larger and more continuous coverage than the net hauls, found over three orders of magnitude (1-3,000 plankton/m^3) difference in acoustic backscatter attributed to zooplankton. From these data, we suggest that the observed zooplankton patches could vary by up to 1000 times the average zooplankton density outside of patches.

The mid-water trawl caught almost exclusively adult walleye pollock. In total, 596 pollock were caught and comprised 93% of the total catch. Additional fish captured included 31 lantern fish (Family Myctophidae), 9 sculpin (Family Cottidae), 2 capelin (*Mallotus villosus*), and 1 chinook salmon (*Oncorhynchus tshawytscha*). The lantern fish were caught in the haul at 125 m, the only trawl haul deeper than 60 m. The pollock averaged 508 mm fork length (range = 400-702 mm) and 870 g wet weight (range = 490-1410 g). The predicted TS was determined using TS=20Log (length) - 66 (Traynor and Williamson 1983). The predicted TS of these pollock coincided with the TS range we used to count pollock-sized targets (Fig. 4). Although there were a limited number of trawl hauls, pollock dominated the catch and the other fish captured in the trawl would have target strengths below our threshold so would not be counted by our echo-counting procedure, except for the one adult salmon captured. Therefore, we assumed that all pollock-sized targets observed during these cruise were adult pollock.

There appeared to be two layers of pollock during these cruises: a shallow layer (less than 50 m deep), and a sparse deep layer around 150 to 200 m (Fig. 5). Although there were few deep trawl hauls made during these acoustic surveys, the trawl data did show the highest catch per unit effort above 20 m (Fig. 6). Based on the shape, distribution, and target strengths of targets below 100 m, and on trawl data from other surveys from 1994-1997 (ADF&G, unpublished data), we believe that these deep targets were also adult pollock. The depth distribution of pollock changed slightly between the two surveys: pollock were more abundant near the surface during the April cruise than during the May cruise, although this difference does not appear significant. The acoustics also showed that there were slightly more pollock-sized targets in the deep layer during May.

Pollock stomachs were found to contain nearly 99% zooplankton (by weight) in April (n=196) and in May (n=34; Fig. 7). In April, calanoid copepods, primarily *Neocalanus spp,* comprised 65% of the stomach contents. In May, however, pteropods were the dominant prey item (43%), while less than 25% of the diet consisted of copepods. Pink salmon were identified on the stomach contents, but due to the break down of tissues during digestion, many fish remains were not readily identifiable and all ingested fish were lumped into a single category. Fish made up less than 1% of pollock diets during both cruises.

We saw pollock-sized targets with plankton patches during both April (Fig. 8) and May (Fig. 9). Although pollock were not always found coinciding with plankton, it appeared that they were more closely associated during the April survey. Indeed, we found positive correlations between pollock density and relative zooplankton density during both surveys in 1995. In general, the correlation between pollock and plankton was better during April than in May. The spatial scales used in the correlation analyses affected the correlation coefficients. In April, more pollock were found near the surface than in May, and the highest r^2 value (0.42) was found by regressing pollock density from 0-50 m in cells approximately 6,500 m long (Fig. 10). In May, we found that the highest r^2 was obtained by including deeper pollock: regressing pollock density from 0-100 m provided the highest r^2 value (0.31), using cells approximately 7,500 m long.

DISCUSSION

The results from our spring surveys in PWS found that post-spawning walleye pollock in Prince William Sound behaved differently than pollock in the Bering Sea and GOA during the summer-winter season. In those areas, adult pollock were found near the bottom during the daytime, with only juveniles commonly found near the surface (Traynor 1986; Bailey 1989). Pollock in the Bering Sea eat mainly euphausiids and larvaceans during the spring (Dwyer et al. 1987), but their spatial overlap with macro-zooplankton has only been assumed (Swartzman et al. 1995). In PWS, we found the highest densities of adult walleye pollock near the surface. Most previous studies have suggested that adult pollock remain deep in the water column (Bailey 1989; Brodeur and Wilson 1996), but this may be a result of sampling effort. When looking at acoustic data, it is essential to remember that sampling volume increases exponentially with range, so while only a few fish may be seen near the surface, they may equate to a high density. For this reason, or because some acoustic surveys are conducted with transducers towed deep in the water column, fish near the surface may have been missed in these previous studies. Our data suggest that the bulk of post-spawning pollock in PWS feed near the surface in early spring to exploit the large *Neocalanus spp.* population. Large copepods composed the bulk of pollock diets during the spring plankton bloom, and are an important food resource for post-spawning pollock in PWS. Paul et al. (1993) showed that for yellowfin sole (*Pleuronectes asper*), a demersal fish, that the spring plankton bloom provides up to 40% of the fishes total caloric intake for the year in the Bering Sea. *Neocalanus spp.* were the dominant zooplankton in April bloom, and could represent a significant portion of the annual caloric intake for adult walleye pollock.

The near-surface distribution of post-spawning pollock in the Sound appears to be to be in response to the availability of prey, as *Neocalanus spp.* undergo a seasonal vertical migration (Cooney 1987). In mid-spring, young copepods migrate up from great depths (400+ m) to respond to the spring phytoplankton bloom, where they remain for a short time. By early summer, the mature copepods have migrated down to 400+ m where they spend the winter. There is also evidence that oceanic copepods enter near-shore and coastal waters in the spring (Incze et al. 1997). We observed both a general decline in copeopod abundance near the surface between late April and late May, and changes in zooplankton patch size and species composition. During April, there were more dense patches of plankton, and more variability in plankton density, than in May. In April, the zooplankton patches were made up almost entirely of *Neocalanus spp*. During May, however, there were fewer high density zooplankton patches, and less variability in plankton distribution. In May, the layers of less patchy zooplankton may have been aggregations of species other than copepods. Pteropods, for example, were much more abundant in the high density areas, and may have been forming the few dense patches we observed during May.

Observations made during this study, as well as other research (Lasker 1975; Leggett 1986; Simard and Mackas 1989; Barange 1994), suggested that climate and currents can influence zooplankton distribution. Gusts of 20 m/s occurred on 23-24 of May 1995, and average daily wind speeds were higher during the May survey than during the April survey (NOAA, unpublished data). The reduced number and density of zooplankton patches and layers near the surface in May could have been the result of the increased winds at that time. In addition, small scale physical mixing from tide rips, Langmuir cells, and internal waves can affect plankton distribution by concentrating plankton in some areas (Haury et al. 1983; Wiebe et al. 1997). On several occasions, we saw a varying depth distribution of plankton layers on a small scale (Fig. 3). The effects of small-scale turbulence on zooplankton patchiness, and the effects of large-scale circulation patterns on zooplankton immigration to, and emigration from, the Sound are not entirely understood at this time, but may affect the number and density of macro-zooplankton available for post-spawning walleye pollock.

Seasonal shifts in adult pollock diets have been reported previously (Dwyer et al. 1987, Bailey 1989, Willette et al. MS submitted). In this study, pollock diets switched from primarily copepods to pteropods; however, another alternate prey, pink salmon fry, are typically found in the top 50 m during their spring out-migration, and are consumed by post-spawning walleye pollock (Willette 1996). The relatively low incidence of fish in diets of pollock we sampled may have been an artifact of the timing and location of the offshore surveys: in PWS salmon fry are usually more abundant in nearshore environments in April and May, before moving into pelagic areas in June (Willette et al., MS submitted). Although fish made up less than 1% of pollock diets during this study, it is important to remember that individual pollock don't need to eat many salmon fry to have a profound effect on salmon survival given the large number of pollock found in the Sound. Assuming there are approximately 25 million adult pollock (ADF&G, unpublished data), and 750 million salmon fry in PWS (Thomas and Mathisen 1993), then salmon survival will be zero if each pollock ate only 30 salmon fry per year. Therefore, it is not hard to imagine that predation by post-spawning pollock could have a profound impact on salmon survival.

Pollock density and macro-zooplankton were positively correlated during this study, and correlations between predators and prey are common in the literature (Schneider 1989; Rose and Leggett 1989; Rose and Leggett 1990; Veit et al. 1993; Deblois and Rose 1995). A positive correlation does not prove a causal relationship; however, since pollock diets were dominated by zooplankton during these surveys, it does support the hypothesis that adult pollock were attracted to and were feeding on macro-zooplankton patches. Even though zooplankton abundance explained less than 50% of the variation in pollock density that was observed, this type of spatial relationship can be difficult to quantify using simple correlation. Spatial associations between predators and their prey are notoriously weak, with correlation coefficients often less than 0.5 (Veit et al. 1993). Rose and Leggett (1990) suggest that positive correlations between predator and prey densities would occur at scales greater than the dimensions of the predator and prey aggregations. Predators, such as pollock, may be found close to their prey, but not right on top of them. For example, strong currents may concentrate zooplankton in some areas, but fish may avoid the strongest currents and feed on the edges of the aggregation. Indeed, we did find that the best correlation was when we pooled our acoustic data into bins larger than the mean patch sizes we observed. The relatively low correlation could also be due to other variables that we haven't examined yet; for example, behavior of fish and zooplankton due to tides, surface mixing, predator satiation, prey avoidance, and the abundance of alternate prey items, such as juvenile fish.

While the quasi-continuous nature of hydroacoustic data is extremely useful for studying spatial distributions, there are several potential sources of error with acoustic data. The small sample volume of the acoustic beam at short ranges, combined with the near-surface distribution and boat avoidance behavior of many fish may have underestimated densities. In addition, target strengths of fish are highly variable and depend on many factors (Traynor and Williamson 1983; Mukai and Iida 1996).

Partitioning acoustic data into different species is essential, but it only as reliable as the methods used to describe the species compostion of the fish assemblage. These potential errors all lead errors in estimates of fish abundance.

There are also problems with our use of acoustics to measure plankton abundance. A 120 kHz transducer was appropriate for measuring fish abundance, the primary objective of these surveys, but this frequency was too low to measure all zooplankton species due to scattering in the Rayleigh region. Errors in the estimation of plankton densities, lengths, and reflection coefficients will all effect the acoustic estimate of plankton biomass (Wiebe et al. 1997). Once again, the partitioning of acoustic data into different plankton species is only as accurate as the methods used to collect plankton. In addition, the coarse echo integration cell size (5 m deep and approximately 50 m long) were not conducive to finding, or describing the small scale patches of zooplankton.

Further research is needed to improve acoustic estimates of zooplankton and fish using different acoustic equipment and techniques. Digital transducers can provide a much finer spatial resolution than analog transducers. The high spatial resolution of digital acoustic data, which is already higher than analog equipment, is largely limited by current computer technology, and is improving a rapid rate. High spatial resolution of digital acoustic data allows for a finer scale analysis of zooplankton and fish patch sizes than with analog acoustic equipment. It also aids in removing unwanted targets before averaging to create the echo integration arrays, thus providing more accurate zooplankton and fish estimates. The use multiple acoustic frequencies further improves separation of fish targets from zooplankton targets. Using exclusively trawls and plankton nets to describe spatial distributions of fish and zooplankton in an area as large as Prince William Sound is futile due to limitations of time and money. By combining these tools with appropriately designed acoustic surveys, it is possible to obtain data with a higher spatial resolution, and covering a larger area, than with net sampling alone.

Understanding the mechanisms of juvenile fish mortality is critical in improving our ability to implement a multi-species management approach to protect the many important fisheries of PWS (Thomas et al. 1997). Understanding the spatial relationship between post-spawning walleye pollock and macro-zooplankton will lead to an increased knowledge of the roles of pollock in the trophic structure of PWS. It also demonstrates the importance of not relying solely on data from other locations (i.e. the Bering Sea) or during only a portion of the year (summer-winter) when attempting to describe the impact of a particular species in an ecosystem.

ACKNOWLEDGMENTS

This research described in this paper was supported by the *Exxon Valdez* Oil Spill Trustee Council for the Sound Ecosystem Assessment Project (Grant Nos. 96320-N and 97320-N). However, the findings and conclusions presented by the authors are their own and do not necessarily reflect the views or position of the Trustee Council. We would like to thank all the crews of the chartered vessels for helping us to collect the data: without their knowledge and experience, this research would not have been possible. The Alaska Department of Fish and Game and the University of Alaska-Fairbanks were responsible for the daunting task of processing the zooplankton and trawl data. A special thanks goes to Mark Willette (ADF&G) for sharing his data on pollock diet, to R. Ted Cooney (UAF) for the plankton data, and to Steven Brandt, Doran Mason, and two anonymous reviewers for their comments on an earlier draft of this manuscript.

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Figure Legends

Fig. 1. Map of Prince William Sound showing sampling locations of acoustic transects from April (dashed lines) and May (solid lines) 1995. Also shown are zooplankton tows (circles) and trawls (triangles) from April (empty symbols) and May (filled symbols) 1995. Note that a some points may not be not visible due to overlapping with other points.

Fig. 2. Zooplankton biomass from vertical net hauls in the top 50 m of Prince William Sound for April and May 1995. The number of hauls (N) is given for each cruise.

Fig. 3. Paper echograms from two acoustic transects during April 1995 showing: A) Plankton layer with varying depth and density, possibly due to localized turbulence, waves or currents; B) Plankton patch with pollock-sized targets associated with areas of high density.

Fig. 4. Target strength (TS) frequencies from acoustic data files (black bars) and estimated TS from walleye pollock captured in the mid-water trawl in Prince William Sound during April and May 1995. Estimated TS were calculated using 20Log (length) - 66 (Traynor and Williamson 1983). The arrows mark the range of TS values that were used to produce estimates of pollock density.

Fig. 5. Depth distribution of pollock-sized targets (± 1 S. D.) from acoustic data collected in Prince William Sound during April and May 1995.

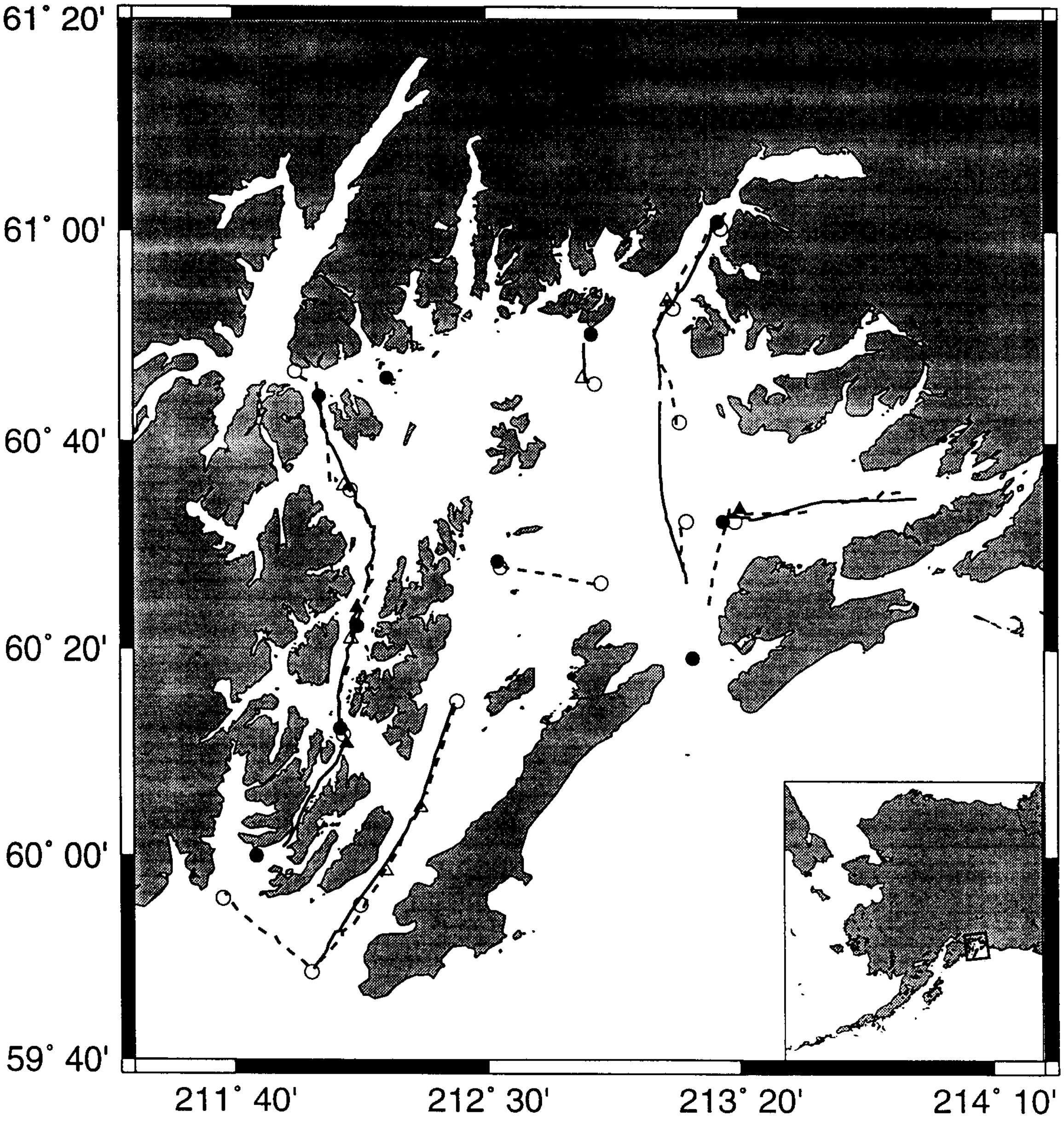
Fig. 6. Catch per unit effort of adult pollock from nine mid-water trawls performed in Prince William Sound in April and May 1995. There were no trawls between 73 and 122 m, or deeper than 138 m. Depth distribution of pollock-sized targets (± 1 S. D.) from acoustic data collected in Prince William Sound during April and May 1995.

Fig. 7. Adult pollock diet composition (percent by weight) in April and May 1995 in Prince William Sound. The sample size (N) is given for each cruise.

Fig. 8. Map of Prince William Sound showing acoustic estimates of pollock density ($\#/m^2$) from 0-50 m in April 1995. Solid circles represent the size and location of zooplankton patches identified from acoustic data. The squares represent the location of zooplankton patches that were too small (< 1,000 m) to be seen on the figure.

Fig. 9. Map of Prince William Sound showing acoustic estimates of pollock density ($\#/m^2$) from 0-50 m in May 1995. Solid circles represent the size and location of zooplankton patches identified from acoustic data. The squares represent the location of zooplankton patches that were too small (< 1,000 m) to be seen on the figure.

Fig. 10. Relationship between acoustic estimates of pollock density and macro-zooplankton abundance (0-50 m) in Prince William Sound. In April (circles and solid line), the best fit was found with pollock abundance from 0-50 m in cells approximately 6,500 m long (r^2=0.4, y=5e^{-08} + 0.0004). In May (squares and dashed line), the highest r^2 (r^2=0.31, y=4e-08 -7e^{-06}) was with pollock density from 0-100 in cells approximately 7,500 m long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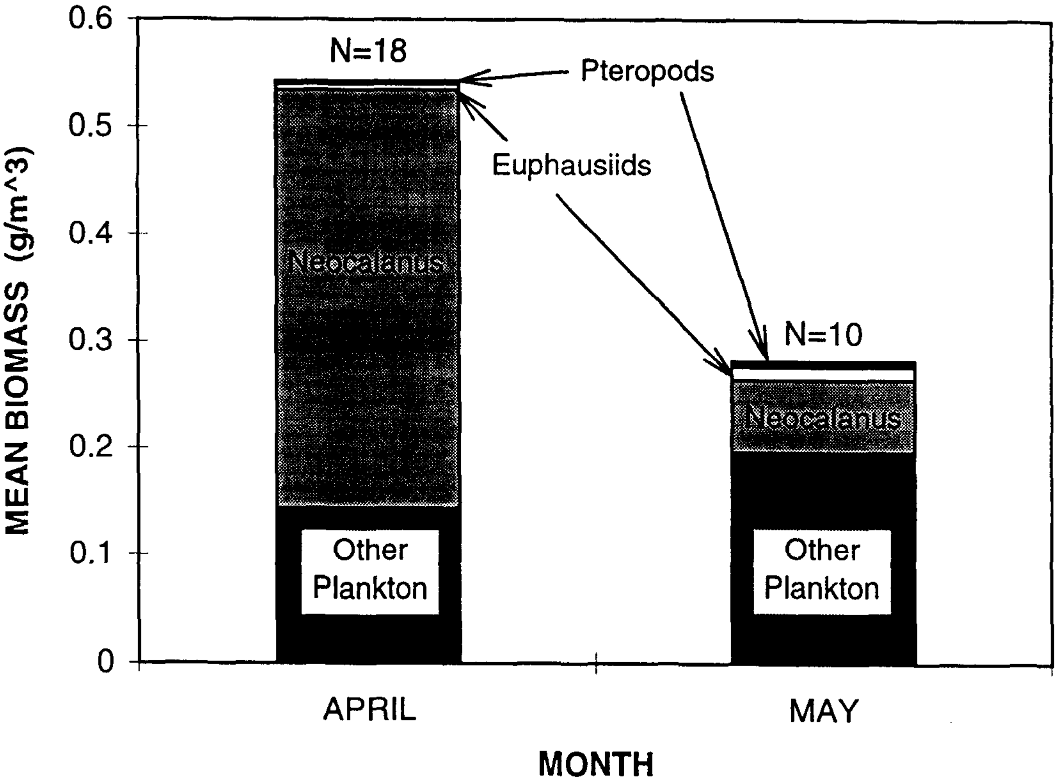
214° 10'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0.5
0.4
0.3
0.2
0.1
0
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N=10
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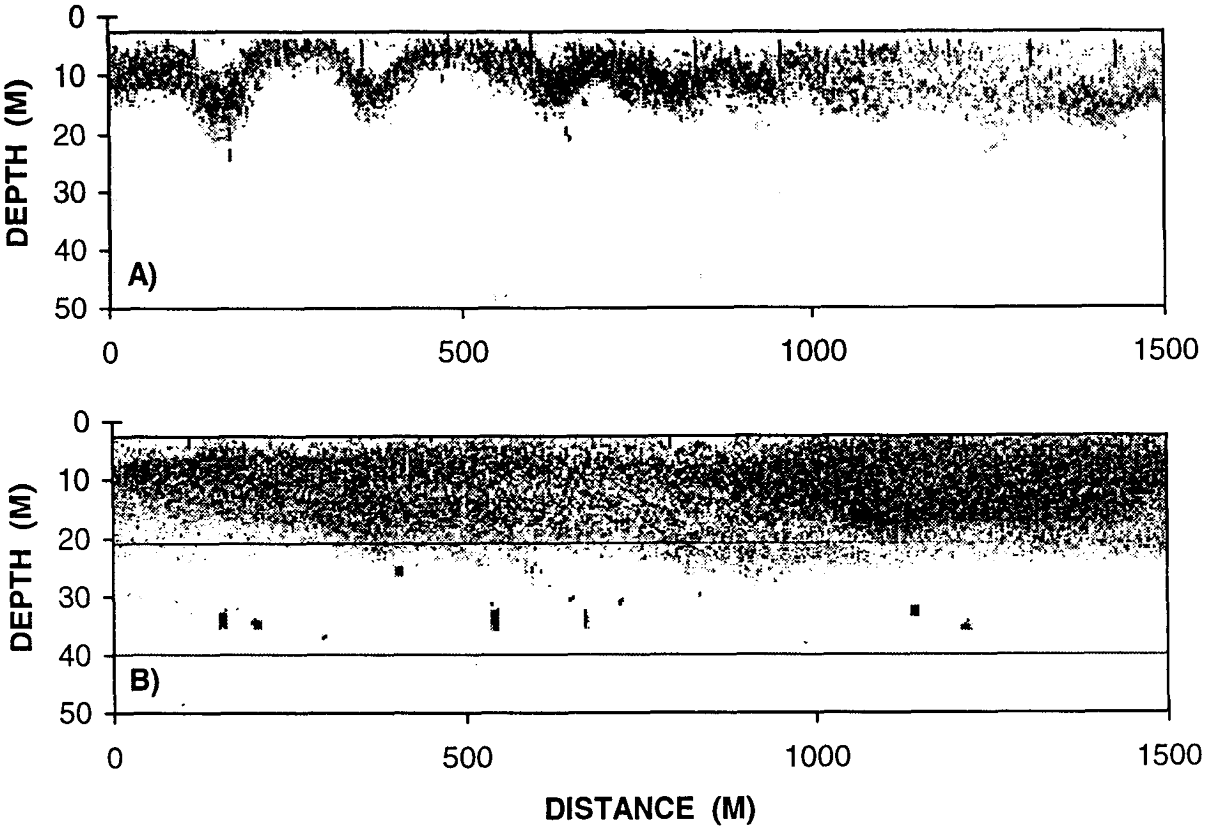
Euphausiids
Neocalanus
Neocalanus
Other Plankton
Other Plankton
APRIL
MAY
MONTH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10
20
30
40
50
DEPTH (M)
A)
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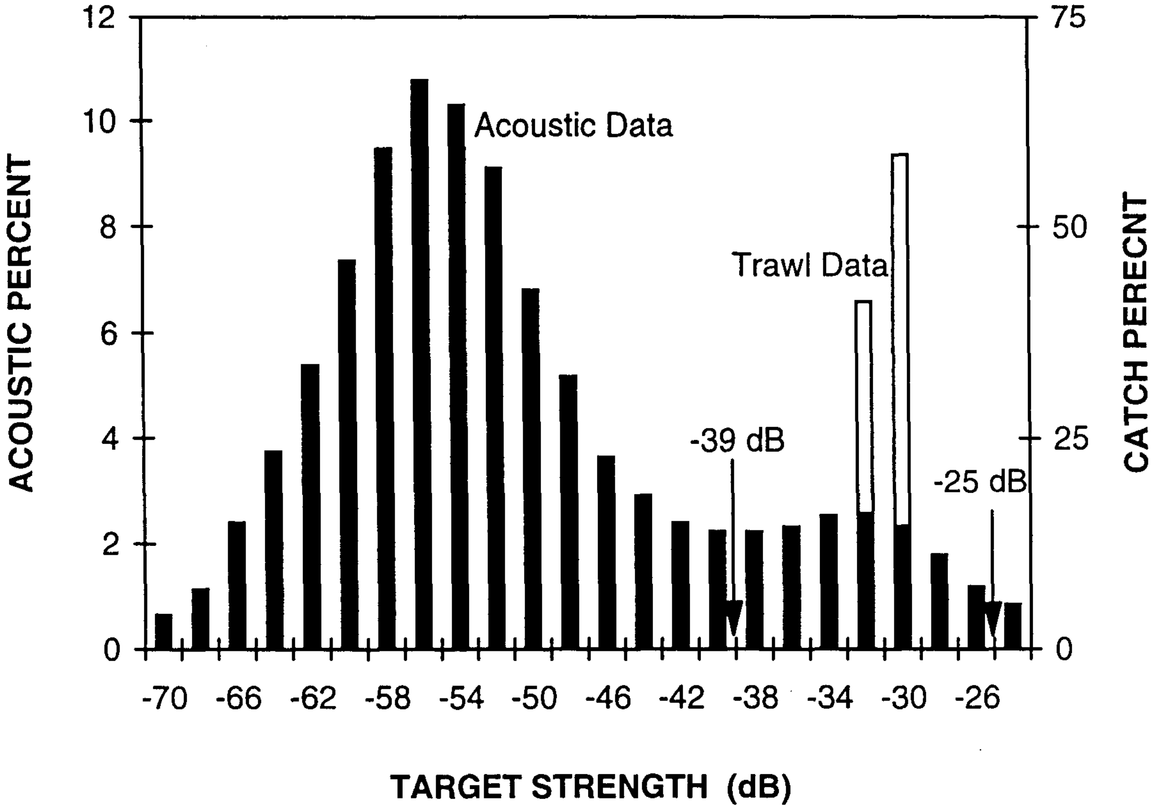
500
1000
1500
0
10
20
30
40
50
DEPTH (M)
B)
0
500
1000
1500
DISTANCE (M)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10
8
6
4
2
0
75
50
25
0
ACOUSTIC PERCENT
CATCH PERECNT
Acoustic Data
Trawl Data
-39 dB
-25 dB
-70
-66
-62
-58
-54
-50
-46
-42
-38
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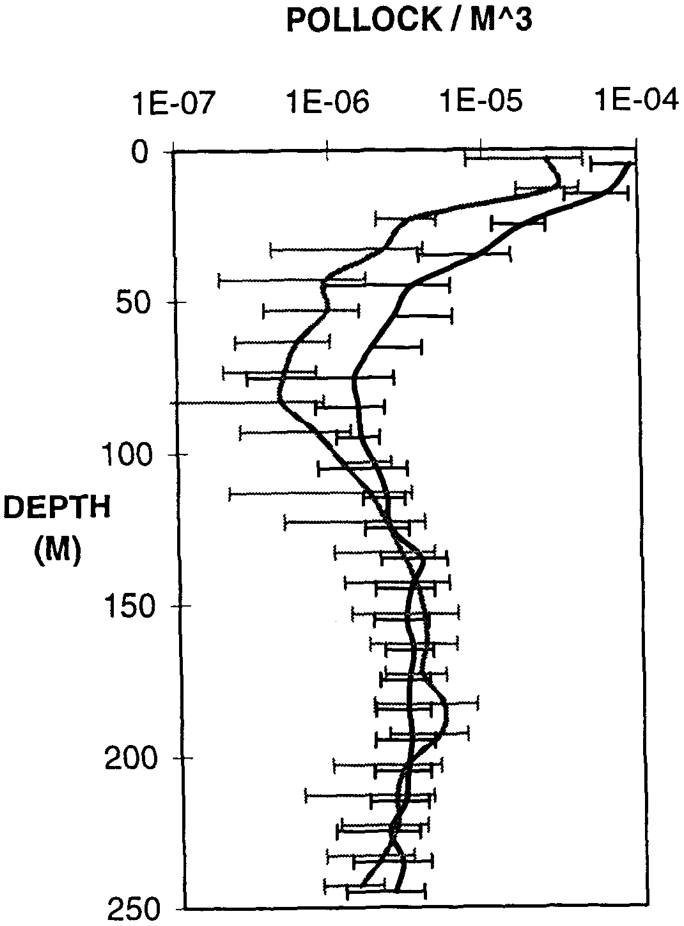
-30
-26
TARGET STRENGTH (dB)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1E-04
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50
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200
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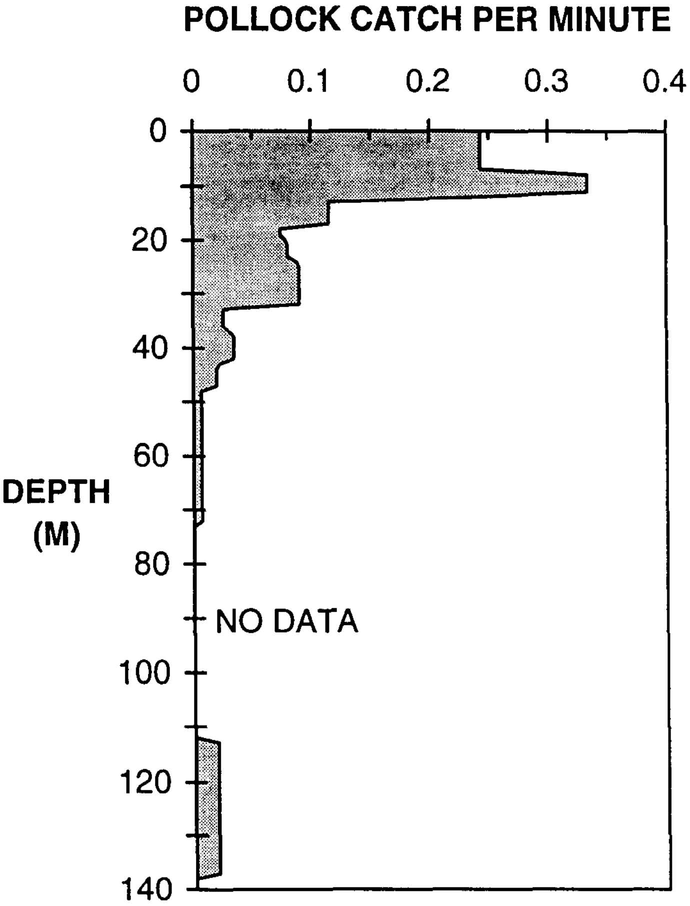
DEPTH
(M)


POLLOCK CATCH PER MINUTE
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0.4
DEPTH
(M)
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100
120
140
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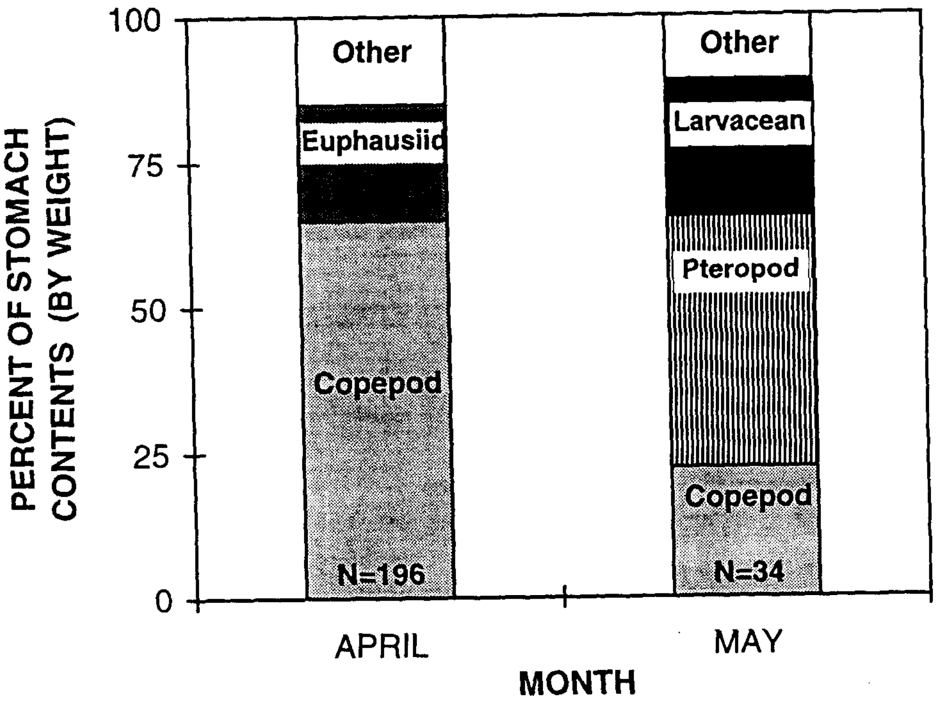
100
75
50
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Copepod
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Other
Larvacean
Pteropod
Copepod
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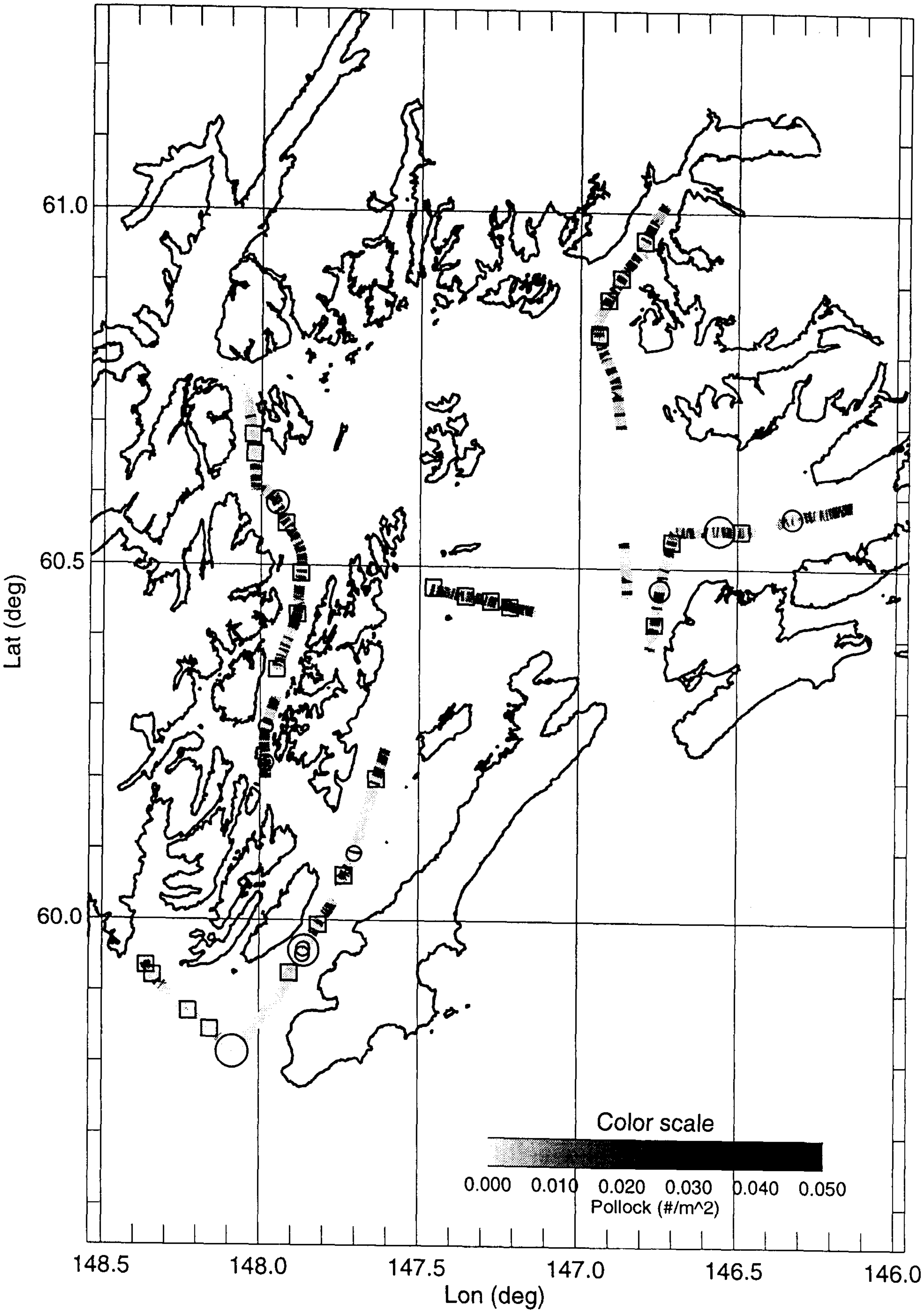
APRIL
MAY
MONTH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60.0
Lat (deg)
148.5
148.0
147.5
147.0
146.5
146.0
Lon (deg)
Color scale
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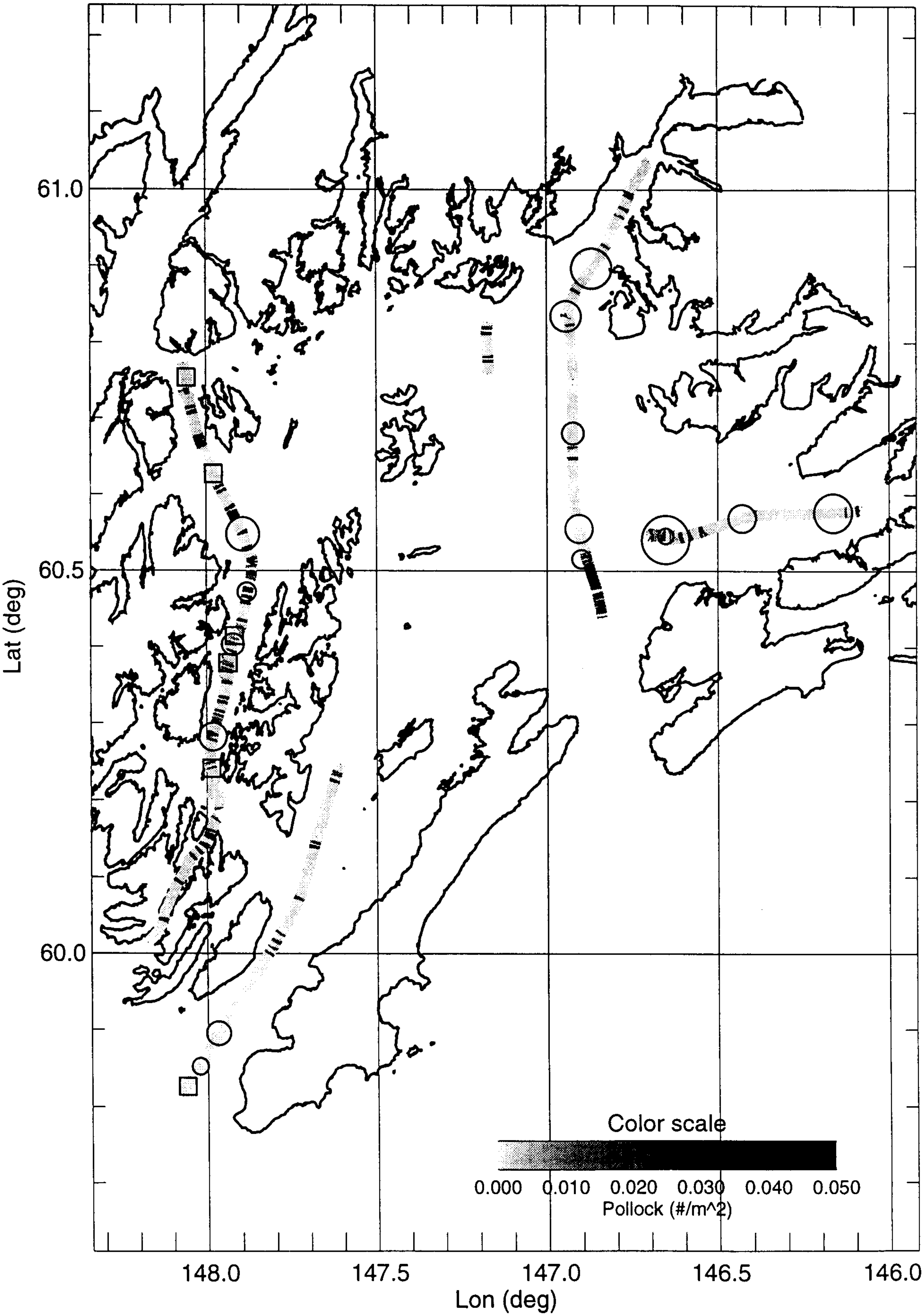
0.010
0.020
0.030
0.040
0.050
Pollock (#/m^2)



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Color scale
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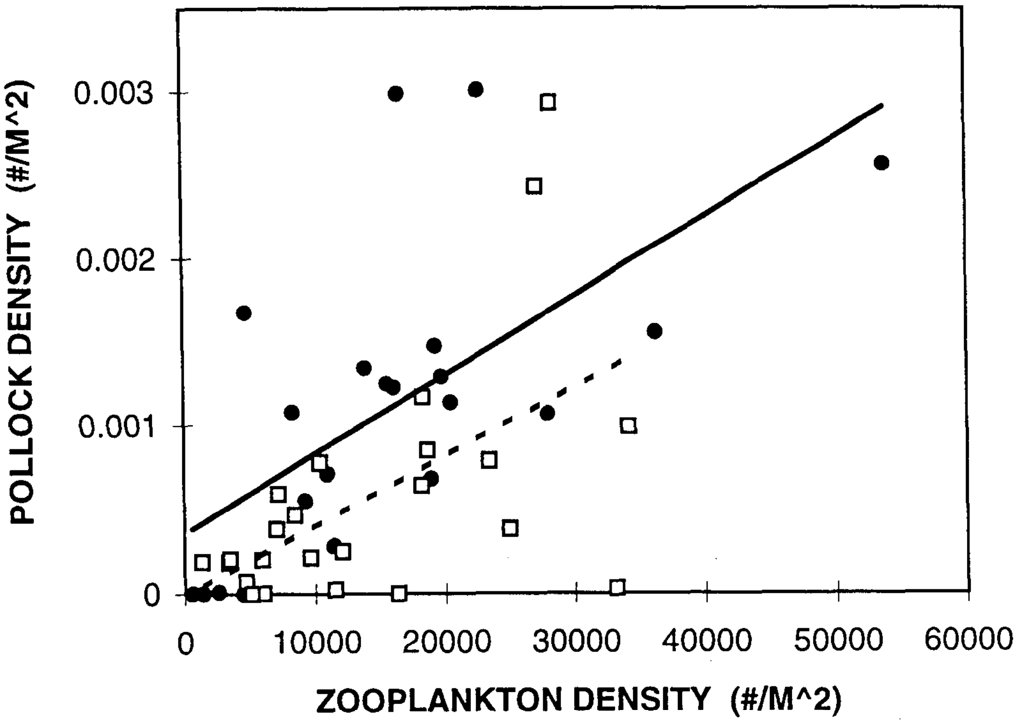
0.050
Pollock (#/m^2)


POLLOCK DENSITY (#/M^2)
0.003
0.002
0.001
0
0
10000
20000
30000
40000
50000
60000
ZOOPLANKTON DENSITY (#/M^2)

Mortality estimates of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska.

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Abbreviated title: Mortality estimates of juvenile Pacific herring

Keywords: juvenile Pacific herring, *Clupea pallasi*, density-dependent natural mortality,

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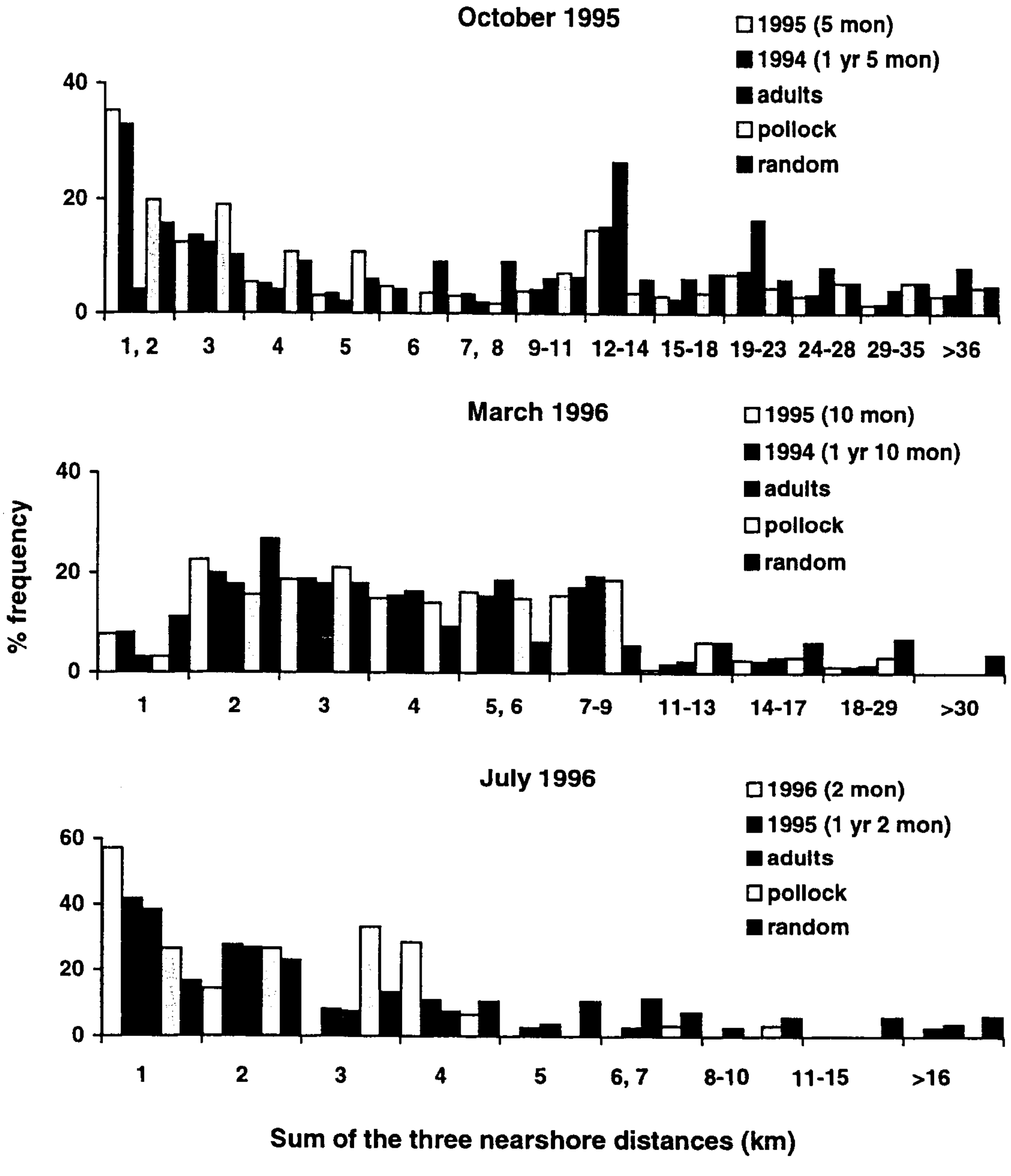

Fig. 6 Stokesbury et al.

Abstract

Pacific herring, *Clupea pallasi*, aggregations isolated within four bays in Prince William Sound, Alaska, were acoustically surveyed from June 1996 to March 1998. Life tables, estimating the amount of natural mortality occurring from metamorphosis until recruitment into the adult fishery, were compiled for the 1995, 1996 and 1997 Pacific herring cohorts within each bay. Severe mortality occurred between August and October in all four bays for young-of-the-year and 1-2 year old Pacific herring. Young-of-the-year Pacific herring were exposed to a second period of high morality between October and March. Intracohort-density-dependent mortality explained 51% of the variability in natural mortality. Intracohort-density-dependent mortality may result from food limitation during the winter, but probably not between August and October as food is abundant. Rather, intracohort-density-dependent mortality may result from shifts in foraging behavior as the risk of predation greatly increases the time juvenile herring forage outside, or on the extremity, of their schools. The slope of the linear equation comparing killing power to Pacific herring cohort density was 0.49 suggesting that although there is a reduction in individual output it is not enough to compensate for the increasing density, therefore the herring population of Prince William Sound is increasing.

Introduction

Pacific herring (*Clupea pallasi* Valenciennes, 1847) dominate the near-shore ichthyofauna of Prince William Sound, Alaska, providing primary forage for pisciovorous fishes, birds and marine mammals and supporting commercial bait, sac-roe, and roe on kelp fisheries (Meyers et al. 1994, Paine et al. 1996). In 1993, four years after the *Exxon Valdez* spilled 36,000 metric tons of North Slope crude oil into Prince William Sound, the Pacific herring population crashed and the fisheries were closed (Paine et al. 1996, Spies et al. 1996). The lack of local life history information combined with the highly variable characteristics of clupeoid populations confounded attempts to determine sources of mortality and the population's recovery time (Meyers et al. 1994, Paine et al. 1996).

Little is know of juvenile herring mortality and spatial distribution (Blaxter & Hunter 1982, McGurk 1993, Tanasichuk 1997). Clupeiod larval mortality rates have been estimated from laboratory and plankton samples (Robinson 1988, Wespestad & Moksness 1990, McGurk 1993, McGurk et al. 1993, McGurk & Brown 1996). Adult natural and fishery mortality rates have been estimated using fishery data and age structure analysis (Beverton 1963, Parmanne 1988, Tanasichuk et al. 1993). Generally, herring from several populations are believed to mix in nursery areas and segregate to different locations prior to spawning (Iles 1971, Hourston 1982, Iles & Sinclair 1982, Sinclair et al. 1985). However, in Prince William Sound each bay appears to be a unique nursery area where juvenile herring are isolated from other groups until their second summer of life (Stokesbury et al. 1999a, Stokesbury et al. 1999b).

We examined the changes in relative density and estimated natural mortality of Pacific herring within four bays in Prince William Sound, Alaska, from May 1996 to March 1998. We hypothesized that the densities and mortality rates of Pacific herring within each bay were unique. Further, we examined the effects of intraspecific density and temporal variability on instantaneous mortality rates to determine if density-dependent mortality occurs within these bays.

Methods

Prince William Sound, Alaska, contains a large body of water separated from the Gulf of Alaska by a series of mountainous islands (Fig. 1). The rocky coastline is irregular with numerous islands, passages, bays, and deep fjords. The Sound has a semi-diurnal tide with a maximum range of 4.4 m during this study.

Four bays, Simpson, Zaikof, Whale, and Eaglek were selected as study sites because they are spatially segregated and appeared to contain isolated aggregations of juvenile Pacific herring (Stokesbury et al. 1999a). These four bays were acoustically surveyed nine times between June 1996 and March 1998 (Fig. 1). During each seven-day cruise, each bay was surveyed three times over 24 hours beginning at 0000 h, 0800 h, and 1600 h.

The acoustic survey vessel (commercial fishing seiner, ≈17 m) followed a continuous parallel transect pattern; transect distances were Simpson Bay = 31200 m, Zaikof Bay = 35024 m, Whale Bay = 31164 m, and Eaglek Bay = 43750 m (Fig. 1). Care was taken to ensure that the same transect was sampled for each diel period during every survey. The acoustic vessel surveyed at 9 to 11 km h^{-1} with a 120 kHz BioSonics 101 echosounder using a preamplified dual-beam transducer towed ≈1 m below the water surface. The acoustic system was calibrated both with a hydrophone and a standard target. The acoustic signals were processed in real-time using the BioSonics ESP 221 echo square integration software and ESP 281 Dual beam software, and the raw signal was stored on digital audio tape (MacLennan & Simmonds 1992, Stokesbury et al. 1999b). Latitude and longitude were recorded simultaneously for each data cell from the GPS navigational system. Echo integration measurements were converted into data cells with 20 m lengths (16 pings per cell, 2 ping s^{-1}) and 1 m width and depth.

Once the acoustic vessel measured a fish school it was sampled to determine species composition and size structure. Fish were captured using a modified bottom trawl in deep water (1.52 x 2.13 m Nor'Eastern Astoria V trawl doors, head rope 21.3 m, foot rope 29.0 m, estimated 3 x 20.0 m mouth, 10.2 cm mesh wings, 8.9 cm middle and a 32.0 mm cod end liner deployed by the Alaska Department of Fish and Game R/V *Pandalus*, ≈20 m), one of two anchovy seines (250.0 x 34.0 m or 20.0 m, 25.0 mm stretch mesh deployed by a commercial fishing seiner, ≈17 m), or a small salmon fry seine in shallow water (50.0 x 8.0 m, 3.0 mm stretch mesh deployed from a 6 m skiff equipped with a 70 horsepower engine). The samples from each collection were speciated and 1000 herring, or the other dominant fish species, were randomly subsampled. Fork length (mm) was measured for all samples and wet weight (g) was recorded from 450 Pacific herring. Size modes of herring, representing young-of-the-year, 1 to 2 year old, or adult fish, were identified (Stokesbury et al. 1999a). Echo integration densities (kg m^{-3}) were converted into number of Pacific herring per size mode (fish m^{-3}). Based on frequency distributions, cells containing the equivalent of <0.5 fish m^{-3} were probably zooplankton and were removed from the data set (MacLennan & Simmonds 1992, Gunderson 1993). Piscivorous fish were dissected and their stomach contents were classified as herring, invertebrates and other fish, or empty.

A length dependent scaling constant was used to convert the reflected acoustic energy into a biomass estimate:

$$\text{TS re:w (dB re:kg)} = -6.0 \log x - 24.2 \text{ dB}$$

where x is the mean fork length (cm) of the fish collected in the area (Thorne 1977a, Thorne 1977b, Thorne 1983a, Thorne et al. 1983, Thorne & Thomas 1990). This equation differs from the more standard regression equation calculated by (Foote 1987) as it derives the target strength as a proportion of weight. Thorne's equation was developed for echo integration primarily using Pacific herring surveys from Alaska and Puget Sound (Thorne 1977b, Thorne et al. 1983). The inclusion of weight adjusts for the wide seasonal and spatial variation in weight-to-length relationship of Pacific herring observed in Prince William Sound (Stokesbury et al. 1999a). Acoustic estimates of Pacific herring densities depend upon the applied target strength equations. This is a limitation of acoustical data as many physical and biological variables affect target strength including depth, temperature, fish orientation, morphology of the fish, fat content, gonad development, and inter and intraschool behavior (Thorne 1983b, Foote 1987, Thorne & Thomas 1990, Misund 1993, Misund & Floen 1993, Misund et al. 1995, Huse & Ona 1996, McClatchie et al. 1996). Our estimates of density are relative and we assume their fluctuations reflect those of the absolute densities of Pacific herring within each bay.

Acoustic transect replicates were completed in two bays. Density estimates from these replicate tranects were compared using a chi-squared test at the 5% level of significance (Sokal & Rohlf 1981). Vertical positions of Pacific herring schools within each bay were examined by comparing their mean depth on a diel scale. When variances were heterogeneous data were transformed using log (x +1) before applying statistical tests. One-way ANOVA's were used to compare differences in means and correlations (Sokal & Rohlf 1981, Winer et al. 1991).

Life tables are a reliable method of determining age-specific mortality and are frequently used when it is possible to follow a group of individuals through time (Begon & Mortimer 1982, Krebs 1989). Prince William Sound Pacific herring spawn in early April. Juvenile age cohorts are easily identified by length frequencies as herring complete about 75% of their somatic growth before first maturity (Cushing 1967, Iles 1971, Winters & Wheeler 1994). Further, Pacific herring appear to remain isolated in bays during their juvenile phase (Stokesbury et al. 1999a, Stokesbury et al. 1999b). These characteristics allowed us to compile life tables.

Life tables estimating the amount of natural mortality occurring between metamorphosis and recruitment into the adult fishery were compiled for the 1995, 1996 and 1997 Pacific herring cohorts within the four bays from June 1996 to March 1998. The number of fish observed (a_x) during one transect survey were compared to the subsequent observation (a_{x+1}) along the same transect during the same diel time period from the next cruise, weeks to months later. If the number of fish within an age cohort observed along a transect was <30 the observation was deleted (Krebs 1989). The "killing -power" ($\log_{10}a_x$-$\log_{10}a_{x+1}$) ranges from 0 to 3 (0 = no mortality, 3 = high mortality) and reflects the rate of mortality between observations (Begon & Mortimer 1982).

Results

Pacific herring migrated to the surface during darkness (Table 1). The range of mean depths varied seasonally but the majority of herring were distributed in the top 20 m during the 0000 h transect for all surveys (Table 1). The 0000 h transects provided the clearest measures of Pacific herring density along all transects. The precision of our acoustical density estimates was moderate. Comparisons of observed herring densities along transects repeated one to four days apart, within the same survey, provided similar fish counts of the dominant age cohorts (Table 2).

Twenty-nine species of fish were collected in association with Pacific herring schools. Sixteen species were piscivorous and 11 preyed on Pacific herring. Walleye pollock (*Theragra chalcogramma*) was the primary predator and 94 of the 294 feeding pollock were preying upon Pacific herring. Thirty-one of the 38 and six of the 23, feeding Pacific cod (*Gadus macrocephalus*) and salmon, respectively, were preying on Pacific herring.

Juvenile Pacific herring endured two periods of high natural mortality. Severe mortality occurred between August and October in all four bays for young-of-the-year and 1-2 year old herring (Fig. 2). During this period densities were often reduced by several orders of magnitude. Juvenile Pacific herring were exposed to a second period of high mortality between October and March (Fig. 2).

Intracohort-density-dependent mortality explained 51% of the variability in natural mortality as the killing power of each Pacific herring size cohort was significantly correlated with the preceding density of that cohort (ANOVA, df = 18, F = 17.39, $r^2 = 0.51$, $p<0.001$; Fig. 3). The slope of the linear equation comparing killing power to Pacific herring cohort density was 0.49 indicating that natural mortality was less than recruitment and therefore density was increasing (Fig. 3). The killing power of each Pacific herring size cohort was not significantly correlated to the total density of herring within each bay (ANOVA, df = 18, F = 3.54, $r^2 = 0.17$ $p = 0.08$; Fig. 3).

Within bays a significant correlation between killing power and cohort density was only found for Simpson Bay (ANOVA, df = 7, F = 9.65, $r^2 = 0.62$, $p = 0.021$). The coefficient of determination (r^2) was high in Whale Bay but the correlation was not significant, possibly due to the low degrees of freedom (ANOVA, df = 4, F = 5.06, $r^2 = 0.63$, p=0.11). Eaglek and Zaikof Bays had no relationship between killing power and density although the degrees of freedom were also low.

The young-of-the-year cohort dominated Pacific herring assemblages within each bay. The killing power values of young-of-the-year herring were significantly correlated to the preceding young-of-the-year density measure (ANOVA, df = 13, F = 8.24, $r^2 = 0.41$, p=0.014; Fig. 4).

Discussion

High natural mortality occurred directly after the young-of-the-year metamorphosed from larvae in late July until the beginning of oceanic winter in late October. This is a period of high somatic growth and food limitation seems unlikely (Stokesbury et al. 1999a). Predation is probably the primary source of natural mortality. Both marine mammals and birds are actively feeding their young as well as increasing their own energy supplies in preparation for migrations (Livingston 1993). In early August the largest influx of predators is the returning wild and hatchery salmon numbering 8,374,327 wild, 20,410,280 hatchery and 4,596,623 wild, 23,702,628 hatchery for 1996 and 1997, respectively (Morstad et al. 1997). Although Pacific herring composed only a small proportion of the salmon stomach contents in May and June they may be more frequently preyed upon from August to October (M. Willette, pers. comm. ADF&G, Cordova, AK). For example, Pacific herring represented ≈26% of feeding salmon and gadids collected with herring schools. Newly recruited young-of-the-year Pacific herring are small, abundant, and aggregated in bays (Stokesbury et al. 1999b). The salmon spawning streams are also located primarily in bays. These Pacific herring would be the last prey the salmon encounter before entering the spawning streams. Interestingly at this time of year the primary tackle used by sport fishers to catch salmon is a silver spoon, which mimics young herring (W. Barber per. comm. University of Alaska – Fairbanks). Simpson and Whale have large wild salmon runs while Eaglek has both a strong wild salmon and hatchery salmon run (M. Willette, pers. Comm. ADF&G Cordova AK).

Pacific herring natural mortality was also high during their first winter from October to March. This natural mortality appeared to result from starvation and predation. Young-of-the-year Pacific herring must store a critical amount of energy during the summer or they will starve during the winter (Paul & Paul 1998, Paul et al. 1998, Foy & Paul in press). The smaller fish within the cohort have the least amount of surplus energy and their survival rate is probably low (Paul & Paul 1998, Paul et al. 1998). Growth data collected from each of these bays supported Paul's conclusions but mortality of larger Pacific herring resulting in negative incremental growth, also occurred (Stokesbury et al. 1999a). Pacific herring may be highly vulnerable to predators during the winter. Hunger suppresses the herring's antipredator behavior resulting in loosely packed schools of mixed size classes (Robinson & Pitcher 1989a, Robinson & Pitcher 1989b, Pitcher & Parrish 1993, Robinson 1995, Stokesbury et al. 1999b). Residential and returning migrational predators increase feeding at the end of oceanographic winter and may select the largest young-of-the-year Pacific herring as they have the highest energy content (Paul & Paul 1998, Paul et al. 1998). Predation varies weight-at-age in other herring stocks by as much as 20% (Sparholt & Jensen 1992).

Separating the Pacific herring population into its trimodal size distribution and examining each mode independently identified intracohort-density-dependent mortality. Shifts in relative

Pacific herring densities along transects could result from immigration and emigration or variations in spatial distribution with each bay. However, dominant size class densities were consistently measured over repeated transects and changes over time on an order of magnitude were readily identified.

Density dependent food limitation may affect growth in herring populations (Iles 1968, Iles 1971, Winters & Wheeler 1994, Tanasichuk 1997). However, studies demonstrating density dependent natural mortality are rare and researchers have concluded that clupeiod stocks tend not to have strong density dependent regulatory mechanisms (Cushing 1967, Blaxter & Hunter 1982).

Intracohort-density-dependent mortality may result from food limitation particularly during the winter, but probably not between August and October when food is abundant (Foy & Norcross in press). Rather, intracohort-density-dependent mortality may result from shifts in foraging time (Walters & Juanes 1993). Herring schools have a strong local effect on their environment as they occupy a small portion of the habitat intensely (Blaxter & Hunter 1982). The risk of predation greatly increases with the amount of time juvenile herring are required to forage outside or on the extremity of the schools, their spatial-behavioral refuge from predators. Therefore, mortality can be density dependent without exhibiting signs of competition such as changes in growth rate due to food limitation (Walters & Juanes 1993). This would explain the intra-cohort-specific natural mortality we observed between August and October as Pacific herring formed dense schools of a single cohort while growth rates appeared to be high in all bays.

The natural mortality sustained by juvenile herring in Prince William Sound was intracohort-density-dependent. The slope of the linear equation comparing killing power to Pacific herring cohort density was 0.49 suggesting that although there is a reduction in individual output it is not enough to compensate for the increasing density (Begon & Mortimer 1982), therefore the Pacific herring population of Prince William Sound is increasing.

Acknowledgments

We thank R. Foy, M. McEwen, N. Peters and G.B. Steinhart, S. Moreland and M. Vallerino for assistance in collecting and processing the data. We also thank the captains and crews of the F/V *Temptation*, F/V *Miss Kayley*, F/V *Kyle David*, M/V *Pacific Star*, F/V *Pagan*, F/V *Cape Elrington*, R/V *Pandalus* and the Alaska Department of Fish and Game, Cordova, for their help. This project was funded by the *Exxon Valdez* Oil Spill Trustee Council through the Sound Ecosystem Assessment (SEA) project to the University of Alaska, Fairbanks, and the Prince William Sound Science Center. However the findings presented by the authors are their own conclusions and not necessarily the Trustee Council position.

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Table 1. *Clupea pallasi*. Mean depths and standard deviations (SD) and ANOVA comparisons of Pacific herring cohorts observed in the four bays acoustically surveyed in Prince William Sound Alaska.

Depth (m)	0000 h		0800 h		1600 h				
Simpson Bay	mean	SD	mean	SD	mean	SD	df=	F =	p=
YOY	13.2	2.01	22.7	2.0	21.4	1.93	2	10.40	<0.001
1-2 year old	14.5	2.04	23.7	2.0	21.6	2.17	2	7.28	<0.001
Adults	17.3	4.36	22.7	3.1	22.7	3.47	2	0.08	0.920
Zaikof Bay									
YOY	18.7	1.92	26.8	2.6	28.8	2.11	2	9.91	<0.001
1-2 year old	14.8	1.39	24.0	1.9	26.1	1.89	2	0.09	0.910
Adults	13.4	1.63	28.8	2.2	29.9	2.26	2	32.7	<0.001
Whale Bay									
YOY	24.4	2.34	24.1	3.1	27.6	2.85	2	0.32	0.730
1-2 year old	20.7	3.04	34.0	3.9	33.3	3.41	2	4.11	0.019
Adults	13.9	8.04	41.7	10.0	44.7	8.65	2	3.9	0.033
Eaglek Bay									
YOY	17.7	3.61	41.0	4.8	32.4	5.88	2	6.18	0.003
1-2 year old	30.2	3.59	48.8	4.3	43.1	5.19	2	6.29	0.002
Adults	30.0	4.45	51.8	5.1	46.2	7.09	2	6.14	0.003

Table 2. *Clupea pallasi*. Repeated measures of the number of Pacific herring observed within each year cohort along a continuous acoustic survey within two bays in Prince William Sound, Alaska; * p <0.01. Comparisons are between each observation for each age cohort, Yate's correction was applied due to the low number of degrees of freedom.

Zaikof Bay; 0800 h	5 Oct. 96		9 Oct. 96		
cohort	observed	%	observed	%	χ^2
1994	21	20	15	79	34.85*
1995	55	94	3	6	78.01*
1996	48	46	56	54	0.51
Simpson Bay; 0000 h	13 Aug. 97		14 Aug. 97		
1995	96	49	98	51	0.00
1996	114	28	297	72	18.96*
1997	9253	53	8286	47	0.20

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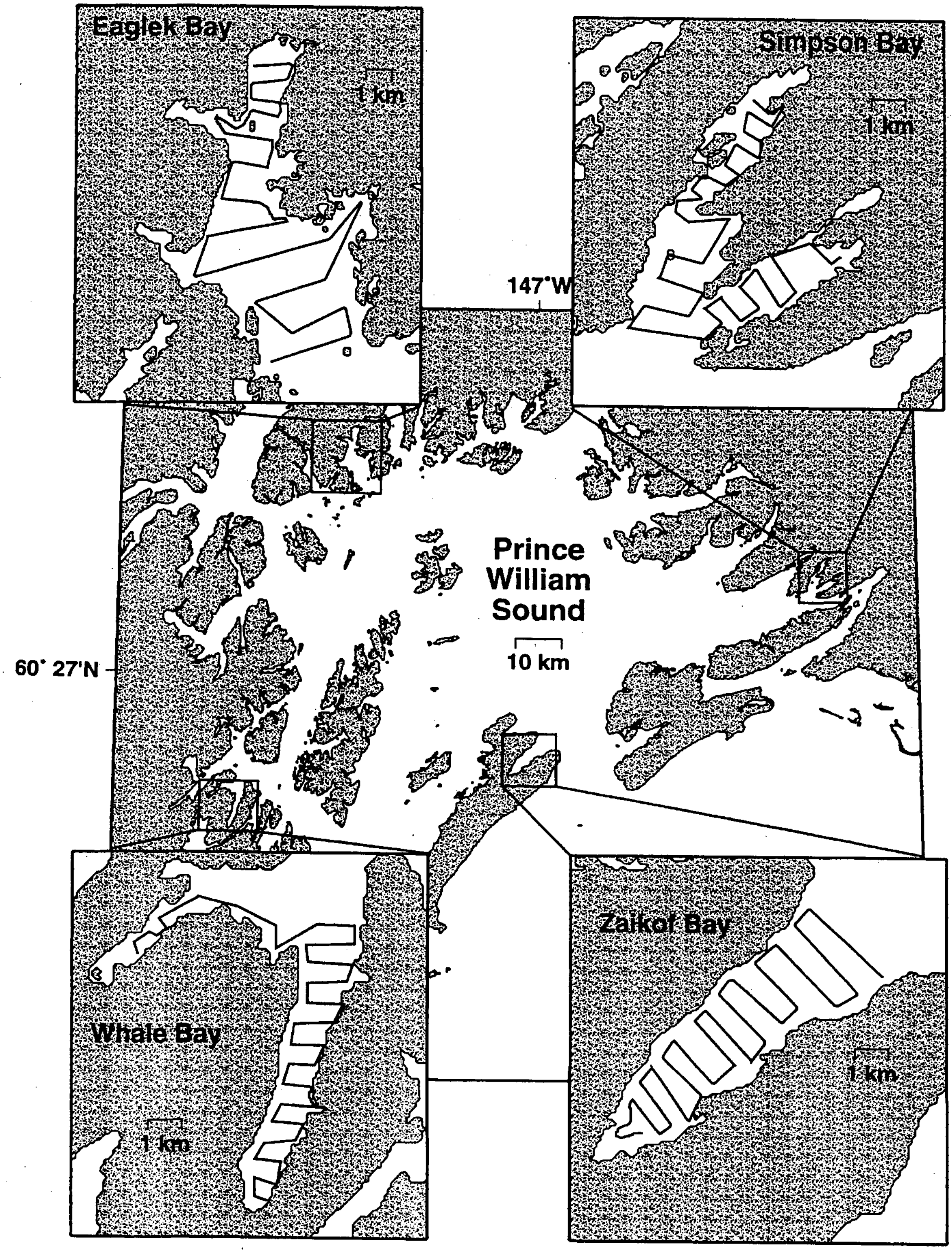
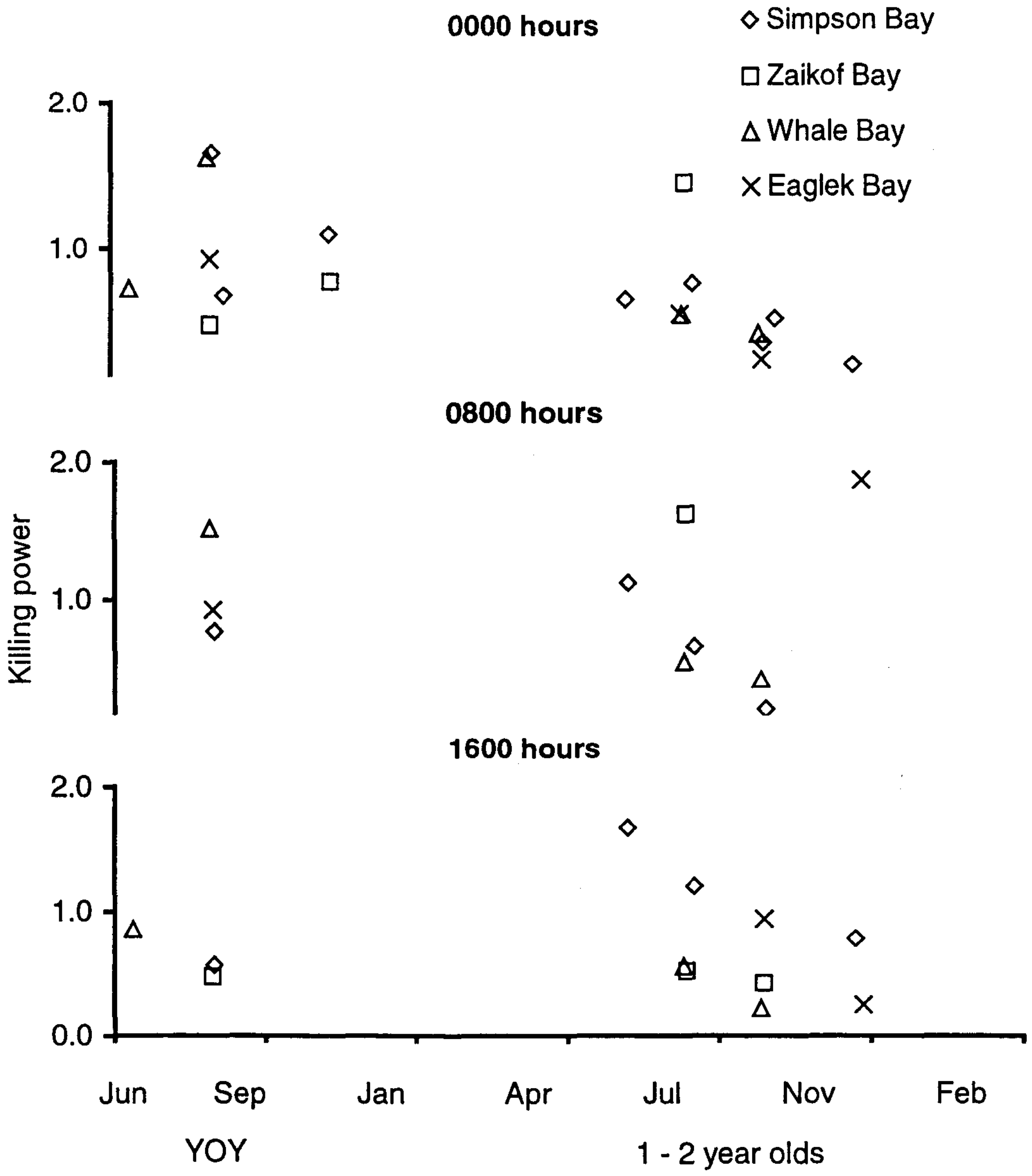


Figure 1. Stokesbury, et al



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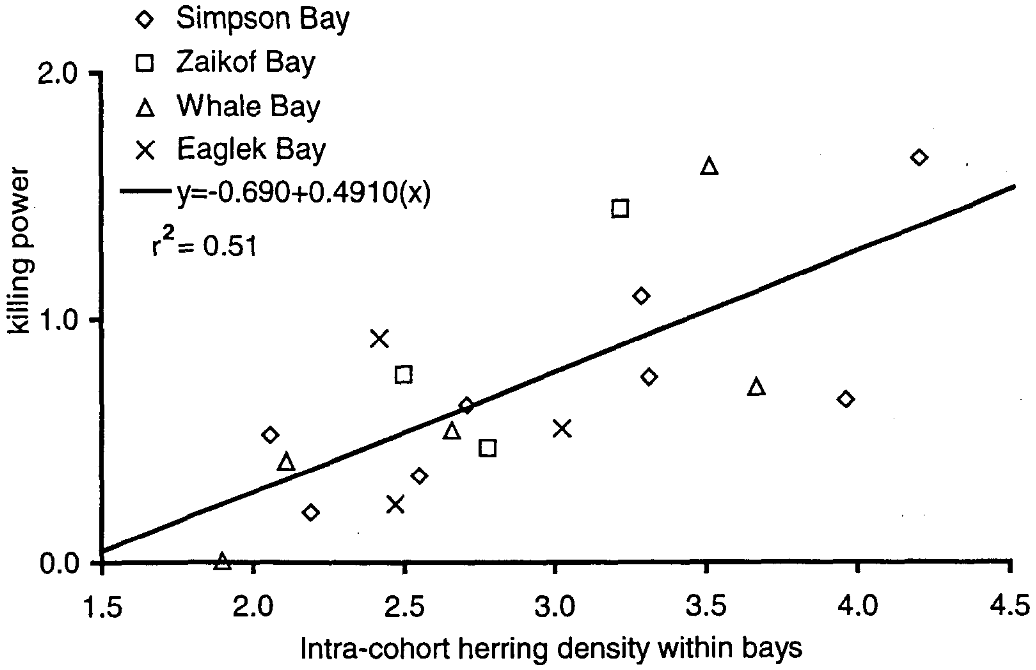

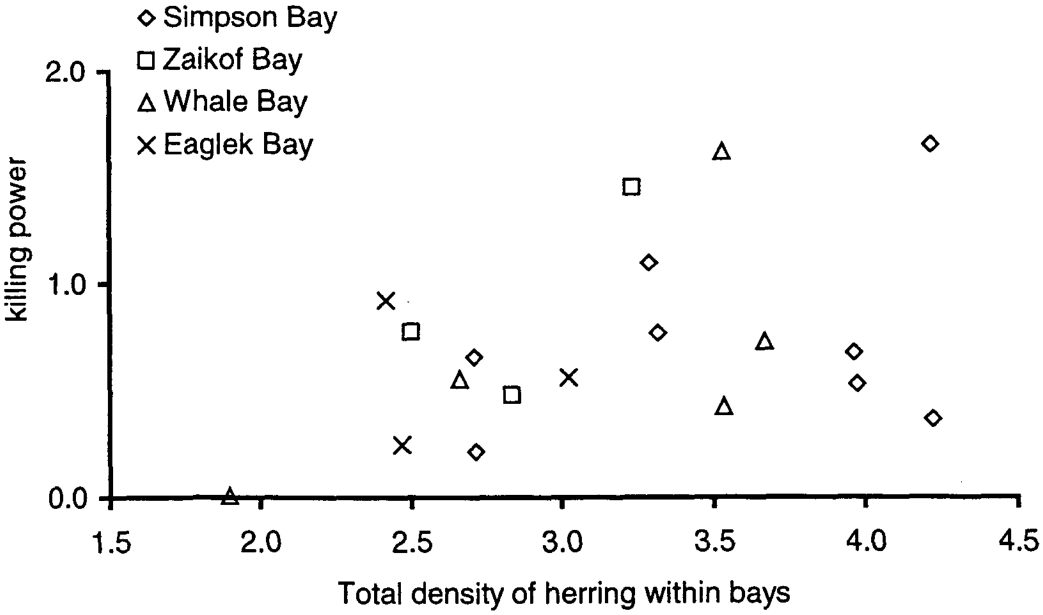

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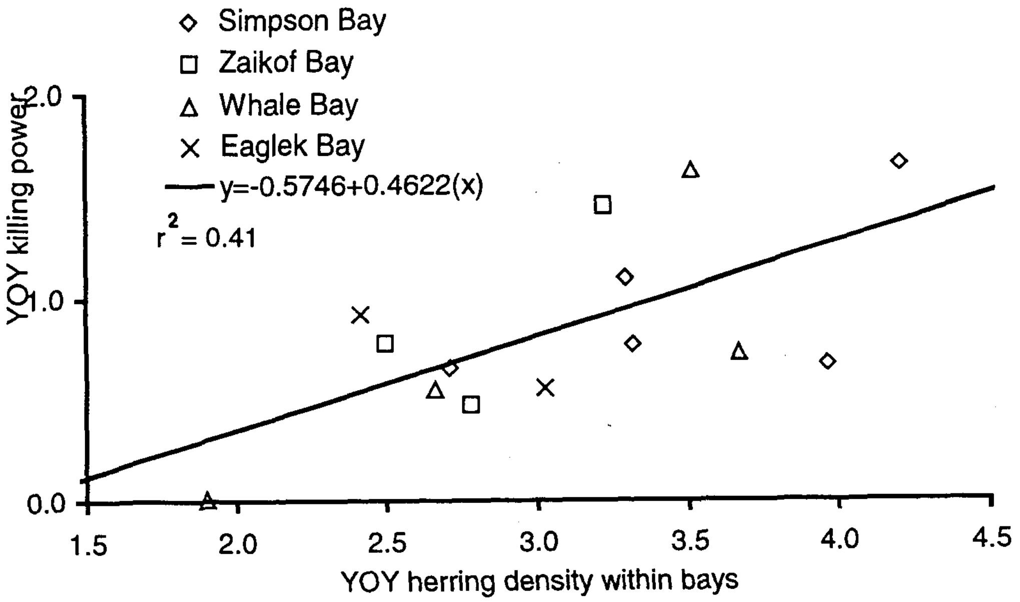

Figure 4. Stokesbury, et al

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1999

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The ecological role of walleye pollock *Theragra chalcogramma* in the trophic structure of Prince William Sound, 1993-1998.

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June 24, 1999

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Abstract

A stock of walleye pollock *Theragra chalcogramma* has been observed to overwinter and feed in Prince William Sound. This stock was composed of three age-related length groups: large-mature fish, the adults (>400 mm, age 4+), small-immature fish, the juveniles (<120mm, age 0) and intermediate sized fish, subadults, (120-400 mm ages 1 to 3). In the winter, the adult walleye pollock were found in highly aggregated groups that were easily accessible to measurement. Echointegration-midwater trawl surveys estimated the abundance of adult walleye pollock to be about 37,000 mt in 1995, 38,000 mt in 1997 and 114,000 mt in 1998. The only other pelagic fish observed to overwinter in the Sound at a comparable abundance was the Pacific herring *Clupea harengus*. This finding indicates the marine food web of the Sound is similar to many other boreal and subboreal systems in that it has a "waist" and that the Sound's food web-waist is composed of two competing planktivores, walleye pollock and Pacific herring. In recent years, this food web-waist has been dominated by walleye pollock but our observations suggest that a few years of high herring recruitment could cause a shift the dominance of the food web-waist. Traditional knowledge and records suggest that herring have dominated the food web waist in the past.

We postulate a feeding mechanism to explain the shifting dominance of the food web-waist. Unlike the juvenile or subadults, after spawning the adult walleye pollock to move to the surface (0-50m) and into the Sound in spring to feed on macrozooplankton, primarily large calanoid copepods *(Neocalanus* spps). We hypothesize that the ability of the adult walleye pollock to feed on *Neocalanus* copepods depends upon high prey density in the form of patches or layers. When patches or layers of *Neocalanus* copepods are available in the spring, the walleye pollock can capture the bulk of the food or energy from lower trophic levels and dominate the food web-waist of the Sound. Furthermore, we suggest that in windy years when surface turbulence is high, the resulting decrease in prey patches reduce the walleye pollock's ability to feed successfully on *Neocalanus* copepods. Conversely, the herring's higher efficiency at raptorial feeding should favor it during windy climate regimes. Since walleye pollock and Pacific herring populations represent the food web-waist in the Sound, they store the bulk of the carbon or potential energy in the Sound's food web. Unless the dynamics of these two taxa are known and considered explicitly, models of the fate of lower level trophic production and the diversity and production of the piscivore assemblage will not represent dominant ecosystem processes.

Introduction

Walleye pollock *Theragra chalcogramma* is well known as a valuable commercial fish, an important forage fish and a dominant marine predator (Dwyer et al. 1987; Livingston 1993; Lloyd and Davis 1988; Springer 1992). The importance of the commercial fishery for walleye pollock is highlighted by the six million ton catch in 1985 worth over $1 billion in ex-vessel income, which made it the world's largest single-species fishery (Anonymous 1996). Surprisingly, this economic importance it is overshadowed by the pollock's ecological importance. Livingston et al. (1997) concluded the number of species in the Bering Sea offshore pelagic fish consumer guild was effectively one due to the super-dominance of walleye pollock.

Traditional understanding of marine food webs suggests they are complex and it is rare when one prey or predator dominates (Russel-Hunter 1970). This is clearly not the case in boreal seas where it is common for food webs to have "waists" where a single or a few taxon in a middle trophic position passes most of the food or energy from lower trophic levels to higher level predators (Rice 1992). Walleye pollock in the Bering Sea are a classic example of a single taxon dominating the food web-waist (Springer et al. 1984, 1987; Livingston 1997). Until recently, models of food webs have not considered cases where one or a few taxon capture the bulk of the lower trophic level production and dispense this energy to the levels above them (Rice 1995). Runge (1988) and Pimm (1991) have both shown that where this occurs that ecologists must first describe how the predators will respond in to changes in the species at the waist before investigating the peripheral structure. Inversely, one is also limited to describe how lower production affects changes in the species at the waist. The dynamics of food webs with waists are so dependent on the one or more species at the waist that the structure elsewhere will have little influence (Runge 1988; Pimm 1991; Rice 1995).

Eastern North Pacific Ocean

Walleye pollock populations throughout the Gulf of Alaska and Bering Sea have been studied since the 1950s (Traynor 1986; Dwyer et al. 1987; Bailey and Dunn 1979; Brodeur and Wilson 1996). Bottom trawl surveys that were initiated in the mid 1960s to assess red king crab *Paralithodes camschatica* were expanded in the 1970s to include demersal fish (Bakkala and Alton 1986). Since pollock was a major component of the trawl catch of demersal fish, these surveys became a major assessment tool. In 1979, the first acoustic-midwater trawl survey was conducted in conjunction with the bottom trawl assessment (Karp and Traynor 1988; Traynor et al. 1990). Subsequently, acoustic surveys were conducted in conjunction with the triennial bottom trawl assessments.

The majority of our knowledge about the walleye pollock's life history characteristics is pieced together from these stock assessment surveys, which were conducted in different areas and primarily in the summer months when surface conditions are most favorable (Karp and Traynor 1988; Radchenko and Sobolevskiy 1993). The pooling of this data has not been considered a major problem since few distinct stocks have been identified in Alaskan waters (Grant and Utter 1980). However in other areas such as British Columbia, many distinct stocks have been identified (Saunders et al. 1988), so there is a need for more information in Alaskan waters to reduce potential confounding due to the pooling of mixed stocks.

Prince William Sound

The 1991 triennial trawl survey assessed the pollock biomass in Prince William Sound at 9,000 mt (Anonymous 1997). This number was used with data from the Gulf to set a harvest quota of 1.5 mt in 1995 (Megrey 1988). However, studies initiated in Prince William Sound after the 1989 Exxon Valdez oil spill (EVOS) revealed a large pelagic population of walleye pollock (Thomas et al. 1997). These findings prompted further studies of walleye pollock with the objective of estimating their distribution and abundance and assess their role as dominant predators that could be influencing the recovery of pink salmon, Pacific herring and other injured species from oil spill damage (Wolfe et al. 1993).

This paper reviews observations of walleye pollock distribution and abundance made by acoustic-midwater trawl surveys conducted from 1994 to 1998 with respect to role walleye pollock play in the trophic structure of Prince William Sound.

Methods

Prince William Sound is a large fjord/estuary that covers an area of approximately 8800-km^2 and has about 3200 km of shoreline along the northern edge of the Gulf of Alaska (Grant and Higgins 1910). Coastal rainforests, high mountains and glaciers border the shoreline of PWS (Thomas et al. 1991). The Sound is exposed to seasonally intense storms moving in from the Gulf of Alaska, resulting in 5-7 m of annual rainfall.

Between 1993 and 1999, we conducted a series of acoustic-midwater trawl-purse seine surveys to determine the distribution and abundance of nekton predators and their influence on the survival of pink salmon fry. These surveys consisted of three spring-summer series (1994-1996) along the outmigration route of pink salmon fry and a series of fall-spring surveys to determine the overwinter abundance and distribution of prespawning walleye pollock (1995, 1997 and 1998) and Pacific herring (1993-1999).

Acoustic sampling

Acoustic data were collected using BioSonics 38 and 120 kHz echosounders with dual-beam transducers. The transducers were mounted on a towfins and towed alongside the boat at a depth of 2 m and at an approximate speed of 3 m/s. The acoustic systems were calibrated before each cruise using a tungsten-carbide ball of known target strength, suspended within the beam of the transducer (Foote and MacLennan 1982; 38 kHz: sl=215.76, pw=0.001, b^2=0.00219, rgn20=-156.474; 120 kHz: sl=225.075, pw=0.001, b^2=0.00107175, rgn20=-159.282). The data was processed in real-time on a laptop computer. Date were geo-referenced and time-coded with a GPS receiver. Echointegration, dual-beam target strength (TS) and GPS data were stored on the computer hard disk and backed up on a tape drive. Raw acoustic signals were stored on digital audiotape and printed on paper echograms.

Post-cruise processing consisted of transferring all PC data to UNIX workstations for data processing and analysis. Software written in IDL was used to apply acoustic calibrations and correct for absorption, remove untracked bottom, identify targets of interest, remove false targets, calculate biomass estimates and produce 2d images of fish distributions. AVS software was used to create 3d visualizations of fish distribution. Echointegration was used on all surveys due to the schooling behavior of the pollock. The target strength of walleye pollock was calculated as -20 Log L-66 (Traynor and Ehrenberg 1979) and then applied to the echointegration arrays to determine density.

Echo counting of pollock-sized targets was used to process spring surveys because the fish were found as single targets in the top 50 meters of the water column. We used a threshold to separate the walleye pollock targets from dense layers of plankton that were present near the surface. The echo-counting technique involved defining the range of possible target strengths that corresponded to an adult pollock. Targets between

–39 dB and –28 dB were counted as pollock using echo-counting software, which were then divided by the sample volume of the acoustic beam and averaged to yield densities in fish/cubic meter.

Multiple targets in the acoustic beam can affect the reliability of any echo-counting technique (Foote 1996). Multiple targets may either overlap just enough to cause the target discriminator to fail to recognize any of the multiple targets or they may sum their individual returns to yield artificially high single target strength. A comparison between the target discrimator and manual counts of pollock sized targets showed that auto counting underestimated the number of targets by 13-28%. We conducted a similar comparison between echo counting and echo-integration showed that echo counting resulted in an underestimate of pollock density by 18-33%. Given the near-surface distribution of the pollock, we also believe that boat avoidance added to underestimation of the absolute densities during the spring surveys. Thus, we consider the echo counts of walleye pollock at the surface in the spring as relative density and conduct only appropriate analyses with these data.

Net sampling

Mid-water trawls and purse seine sets were made during the hydroacoustic surveys to provide target verification and biological information. The trawl measured 40 m x 28 m and was equipped with a net sounder. The cod end of the trawl was lined with a 1.5 cm stretch mesh to retain small specimens. The depth and location of the trawling was directed to the depth of fish targets to verify acoustic targets. The length of trawl hauls was approximately 30 min at depth. Fish from the catch were identified, weighed, measured and had their stomachs removed and preserved in a 10% buffered formaldehyde solution for later diet analysis (Willette et al. 1999). A modified commercial anchovy purse seine was used to sample fish targets in the nearshore areas.

Vertical zooplankton tows were collected using a 0.5-m ring net with 333 um mesh. The net was towed vertically through the top 50 m at several locations on each survey (Cooney et al. 1999). The samples were preserved in a formalin solution. In the lab, the zooplankton were enumerated, measured and identified to species. The mean length of each species was used to calculate the mean weight and then multiplied by the number of individuals in the sample to yield biomass estimates.

Results and Discussion

In the winter of 1995, 1997 and 1998, echo integration-trawl surveys were conducted in PWS to determine the distribution and abundance of adult pollock after commercial fishery operations so there was prior knowledge of the areas where the adult pollock were concentrated. In the fall of 1995 to spring of 1996, reconnaissance surveys of PWS verified that there were no additional concentrations of pollock residing in the Sound and that the only other species of comparable biomass was the adult Pacific herring (Figure 1). The depth distribution of the prespawning pollock in PWS areas has ranged from 150-200 m over the study period (Figure 2). The length of the adult pollock caught on these surveys ranged from 23-69 cm (Figure 3 a,b,c). We estimated the biomass to be approximately 38,000 mt in 1995, 37,000 mt in 1997 and 114,000 mt in 1998.

In contrast to the adult pollock biomass, the adult herring biomass was low. The Pacific herring stock collapsed in 1993 after an outbreak of viral hemoragic septicemia (Kocan et al.1999; Marty and Meyers 1999). We estimated the biomass at 20,000 mt in the fall of 1993 and 13,000 mt in the fall of 1994. In 1995 and 1996, we observed recruitment and a resulting increase in the biomass of herring from 23,000 mt to 38,000 mt. After commercial fisheries in 1997 and 1998, the stock biomass was observed to decline to 17,000 and 18,000 mt, respectively. In the three years with comparable estimates the ratio of adult pollock to adult herring ranged from 1:1 to 6.33:1 (37/23 in 1995, 38/38 in 1997 and 114/18 in 1998). Between 1993-1999, walleye pollock and herring were the only two species that were observed to form overwintering schools of with biomass greater than 1000 mt.

These results show that the pelagic food web in Prince William Sound has a "waist" (Rice 1995) and that two species, walleye pollock and Pacific herring share the food web-waist. In contrast, the food web-waist of the Bering Sea is occupied by solely walleye pollock (Springer et al. 1984, 1987; Livingston 1997). However, it is important to note that if the summertime, offshore sampling design used in the Bering Sea (Traynor et al. 1990) were applied to Prince William Sound, like the Bering Sea, the walleye pollock would be the sole taxon in the food web-waist. In the 1950-1970s, there were major commercial and reduction fisheries (for food, oil and fishmeal) for Pacific herring in from Prince William Sound to the Bering Sea (ADF&G). This suggests that the Pacific herring and other fat-rich forage fishes (capelin and sandlance) may have been the dominant taxon of the food web-waist prior to the 1970s. Presumably after a climate shift, a groundfish-dominant trophic structure developed that persists to this day, which caused a massive reorganization of the higher predators (Anderson et al. 1999).

The recruitment of Pacific herring between 1994 and 1996, the recent (1980-1993) records of herring in Prince William Sound (Anonymous 1999) and the historical records (1900-1999) of the herring fisheries in the Eastern North Pacific suggest that the Pacific herring may compete with walleye pollock for the dominant taxon position of the food web-waist. If so, the mechanism for this competition and how climate forcing might influence it is of critical importance to explain shifts in trophic efficiency and higher trophic level predator production.

Postspawning, spring feeding migrations

In April after spawning, the distribution of adult walleye pollock in the Sound is highly dynamic (Figures 4 a,b,c,d). During this period the adult pollock were found at the surface as single fish and often mixed in with the zooplankton layer (Figures 5,6,7,8). Net sampling showed that the zooplankton layer was dominated by *Neocalanus* copepods in the early spring (Figure 9, 10), which was the primary prey of the adult walleye pollock (Figure 11). This feeding behavior was observed in the Bering Sea where the timing is lagged by about a month (Yoshida 1994). In the Sound, the vertical distribution of the walleye pollock changes rapidly in the spring suggesting the adult pollock track *Neocalanus* copepods through their spring ontogenetic migration (Figure 12).

In the spring, the adult pollock switched to pteropods and other macrozooplankton when the *Neocalanus* began leaving the surface on the reverse of their annual ontogenetic migration to the surface (Cooney 1987). Willette et al. (this issue) shows that when these macrozooplankton prey become less unavailable that the pollock switch juvenile fish. Walleye pollock are well known for cannibalism (Brodeur and Wilson 1996) and it is likely that the bulk of the juvenile fish consumed by the adult pollock are their young.

Paul et al. (1993) showed that over 30% of the total energy consumed in the year by yellowfin sole were derived from the spring zooplankton feeding. Given that a benthic predator, such as yellowfin sole, can derive such a large portion of its annual caloric intake from a near-surface pelagic prey resource indicates the relative ecological importance of spring feeding on macrozooplankton. The pelagic planktivores, such as walleye pollock and Pacific herring, may receive even more of their annual caloric intake from *Neocalanus* copepods in the spring. In the early spring, the adult pollock are emaciated after spawning so initial feeding success is important to growth and survival. The spring zooplankton bloom is probably the first large food supply available for this purpose. Corroborating the importance of this behavior is that the highest growth rate of the season is observed during the period when adult pollock are feeding on *Neocalanus* copepods (Figure 13). Since food web-waist taxon are classified by their ability to capture the bulk of the lower trophic level production (Rice 1995), and *Neocalanus* copepods represent a major pathway for capturing lower-trophic level production, we consider this spring feeding behavior the adult walleye pollock as a mechanism to explain competition between pollock and herring to dominate the food-web-waist.

Climate affects on filter feeding by adult pollock

Willette et al. (this issue) found the number of copepods in the adult walleye pollock stomachs range up to 1200. This number of prey of such small size suggests the pollock are filter feeding. Anatomical studies have shown that adult walleye pollock have a fine gillrakers that would be efficient for filter feeding (Matsubara 1943; Okada 1955; Wilimovsky et al. 1967). Wright et al. (1982) suggests the importance of fine gill rakers that allow a fish to filter feed increases a fish's competitive advantage and ultimately its fitness. Despite that direct observations of walleye pollock filter feeding have not been made, given the size of *Neocalanus*, the numbers consumed and the gill raker structure, filter feeding is a plausible feeding mechanism.

Whether filter feeding or not, there is a positive correlation between *Neocalanus* dominated patches of macrozooplankton and the density of adult walleye pollock (Figures 14, 15 and 16). The vertical distribution of the walleye pollock in the spring suggests that they track their primary prey, *Neocalanus* copepods (Figure 12). Due to the disparity in size between the adult pollock and their *Neocalanus* prey, we hypothesize that the formation of high density patches or layers of copepods is important to the adult walleye pollock's ability to exploit the spring zooplankton bloom. Leong (1970) demonstrated that a prey density threshold existed where northern anchovy *Engraulis mordax* switched from raptorial to filter feeding.

Davis et al. (1997) simulated the effects of physical turbulence on zooplankton patches showing patch dissipation and reduced growth in planktivores. Knowing the importance of *Neocalanus* feeding to pollock growth and the pollock must be sensitive to prey density for feeding success, we hypothesize that physical turbulence could be a major mechanism causing interannual and decadal variability in the feeding success of walleye pollock. With zooplankton patches dependent on low turbulence conditions and the adult walleye pollock dependent on the patches to successfully feed on zooplankton, we refer to this mechanism as the patch-dependence and response hypothesis.

Many investigators have referred to climate regime shifts based upon water temperature changes (Royer et al 1993; Muter et al.1995; Bailey et al. 1995). Thomas and Mathisen (1993) and Hollowed et al. (1998) and many others have shown positive correlations between temperature and fish production without proposing a direct mechanism. Bailey et al. 1995 concluded that warming conditions result in lower survival and production of Pacific herring and higher survival and production of walleye pollock. Bulatov (1988) shows that strong year classes of eastern Bering Sea pollock appear in warm, calm years. However, this only reflects the production of one year class of the pollock population and such trends are not supported in the western Bering Sea or Gulf of Alaska (Muter et al. 1995). The walleye pollock population is a complex assemblage of several age classes that are cannibalistic on each other at specific life history stages so inconsistency in the results from single cohort analysis is not surprising.

In contrast to temperature as the key physical condition driving this change in species, the patch-dependence and response hypothesis depends upon a turbulence-based mechanism. Turbulence is driven by the same Aleutian low, cyclonic storms that lower and raise the water temperatures in the Eastern North Pacific. Thus, we hypothesize that windy years create the turbulence that breaks up zooplankton prey patches, which results in failures of the adult pollock foraging. Likewise, relatively calm conditions allow walleye pollock to potentially double their annual intake of energy from the food web. If this patch-dependence and response hypothesis is supportable, it provides us with a plausible mechanism that links climate forcing with the walleye pollock dominance of the food-web-waist. Alternately, it also provides explanation for herring and possibly other fat-rich fishes, which are smaller and more efficient raptorial feeders (Stephens and Krebs 1986; Crowder 1985) to dominate the food web-waist.

In the Southern California blight, a dominance cycle exists between the two primary pelagic species, northern anchovy and sardine (Baumgartner et al. 1992). The northern anchovy is filter feeder as an adult, which is similar to the role that we hypothesize for the adult pollock. The California sardine has a similar feeding behavior to the Pacific herring being more of raptorial feeder than a filter feeder. Thus, in both regions we have competition between two dominant pelagic fishes where one is primarily a raptorial feeder and one that is specialized to filter feed. Unfortunately, without the deep anoxic basin in the North Pacific, that provided Baumgartner et al. (1992) the historical record of the Southern California sardine-anchovy cycle, we cannot test for a long-term dominance cycle between Pacific herring and walleye pollock.

Implications to the food web

Pinniped and seabird populations in the north Pacific are in decline (National Research Council 1996; Livingston et al. 1999). Species in decline are piscivorus (e.g. Steller sea lions, fur and harbor seals, murres and kittiwakes). Declines were first detected in western Alaska during the 1970s and were later detected elsewhere (Alaska Sea Grant College Program 1993).

Correlations between many independent observations strongly suggest food limitation as the reason for these declines but to date the underlying mechanisms have not been verified. Competition with commercial fisheries has been suggested as a mechanism, in part because the declines coincide with major growth in the fishing industry in the region (National Research Council 1996). Confounding this hypothesis is growing support for a "regime shift" hypothesis, which explains major changes in marine animal production on the basis of climate change (Livingston et al. 1999). Other possible causes, such as direct mortality related to fisheries, increased predation, disease, human take, disturbance at rookeries, or mortality from pollution are not similarly implicated.

Restrictions to fisheries, especially in the vicinity of Steller sea lion rookeries, have been suggested and in some case imposed (National Marine Fisheries Service 1999) on the assumption that fisheries depletion of pollock and other forage fish stocks has contributed to the declines. We refer to this idea as the "pollock-limited" hypothesis because of the inference that access to more pollock would reduce nutritional stress (this idea is also referred to as the depletion hypothesis). A competing hypothesis argues that marine regime shifts, possibly fueled by climate change, have resulted in an increase in pollock stocks at the expense of fat-rich fish (herring, sand lance, capelin). We refer to this as the "herring-limited" hypothesis. This idea incorporates another that is known as the "junk-food hypothesis" because it holds that the available diet of pollock is insufficiently energy-rich to support population growth in these species (Alaska Sea Grant College Program 1993, Roby et al. 1999). We have just added differential handling costs of pollock versus herring to the energy content idea.

The mechanism of food limitation differs between the herring-limited and pollock-limited hypotheses. Pollock may have been depleted or their distribution so disrupted by commercial fisheries that marine birds and mammals are starving for the lack availability of this food (pollock-limited hypothesis). Alternatively, piscivores are feeding on an abundance of pollock in the absence of adequate herring, but pollock is much more costly to catch when compared to herring and is nutritionally inadequate during at least one life stage critical for population growth (herring-limited hypothesis).

When escaping predators, small groups of herring, sand lance *Ammodytes hexapterus* and capelin *Mallotus villosus* have been observed to break away from larger, schools deep in the water column, flee to the surface and form high density, near-surface schools, commonly referred to by fishermen as bait-balls (Thorne and Thomas 1988). It is our hypothesis that pollock do not behave in this manner, but instead may flee downward and disperse when attacked by predators. We suggest that foraging costs on pollock and herring differ due to these species-specific schooling and predator-avoidance behaviors, as well as to the different fat content of the fish. Under the pollock-limited hypothesis, the effects of reduction and dispersal of pollock schools by commercial fishing may be cumulative and reduce pollock availability as food. Under the herring-limited hypothesis, declines in herring may force sea lions to forage on pollock, a prey that is inadequate by virtue of both its low energy concentration and the high energy expenditure required to feed on deep and dispersed schools.

When herring (and other fat-rich fish) aggregate at the surface, they fall prey not only to deep diving predators but also to other predators that cannot dive deep. Thus, just due to the escape behavior these energy-rich prey are available to support the production of a much wider diversity of marine animals. This surface-aggregating escape behavior of herring (and sand lance) may reduce the cost of capture for predators and increase the difference in net energy intake between a diet of pollock and a diet of herring. The predation event that disturbs deep schools of herring and causes the formation of near-surface bait-balls is currently unknown but could include a wide range of individual or combinations of predators, or even specific physical conditions as the catalyst (Thorne and Thomas 1988). Possible catalysts may include or deep-foraging predators such as humpback whales, sharks, or diving birds (Chilton & Sealy 1987) that disturb deep schools and chase fish toward the surface and the occurrence of such events appears correlated with tidal current velocities at specific locations (Thorne and Thomas 1990). Such a catalyst has been suggested as a mechanism for increased foraging efficiency in mixed-species flocks of seabirds (Hoffman et al. 1981, Chilton & Sealy 1987). Predators that modify prey behavior in a manner that makes the prey more accessible to other predators are referred to as "facilitating predators" (Hoffman et al. 1981, Kotler et al. 1992). Thus the energy gains available to predators on herring schools may depend on the presence of one or more co-occurring facilitating predators and these events may be tightly linked to physical conditions such as tide and bathymetry.

We hypothesize that a herring-rich system supports higher diversity and biomass of birds and mammals than are possible in a pollock-rich system, due to both differences in energy content and escape behavior of the fish. By linking this herring-limited hypothesis with the findings of this research that explain why pollock and sometimes herring dominate the pelagic fish guild to become the "waist taxon" of the pelagic food web (Rice 1995; Livingston et al. 1997; Thomas et al. 1999), we hope to develop better understand how climate change affects the makeup affects the diversity and productivity of higher trophic level predators, the seabirds and mammals, in the North Pacific. Thomas et al. (1999) refers to this as the middle-out hypothesis, where a couple of super-dominant, multi-year class, planktivores (pollock and herring) capture the bulk of the one and two-year carbon (*Neocalanus* is a two-year animal) being produced in Prince William Sound, while the ratio of planktivore abundance determines the energy available to different suites of higher trophic level predators, the seabirds and mammals.

Finally, as Runge (1988), Pimm (1991) and Rice (1995) contend, these results imply that studies of higher trophic level predators such as Steller sea lions, harbor seals, common murres and other declining, damaged or endangered species in Prince William Sound, the Gulf of Alaska and probably the eastern North Pacific Ocean must be based upon knowledge of the dynamics of walleye pollock and Pacific herring stock dynamics to determine changes due to climate and anthropogenic impacts such as commercial harvesting, oil spills, hatchery practices, etc.

Acknowledgements

We would like to thank all those who have helped us in the Sound Ecosystem Assessment Program, Cordova District Fishermen United, Alaska Department of Fish and Game and the National Marine Fisheries Service. We thank the EVOS Trustee Council for financial support but we have been instructed to state that the opinions stated herein are not those of the Council. Special thanks go to the residents, Alaska Natives, fishermen and public of Cordova and Prince William Sound who made the Sound Ecosystem Assessment Program possible through their grass roots support.

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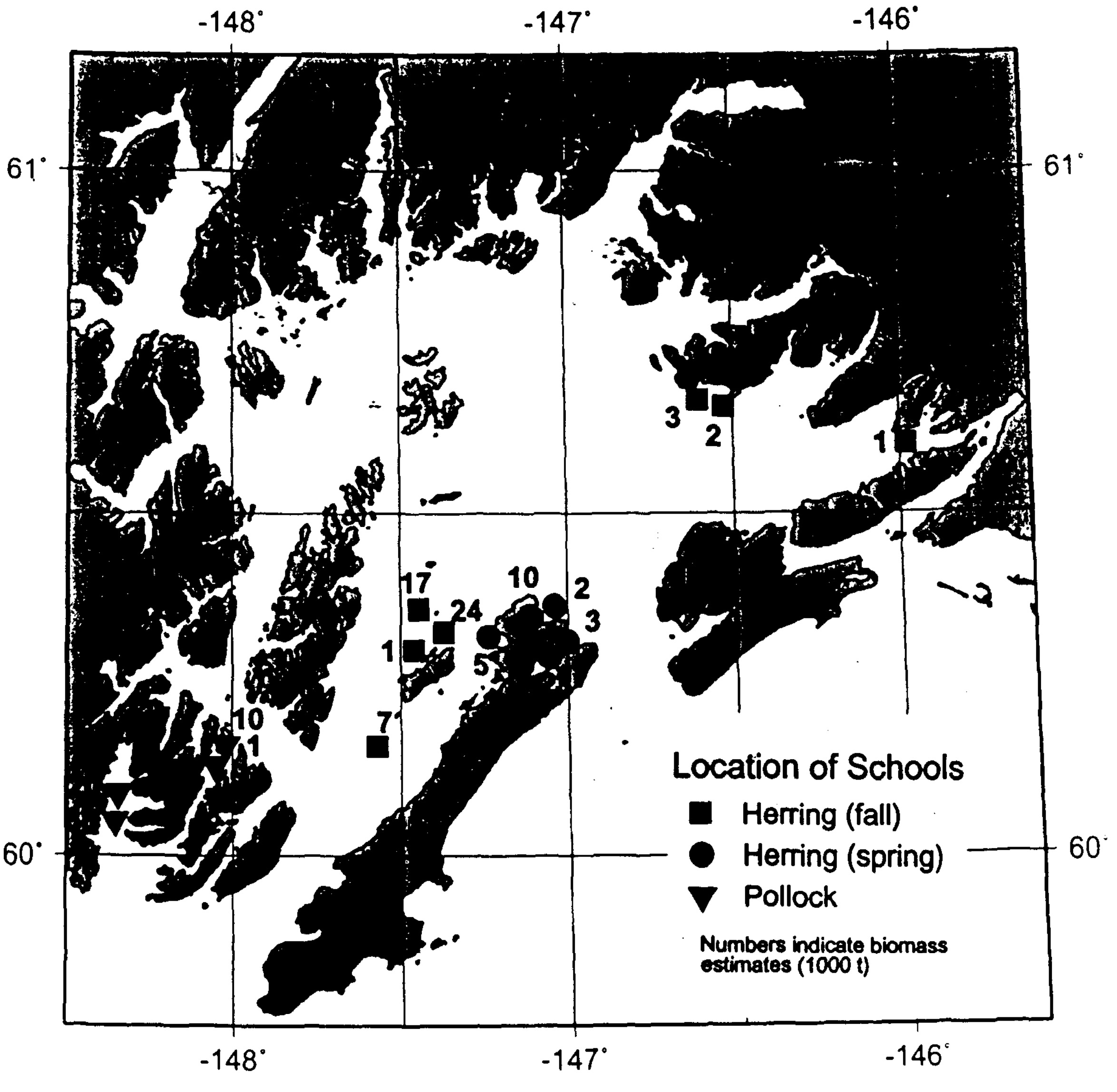
Prince William Sound, Alaska



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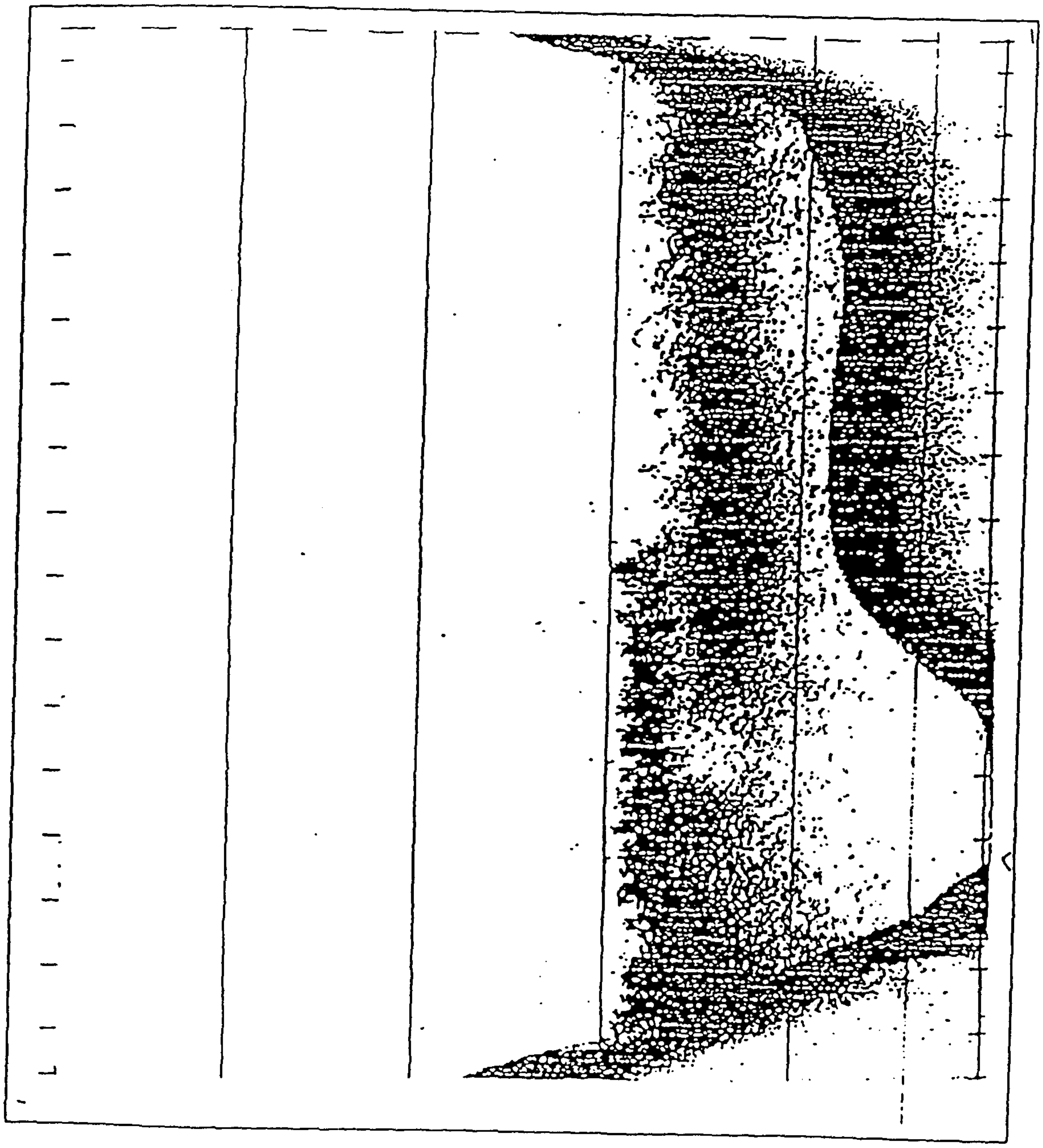

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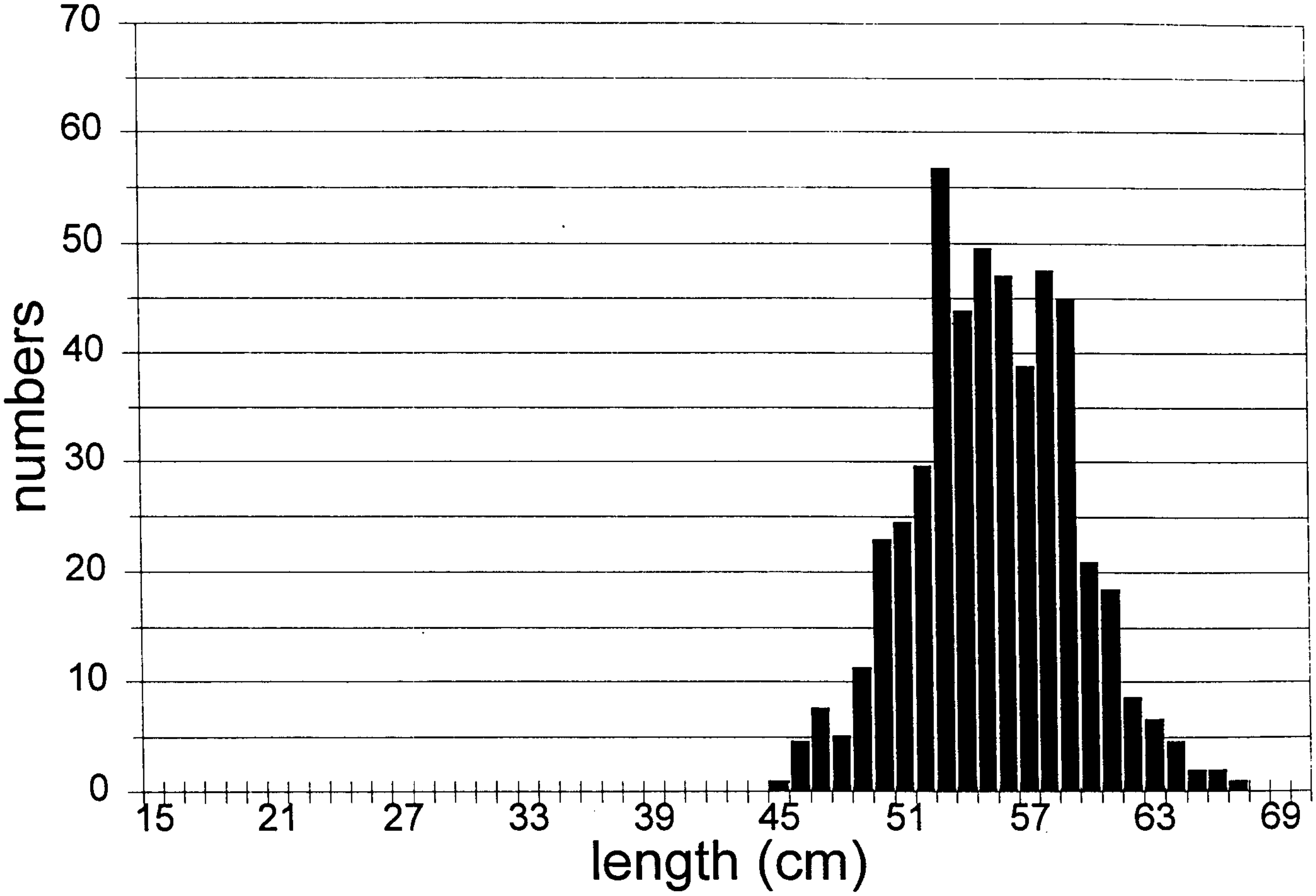
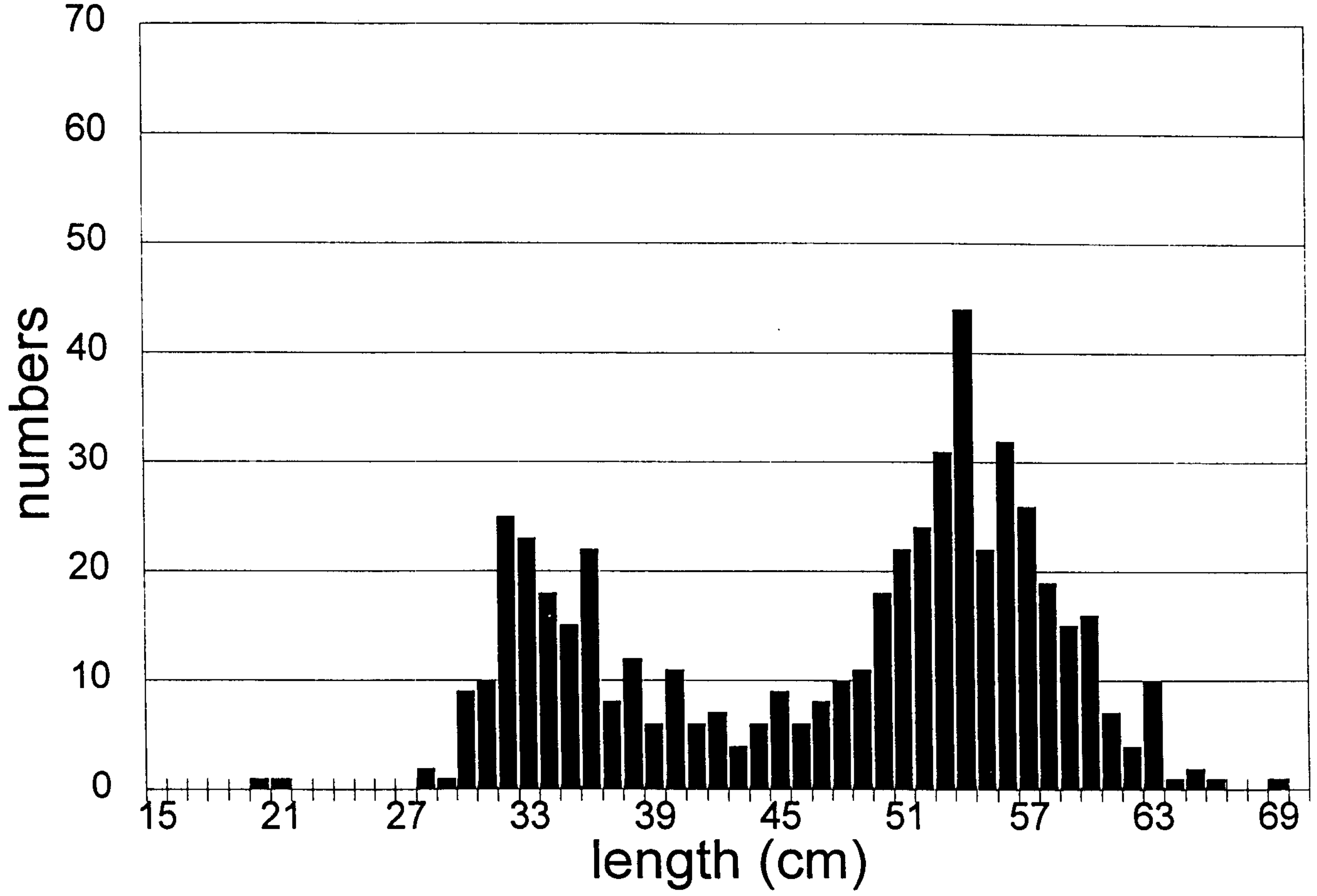


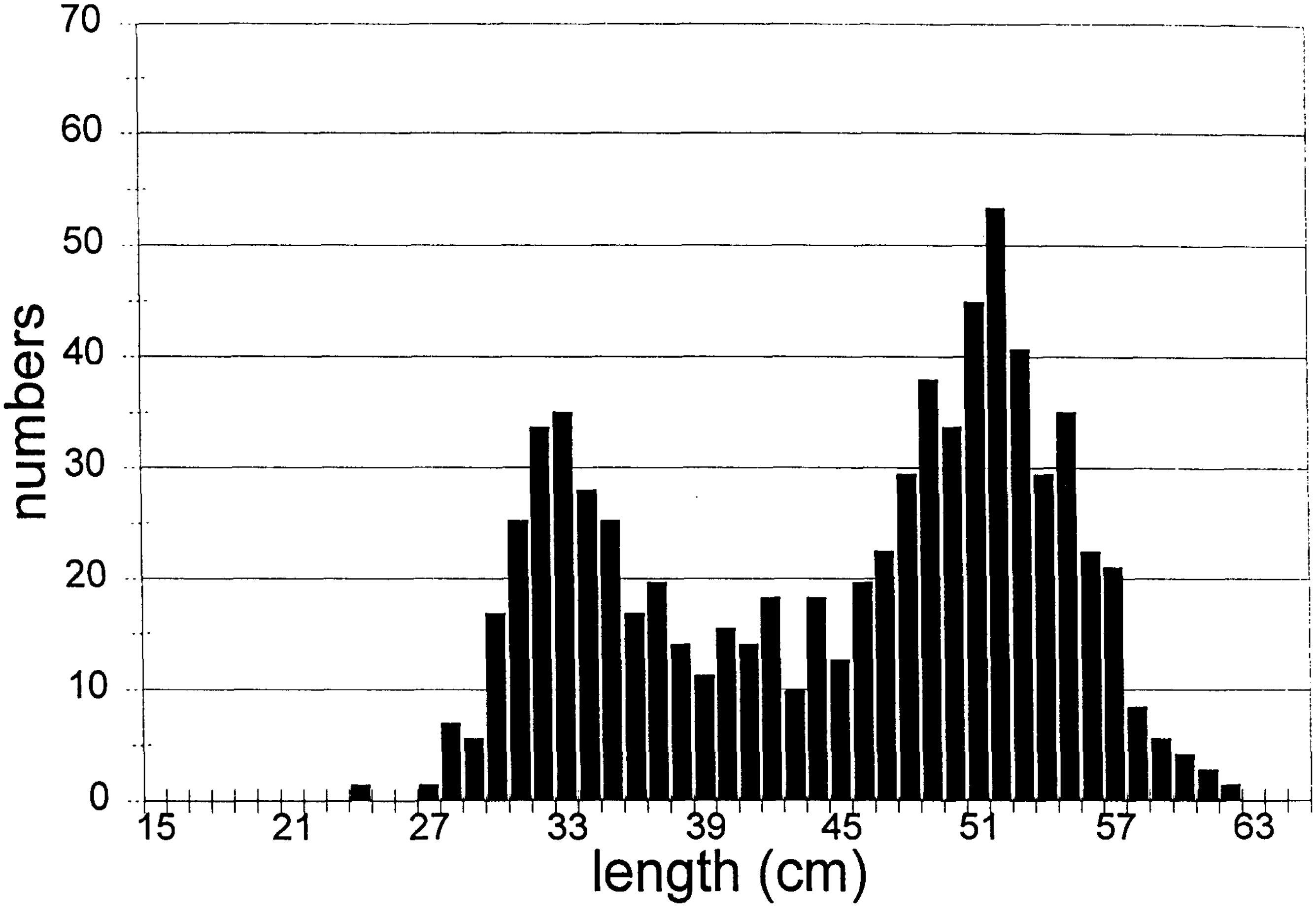
70
60
50
40
30
20
10
0
numbers
15
21
27
33
39
45
51
57
63
69
length (cm)

F 3A.



70
60
50
40
30
20
10
0
numbers
15
21
27
33
39
45
51
57
63
69
length (cm)

F3B



F3c

Pollock Distribution and Density : May - July, 1994

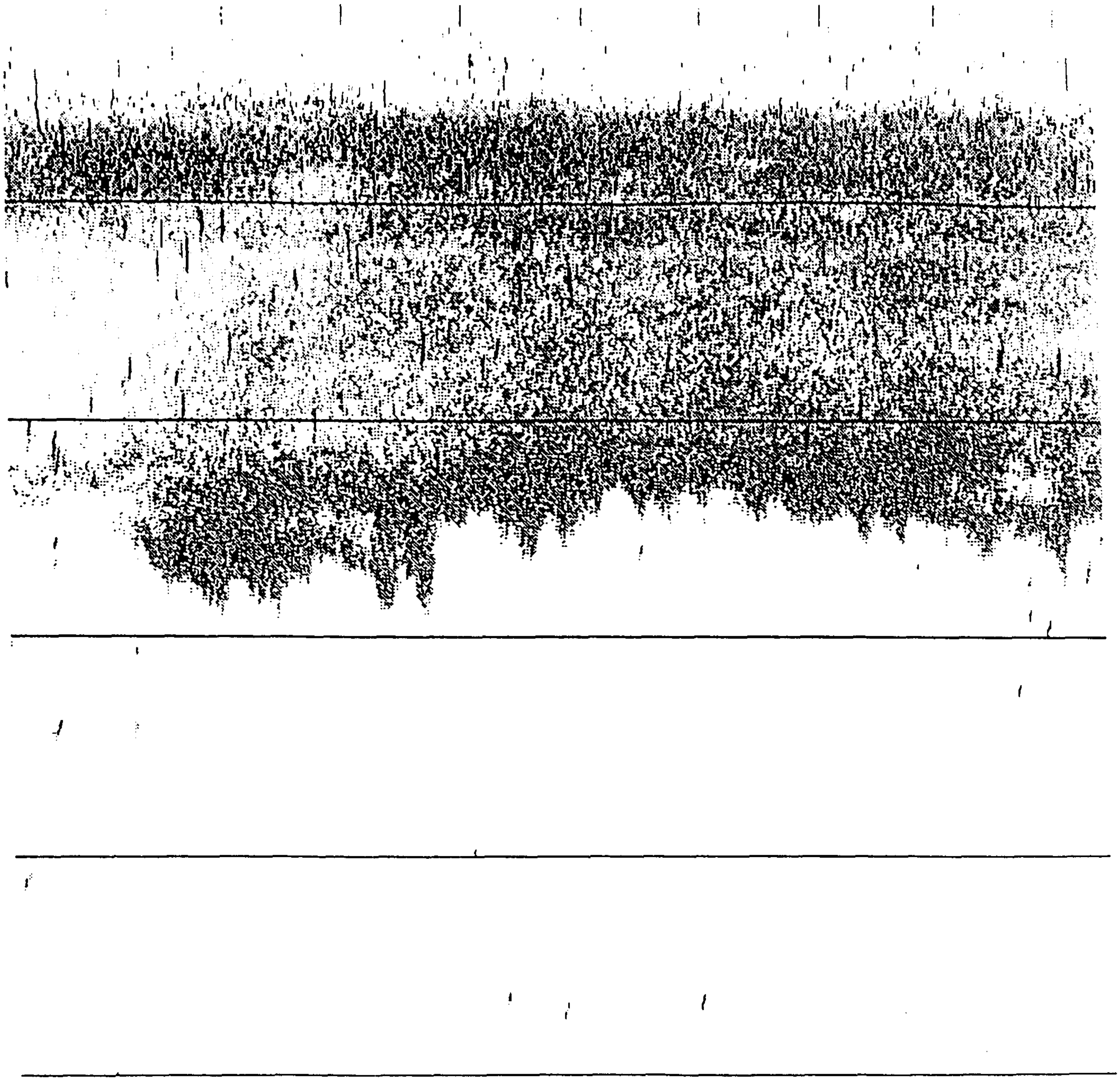
Pollock - Early May

Pollock - Late May

Pollock - Early June

Pollock - Mid July

F4 A, B, C, D



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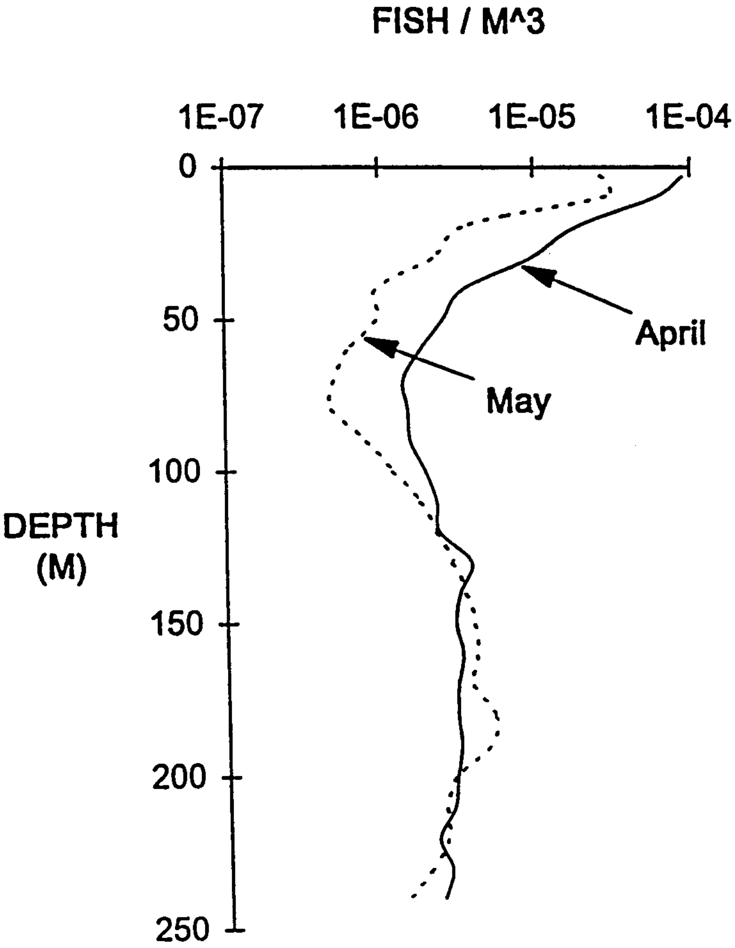
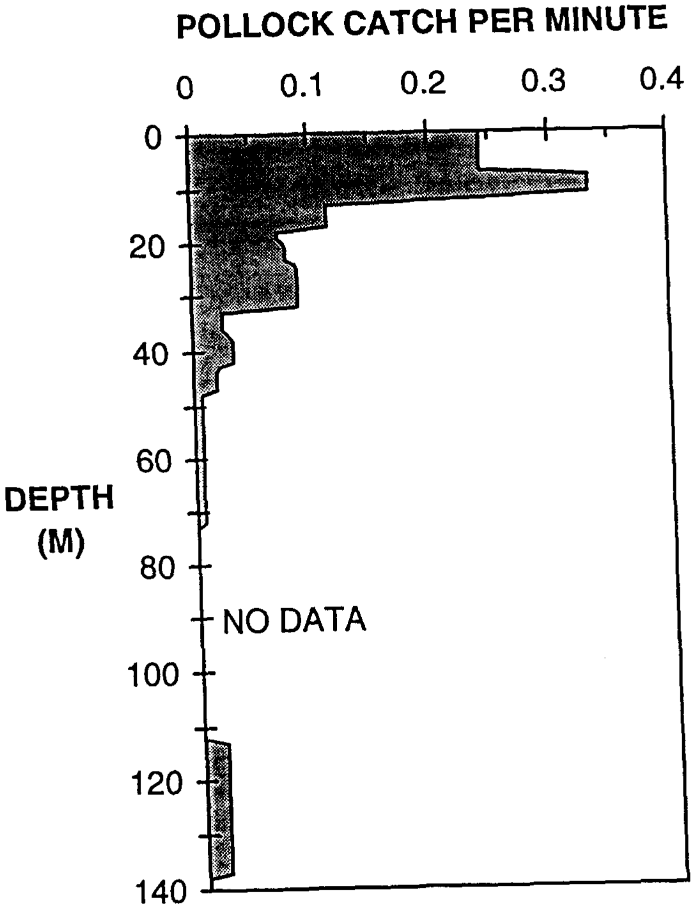
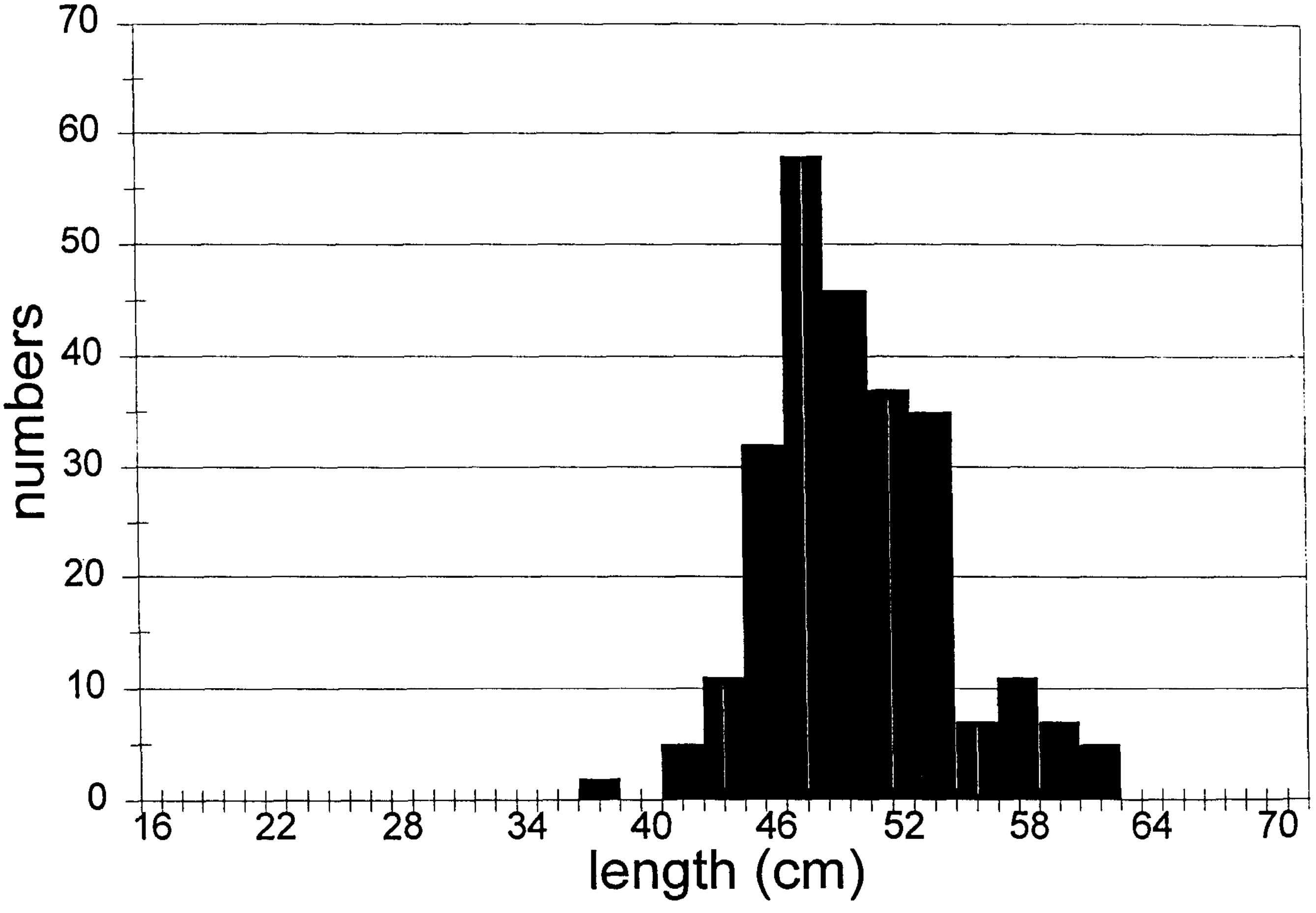

FISH / M^3
1E-07
1E-06
1E-05
1E-04
0
50
100
150
200
250
DEPTH
(M)
April
May

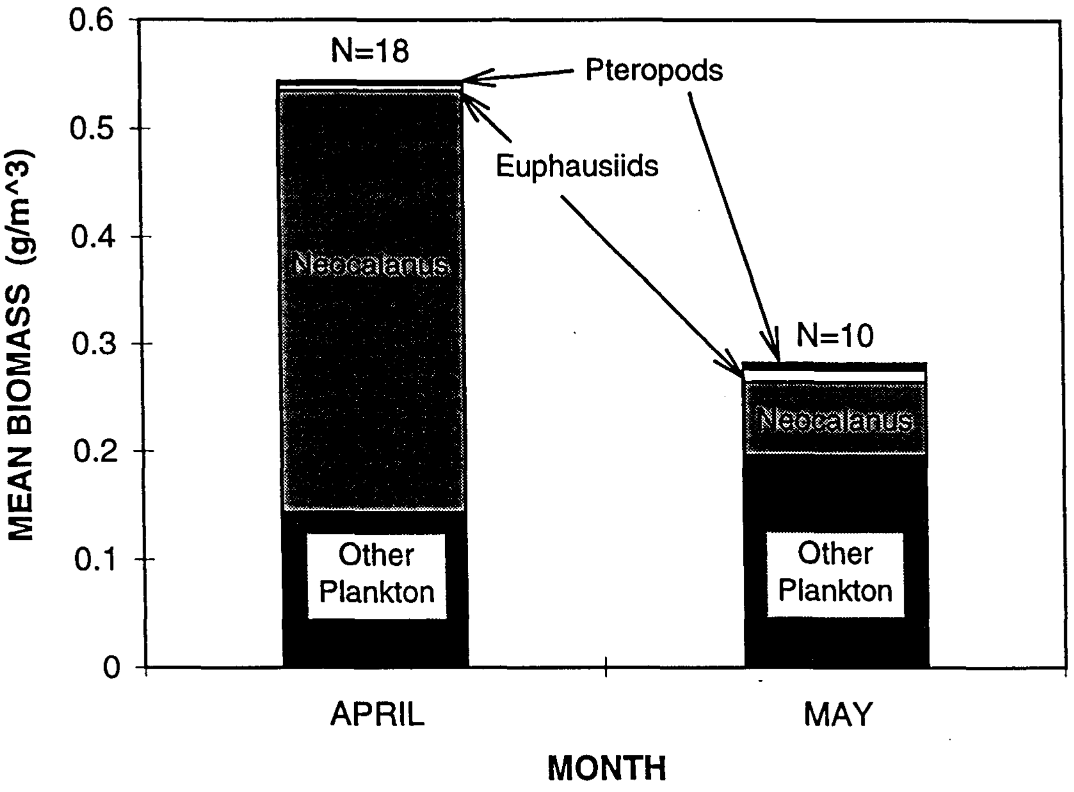
F6


POLLOCK CATCH PER MINUTE
0
0.1
0.2
0.3
0.4
DEPTH
(M)
0
20
40
60
80
100
120
140
NO DATA

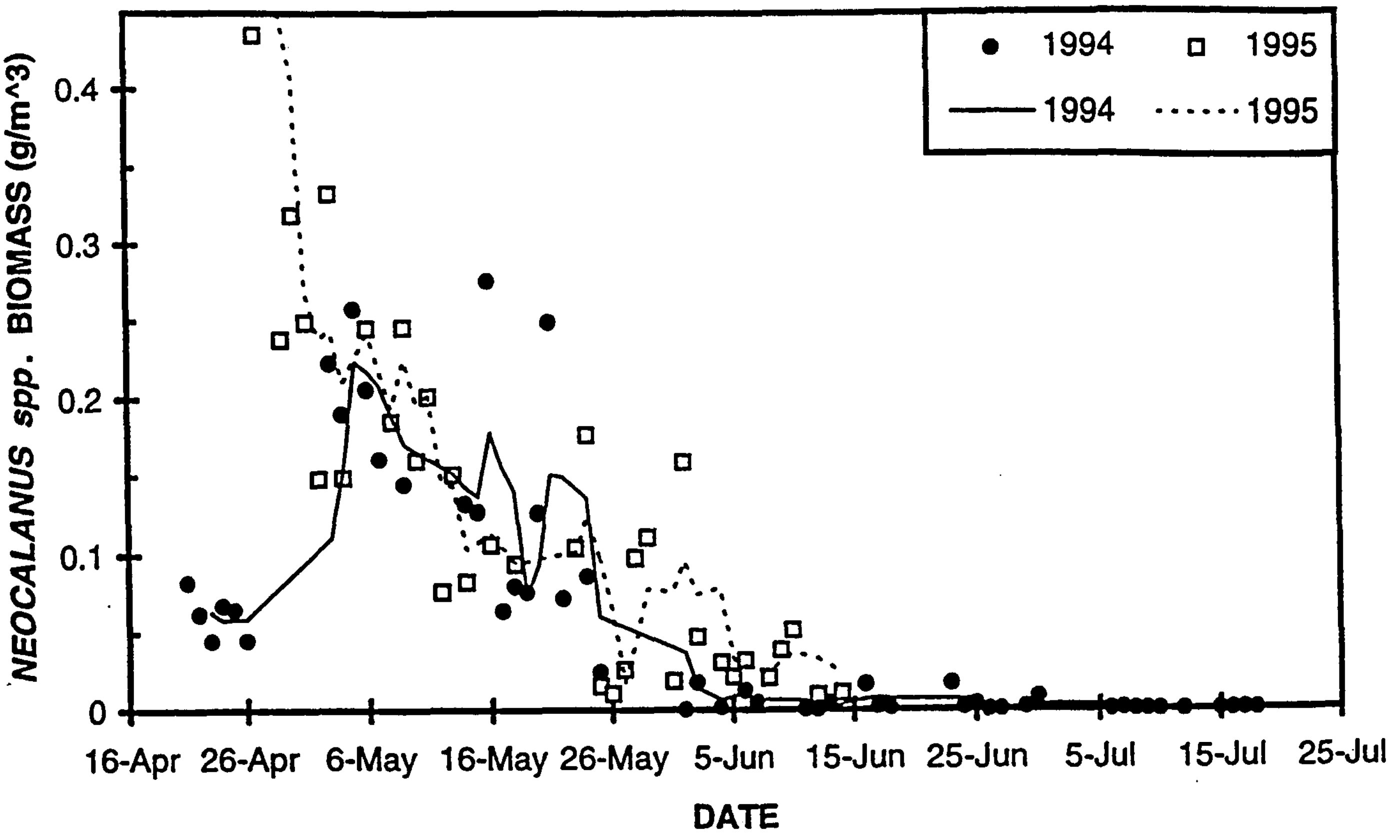
F7


70
60
50
40
30
20
10
0
numbers
16
22
28
34
40
46
52
58
64
70
length (cm)

F8

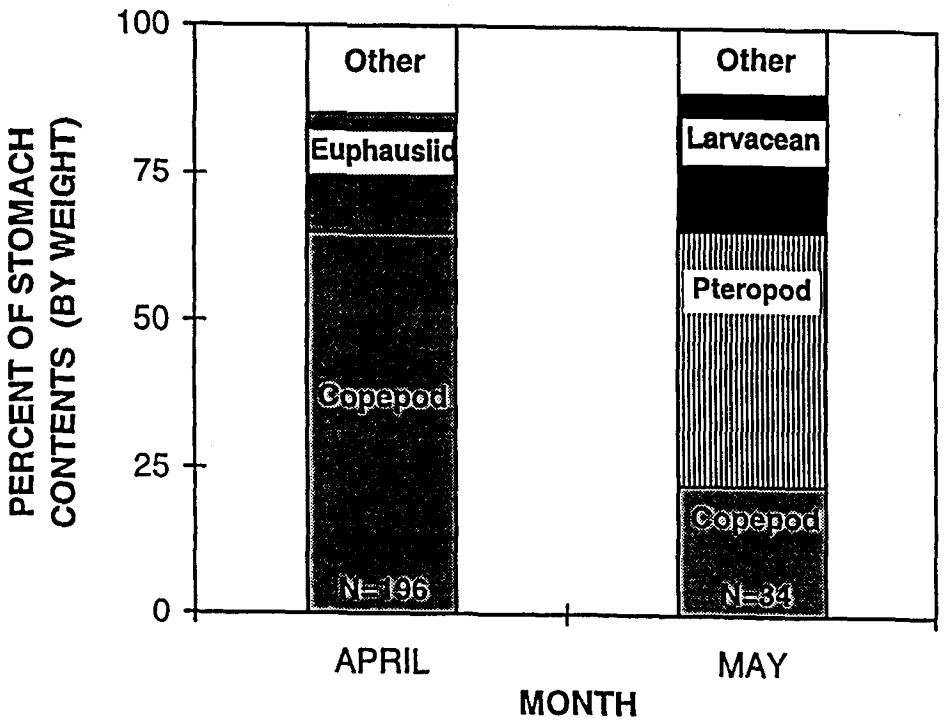

0.6
0.5
0.4
0.3
0.2
0.1
0
MEAN BIOMASS (g/m^3)
N=18
Pteropods
Euphausiids
Neocalanus
Other Plankton
N=10
Neocalanus
Other Plankton
APRIL
MAY
MONTH

F 9



● 1994
□ 1995
—— 1994
······ 1995
NEOCALANUS spp. BIOMASS (g/m^3)
0
0.1
0.2
0.3
0.4
16-Apr
26-Apr
6-May
16-May
26-May
5-Jun
15-Jun
25-Jun
5-Jul
15-Jul
25-Jul
DATE

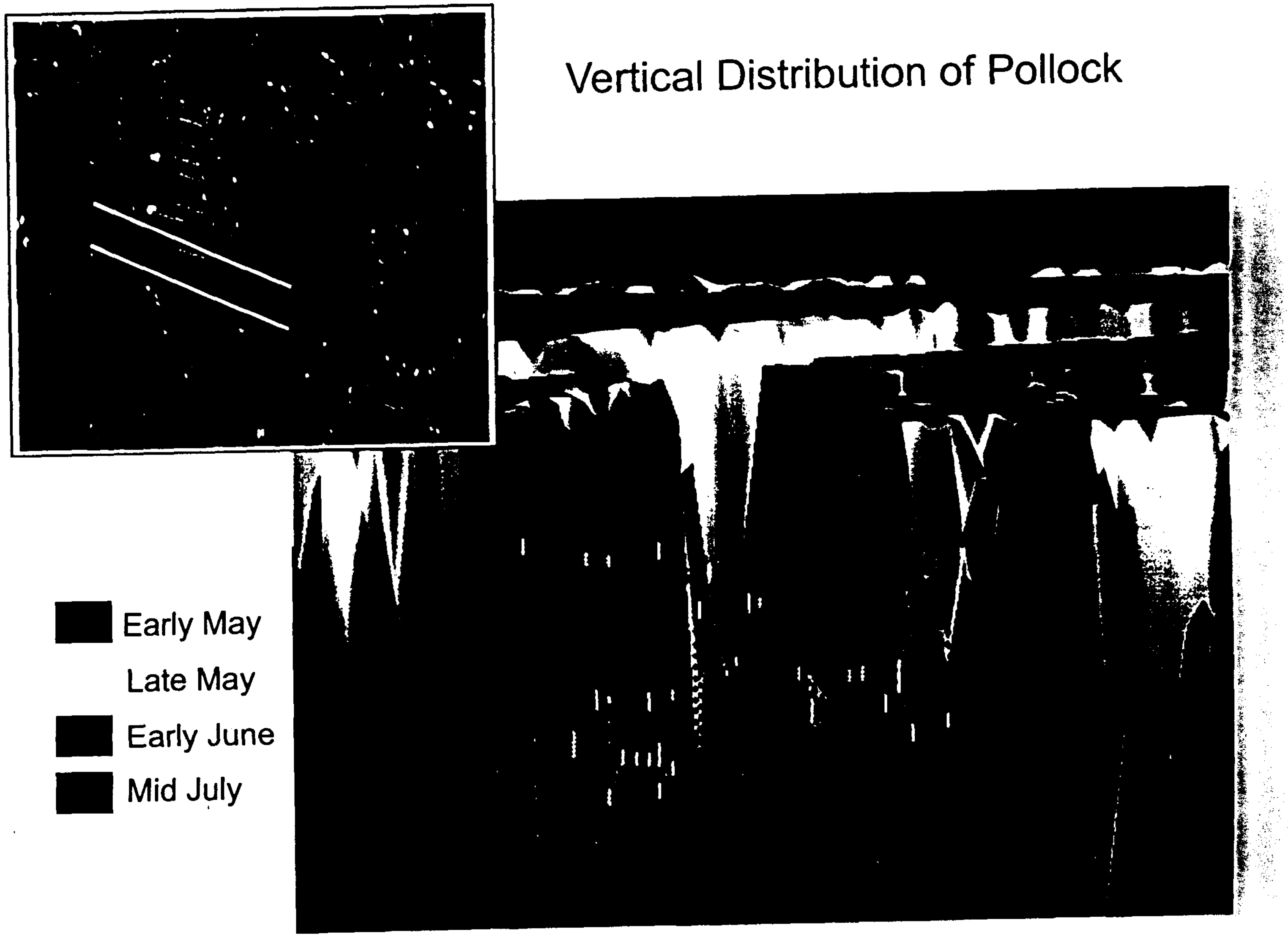
F-10



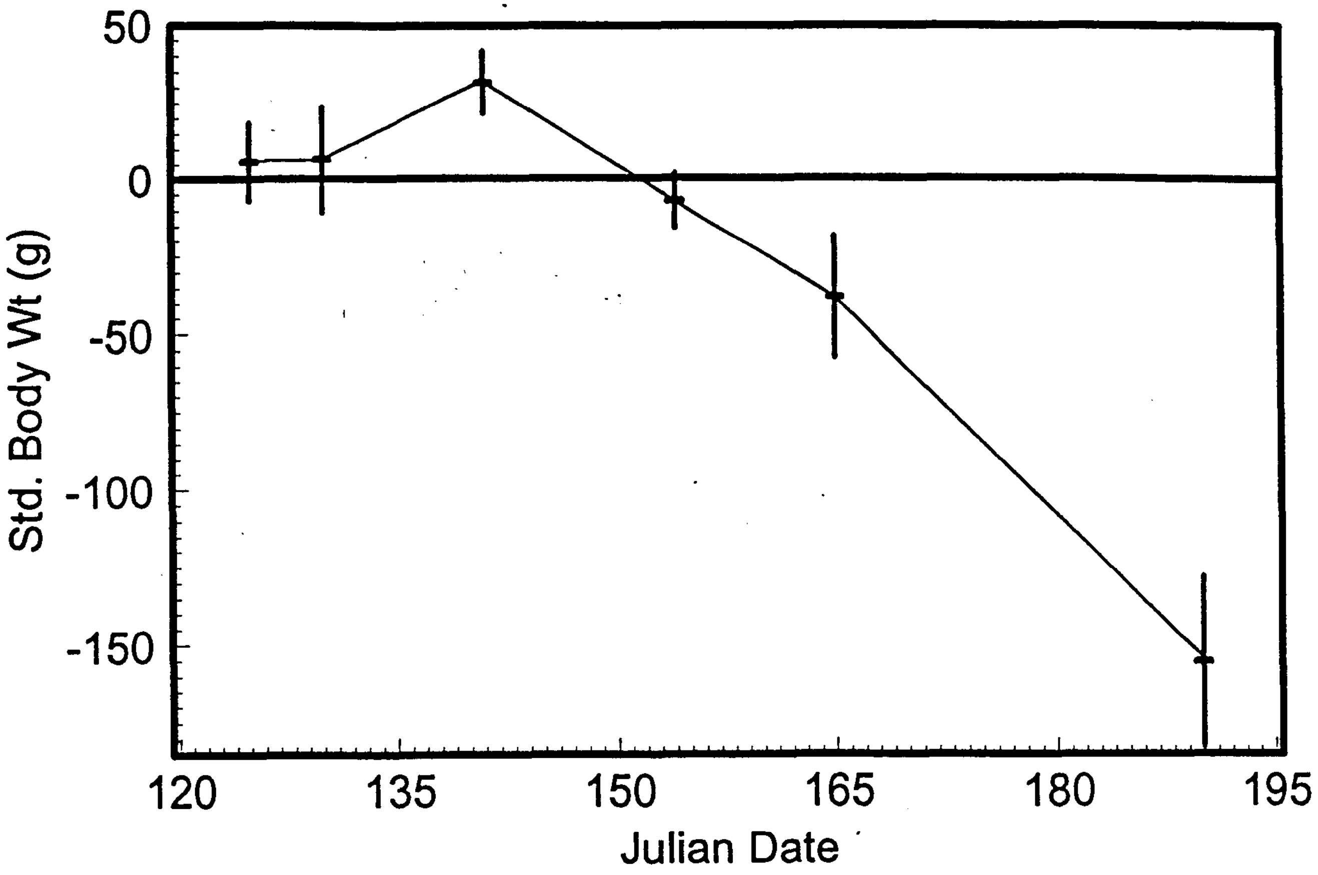
100
75
50
25
0
PERCENT OF STOMACH CONTENTS (BY WEIGHT)
Other
Euphauslid
Copepod
N=196
Other
Larvacean
Pteropod
Copepod
N=34
APRIL
MAY
MONTH

F-11

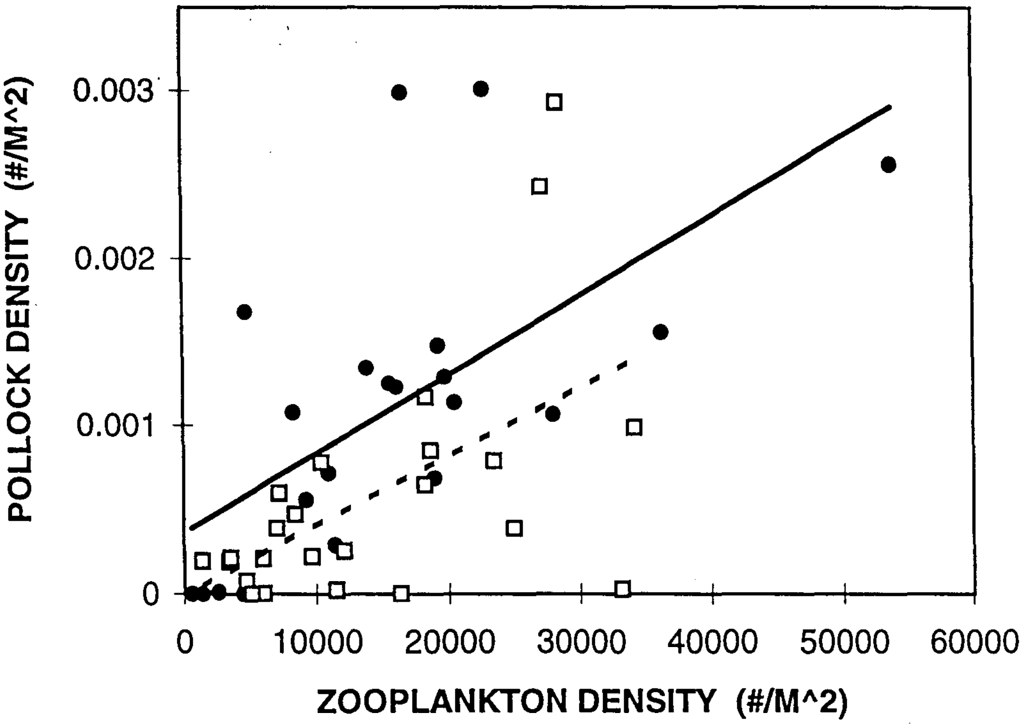
Vertical Distribution of Pollock



F12

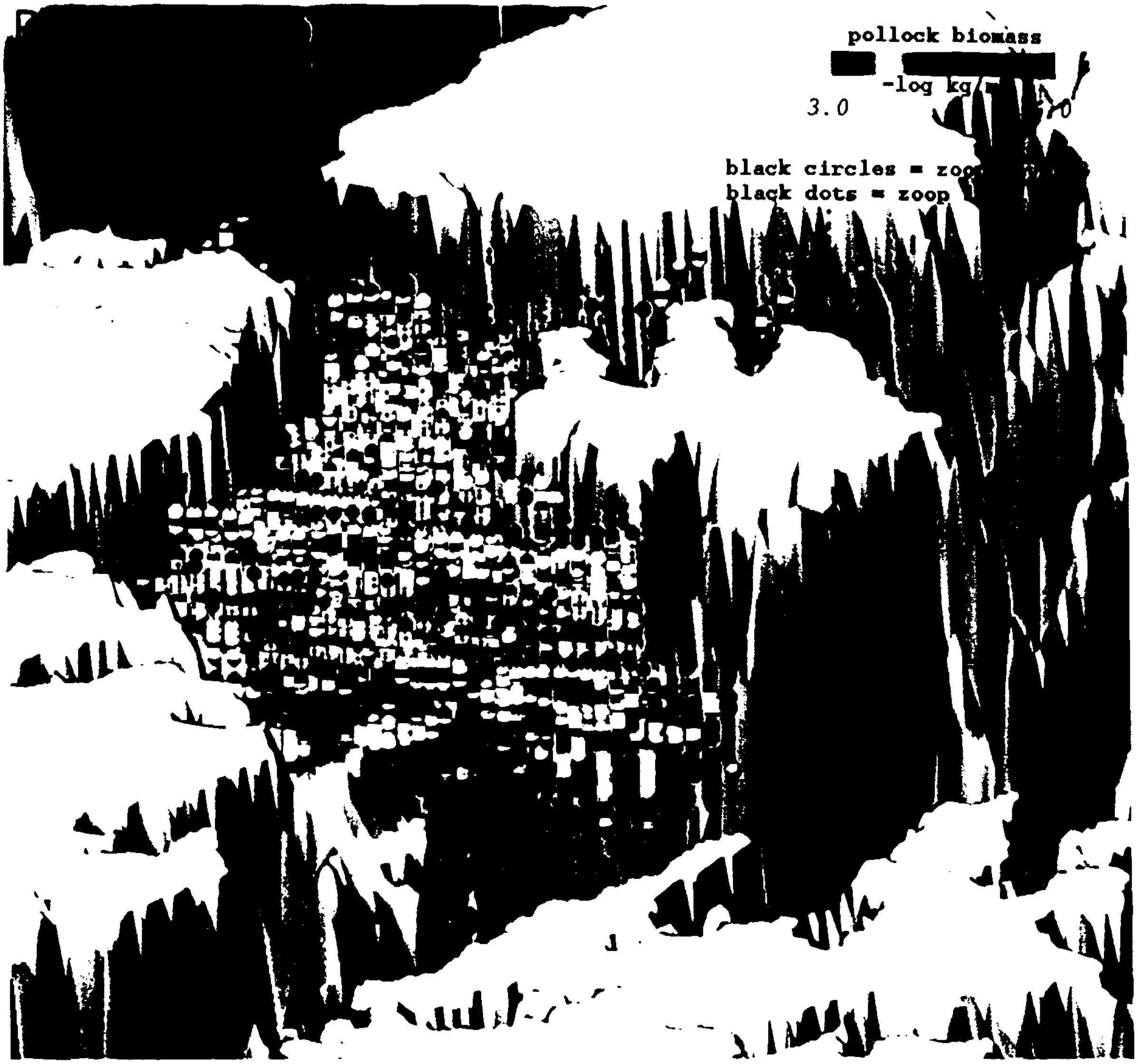


F 13

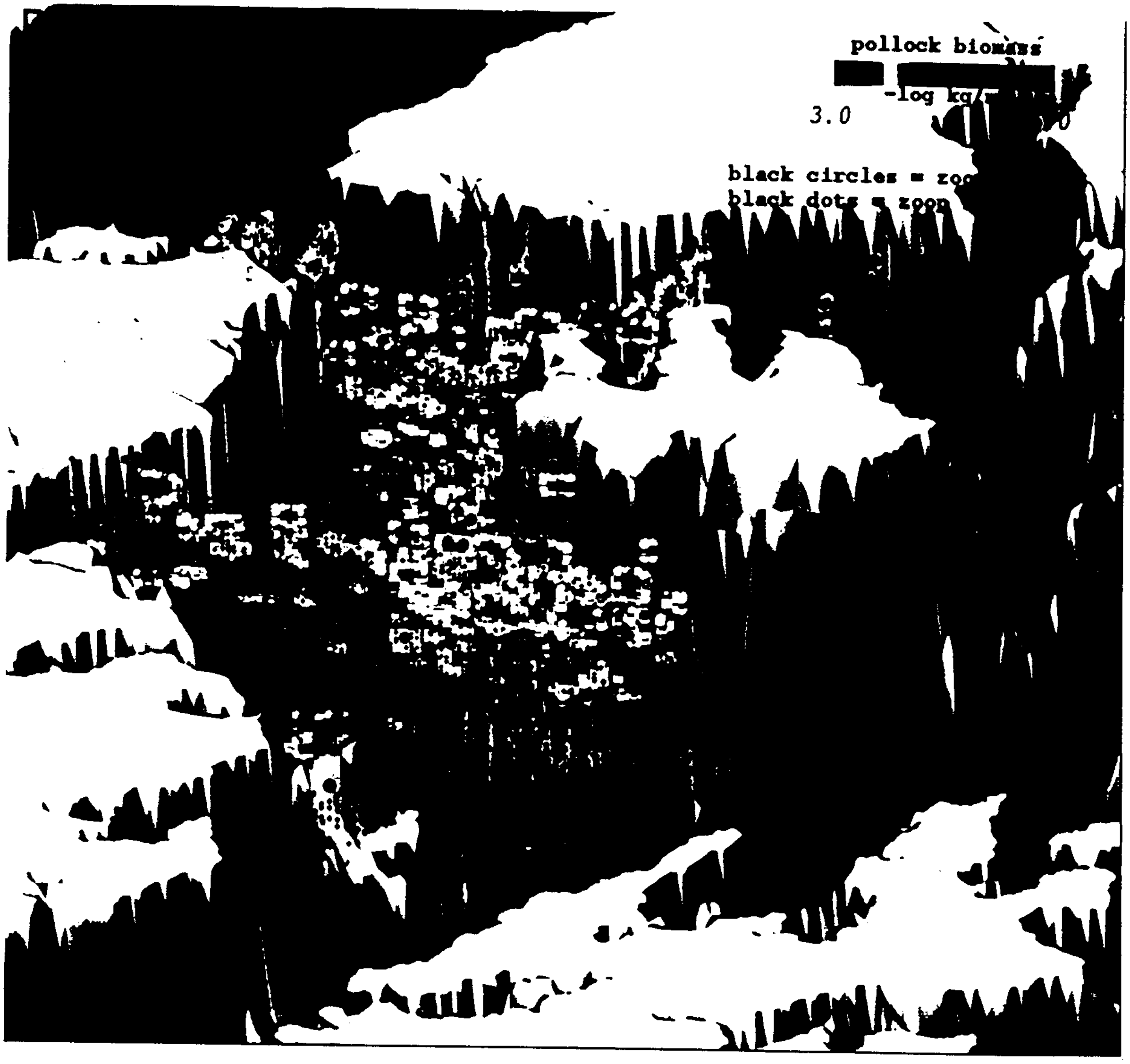


POLLOCK DENSITY (#/M^2)
0.003
0.002
0.001
0
0
10000
20000
30000
40000
50000
60000
ZOOPLANKTON DENSITY (#/M^2)

F 14



F 15



F -16

Chapter 3 – Thomas et al.
1997

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Development of an Ecosystem Model for Managing the Fisheries Resources of Prince William Sound

Second World Fisheries Congress

28 July-2 August 1996

Brisbane, Australia

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July 1996

INTRODUCTION

In 1988-90, a group of scientists working on the Ocean Ecosystem Dynamics Program (GLOBEC) of the National Science Foundation concluded that our inability to predict changes in marine fish populations has prevented us from separating natural and anthropogenic impacts (Cullen 1988). Using the GLOBEC program as a guide (GLOBEC 1991), in 1994, the Sound Ecosystem Assessment program

(SEA) was implemented to develop better predictive tools for fish production in the Prince William Sound, Alaska. SEA assumes that the physical (temperature, turbulence, currents, etc.) and biological (predators, prey and competitors) environment are major contributors to patterns of abundance and production of marine animals.

After failures in recruitment of Prince William Sound pink salmon *Onchorhynchus gorbuscha* and Pacific herring *Clupea harengus pallasi* in 1991-93 (Thomas and Mathisen 1993; ADF&G 1996), these stocks were classified as damaged by the EXXON VALDEZ oil spill Trustee Council (Wolfe et al. 1993). Efforts to restore these stocks are confounded by the poorly understood effects of climate, food and predators. These factors have been shown to account for up to 99.8% mortality in the early marine period for these fishes (Hjort 1914; Parker 1968; Ricker 1976; Hartt 1980; Bax 1983). During this period, slow growing individuals sustain a higher mortality because they are vulnerable to predators for a longer time (Parker 1971; Ricker 1976; Healey 1982; West and Larkin 1987). The long-term goal of the SEA program is to improve forecasting of fish recruitment in Prince William Sound.

The approach is to measure specific physical and biological conditions for input into numerical models. However, a more immediate need is to incorporate new knowledge of these species, where possible, into the ongoing management and restoration programs. Here we focus on the problem of measuring fish populations and the application of contemporary methods to improve accuracy and precision of biomass estimates.

More immediate concerns

The development of new measurement techniques to determine abundance and distribution of nekton and plankton is a prerequisite for testing the underlying hypotheses of the SEA models. Although model development is an eight to ten year goal, there is no reason why the new information on stock abundance, distribution and interactions cannot be used to create more effective restoration and management programs. Since pink salmon, Pacific herring and walleye pollock are all commercially exploited stocks, the establishment of exploitation rates have direct implications on restoration.

Presently, the stocks, pink salmon, herring and walleye pollock are all managed independently by establishing single-species harvest strategies. Single species harvest strategies are often based upon spawner-recruit relationships and stock assessment information. Missing are the effects of physics and other populations on the stock. With support that these species are influenced by climate-driven, predator-prey mechanisms and the acquisition of reasonably accurate, direct estimates of these stocks, an opportunity exists for testing the efficacy of multi-species management.

This paper addresses the findings after two years of the SEA program. Specifically, we review developments in the ability to measure the abundance and distribution of two dominant species (pollock and herring), and the implications of new information on current fisheries restoration and management.

METHODS

Prince William Sound is a complex fiord/estuary located at the northern margin of the Gulf of Alaska (Figure 1). High mountain peaks in excess of 4000 m border the Sound and receive the brunt of the seasonally intense cyclonic storms from the Gulf (Thomas et al. 1991). Depths exceeding 400 m occur in the western and central portions of the Sound which support overwintering populations of oceanic copepods.

Sampling design

The acoustic surveys were run from a variety of charter vessels according to standard echo integration practices (MacLennan and Simmonds 1992) using sphere-calibrated BioSonics 101,120 kHz and 102, 38 kHz dual beam and BioSonics ESP/EI and DB software programs. Each sonar system was equipped with a GPS receiver to geo-reference acoustic data. Echo integration, dual-beam target strength and GPS data were stored on hard drives and backed up on magnetic disks/tapes. Unprocessed data were stored on DAT recorders. The parameters of the two acoustic systems were: 120 kHz /SL = +225.075 dB, RG = -159.282dB, b2 = 0.0010718, PD = 0.4 ms;

38 kHz /SL = + 215.784, RG = -144.474, b2 = 0.00219, PD=1.0 ms.

Long day-lengths necessitated daylight surveys to monitor predator densities in the spring. Otherwise the acoustic surveys were conducted at night (Burczynski et al. 1986). Only red running lights were used on nighttime surveys to minimize boat avoidance and search-light sonars were used to monitor school behavior relative to the vessel track. The spring predator (walleye pollock) surveys took place mainly in the Wells and Perry Island Passages, in the northeastern corner of the Sound. This was to take advantage of the release of over 500 million salmon smolt by the hatcheries in this area. The fall-winter prespawning surveys of adult herring and pollock took place mainly in the north Montague Straits and Port Bainbridge areas. Since 1993, we conducted 11 spring predator surveys and eight fall-winter prespawner surveys.

On all surveys measurements were made on systematically stratified grids of parallel transects. On the prespawner surveys the grids were conducted only over fish school groups. This was the second of a two-stage survey design, with the first stage a search for school groups. Cochran (1977) describes the algorithms for estimating biomass and variance and discusses the biases associated with single and two-stage, stratified-systematic sampling designs. All acoustic sampling was supported by midwater trawl or purse seine catches to collect biological information.

Data Analysis

Batch processing to transform 2d arrays of acoustic targets from dB to kg and numbers, estimate and visualize biomass were conducted after transferring the data to a UNIX workstation. All data are stored in the appropriate format for post processing using Interactive Data Language (IDL), and Advanced Visualization systems (AVS) software.

Measured target strengths of individual fish were compared with length data of fish captured by the nets. To establish a fish size-target strength relationship, we used the relationships advanced by Thorne (1983 for target strength per kg versus length, Traynor and Ehrenberg (1979) for walleye pollock target strength versus length, and MacLennan and Simmonds (1992) for Pacific herring target strength versus length. Weighted mean densities and their variances were computed and extrapolated to biomass and 95% confidence limits using the delta method (Seber 1973).

Visualizations of biomass survey data were made using AVS. Geo-coded volume backscatter values were stored in a 1-d scatter arrays and displayed as scatter- dot clouds in 3-d space to view sampled locations. The 1-d scatter array was then converted to 3-d unstructured cell data (UCD) format. In UCD format each point is identified by its spatial relationship to neighboring points. Interpolation using Delauney triangulation

was used to generate the UCD structure. The 3-d UCD volume was converted to a geometry by applying a user-specified color map to the nodes and then displayed and manipulated in the AVS geometry viewer. Finally, serial slices throughout the UCD volume were taken using horizontal planes to show truncation of school group measurements. Isosurfaces of the school groups were examined at various thresholds, rotated in 3-d space and animated as time sequences to select views that best describe the truncation problem.

RESULTS AND DISCUSSION

Implications of new biomass information

Six surveys of prespawning herring and two of prespawning pollock were conducted between 1993-1996. Both species occur in highly aggregated school groups that are distinct enough in their vertical distribution and density that identification of their acoustic targets is not an issue. Only twelve school groups of herring in excess of 1000 mt were observed on the six surveys over three years (Figure 1). Only four school groups over 1000 mt of pollock were observed on two surveys in 1995 (Figure 1).

Four of the 12 herring concentrations were surveyed twice to determine repeatability of the measurements. In fall 1993, we estimated the same school group on Applegate Rocks to be 12,875 and 16,442 mt; in spring 1995, we estimated the same school group in Rocky Bay to be 10,480 and 8,050 mt; in winter 1996, we estimated the same group of fish in Zaikof Bay at 26,309 and 20,097 mt; in the spring of 1996, we estimated the same group of fish in Stockdale Harbor at 3,227 and 3,791 mt.

Upon close inspection, the largest source of error in estimates from the repeated transects over the herring or pollock aggregations is the lack of adequate coverage of the fish concentration. Figures 2-6 show the results of five consecutive surveys on a concentration of herring in Stockdale Harbor. The school isosurfaces show that the measurement of the herring school group was severely truncated on surveys #1 (Figure 2), #3 (Figure 4) and #5 (Figure 6), but not on surveys #2 (Figure 3) and #4 (Figure 5). The nearshore affinity of walleye pollock suggests that truncation of measurements is also a problem on their surveys. The biomass estimated on #2 and #4 were 3,227 and 3,791 mt, whereas the biomass of the other three surveys never exceeded 1,700 mt.

Another aspect of repeatability is the fall to winter-spring estimates. The fall 1994 and spring 1995 estimates of adult herring biomass were both about 13,000 mt. The fall 1995 and winter 1996 estimates of adult herring biomass were about 24,000 and 23,000 mt. The observed increases from spring to fall are due to recruitment and little overwinter mortality has been observed. Finally, in 1995 the biomass of prespawning pollock in Port Bainbridge was estimated to be 27,366+/- 7,227 mt from a survey of nine parallel transects.

The fact that there are so few school groups of prespawning herring and pollock in the Sound region, and that they do undergo localized movements which can allow good coverage if the surveys are continually repeated, suggests the use of a two stage survey design: (1) use aerial and sonar searches to locate the school groups, and (2) remain with the school group until repeatable measures are made.

These findings suggest that making "corrections" for fish too close to the shore (Hampton 1996) for Prince William Sound herring and pollock can result in unacceptable inaccuracy in the biomass estimation. Adoption of two stage procedure should result in repeated estimates of school group biomass within 10% of each other.

The single-species paradigm

Currently, the three dominant pelagic fish populations in the Sound, pink salmon, Pacific herring and walleye pollock are also three of the most important commercial fishes. As is the tradition in fisheries science (Hilborn and Walters 1992), each fishery is managed separately and with sparse data. With new information generated by the SEA program on abundance, distribution and interaction there is the possibility to take a multispecies approach and minimize the potential for contradictions between restoration and management activities.

The status of the pink salmon is somewhat independent of the system because 90% are produced by hatcheries (Thomas and Mathisen 1993), and they only spend 3 months in the Sound as juveniles before migrating to the ocean to feed (Willette 1993), and about two-three weeks in the Sound as adults while migrating to spawning areas. In contrast, Pacific herring and walleye pollock spend much of their life histories in the Sound.

The Sound's Pacific herring stock has been too low to support commercial harvests since 1993 (ADF&G 1996). Concurrently, the Sound's walleye pollock stock is considered to be part of a declining Gulf of Alaska stock (NMFS 1996). Thus, the Sound's walleye pollock are being harvested at a reduced exploitation rate (9% in 1995). Since the status of the Gulf of Alaska pollock stock is determined by a model prediction for the west-central stocks, where the predictions do not agree with survey data, this harvest rate is at least controversial. With recent findings that the walleye pollock and herring are the two dominant, competing pelagic species in the Sound, there is a concern that the current management strategy to build the pollock stock may contradict the restoration of the herring stock.

Walters et al. (1986) found herring survival to recruitment to be negatively related to cod abundance *Gadus macrocephalus*. Analysis of cod stomach contents supported the estimated mortality rates. We have found that walleye pollock are the primary predators of young pink salmon and herring. Thus, a negative correlation between walleye pollock abundance and the recruitment of herring is a good hypothesis for testing.

Sainsbury (1988) proposed that managers set up experimental fishing regimes for multispecies analysis. Present fishing regimes in the Sound are established independently for the walleye pollock, Pacific herring and pink salmon by the Alaska Department of Fish and Game and National Marine Fisheries Service, hence they are already subjects of an ongoing experiment. With both of these agencies represented by the EVOS Trustee Council there is unprecedented opportunity to merge information from both management and restoration programs and evaluate a multi-species management approach.

Hilborn and Walters (1992) identified the data requirements for multispecies biomass dynamics and age structured models as too demanding or expensive for practical utility. However, we anticipate that GLOBEC and SEA research and development programs will produce remote sampling methods that are accurate and cost effective enough to satisfy both the accuracy and cost constraints. To illustrate, one survey is less than $50KUS. Such are well within the amount that and costs can be borne by test fishing revenues (Thomas 1992). Such monitoring will also serve our long term goals by providing the information needed to initialize and verify the next generation numerical models for predicting fish population changes (GLOBEC 1991).

In-season management for escapement

We show that acoustic measurement techniques can make repeatable estimates of the size of herring and pollock school groups in the Prince William Sound region. Repeatable measurements of biomass have been made both within and between fall and spring surveys. The largest source of error in the biomass estimation procedure is truncation of the school groups by the survey volume. Visualization techniques have been developed to provide criteria for accepting repeated measurements as replicates. Use of new criteria for repeating biomass estimates in the field is expected to produce the accuracy needed for implementing in-season management practices. The implementation of in-season management practices can protect marine fish stocks and allow weak stocks to rebuild prior to having predictive models.

Current management of the walleye pollock fishery could be contradictory to the restoration of the collapsed herring stock and production strategies for hatchery salmon. With the ongoing SEA research program, we recommend that management agencies take advantage of this opportunity by experimenting with multi-species harvest strategies and implementing in-season management practices for herring and pollock.

Predictive Models

With short-term concerns over conservation of stocks satisfied by using accurate estimates of fish biomass to implement in-season management practices, research can focus on the development of predictive models. Accurate monitoring of the fish biomass is also essential for initializing and verifying model predictions. Thus, with the development, refinement and implementation of monitoring programs to accurately assess fish stock biomass, conservation practices and eventually, the prediction of animal population change is possible. Since the ability to predict animal population change is a prerequisite to the separation of natural and anthropogenic effects, we have a pathway to developing the ability to assess the effects of fishing, hatchery practices, oil spills and other man-induced impacts on natural populations.

SUMMARY

The Sound Ecosystem Assessment (SEA) program is developing and applying new survey designs to estimate the abundance and distribution of dominant fish stocks (Pacific herring and walleye pollock) in Prince William Sound. The long term goal is the development of numerical models to improve the prediction of fish population change. However, accurate estimates of biomass are not only needed to initialize and verify model predictions but are essential for implementing conservation practices that will sustain healthy fisheries. The current management of the walleye pollock fishery could be contradictory to the restoration of the collapsed herring stock and production strategies for hatchery salmon. We support the implementation of a biomass monitoring program for herring and pollock stocks in the Sound and the development of in-season management practices. Furthermore, we urge the adoption of experimental multi-species harvest strategies while the three dominant species (herring, pollock and salmon) are being monitored for changes in biomass. We see this to be an unprecedented opportunity for fisheries science to evaluate a new management paradigm.

ACKNOWLEDGMENTS

This research is funded by the EVOS Trustee Council. We thank the Council and its staff, the SEA program researchers, local area managers and Prince William Sound Science Center personnel and associates for support of this research. Special thanks goes to the fishermen in Prince William Sound who have contributed valuable insight on the fish distribution and behavior and are second to none as vessel skippers.

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LIST OF FIGURES

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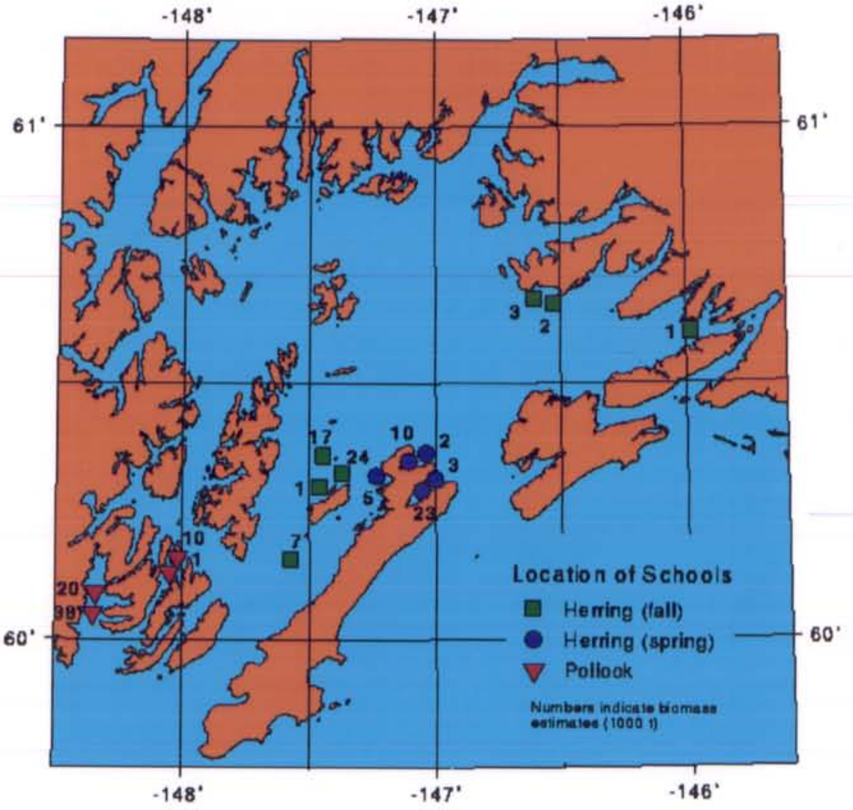

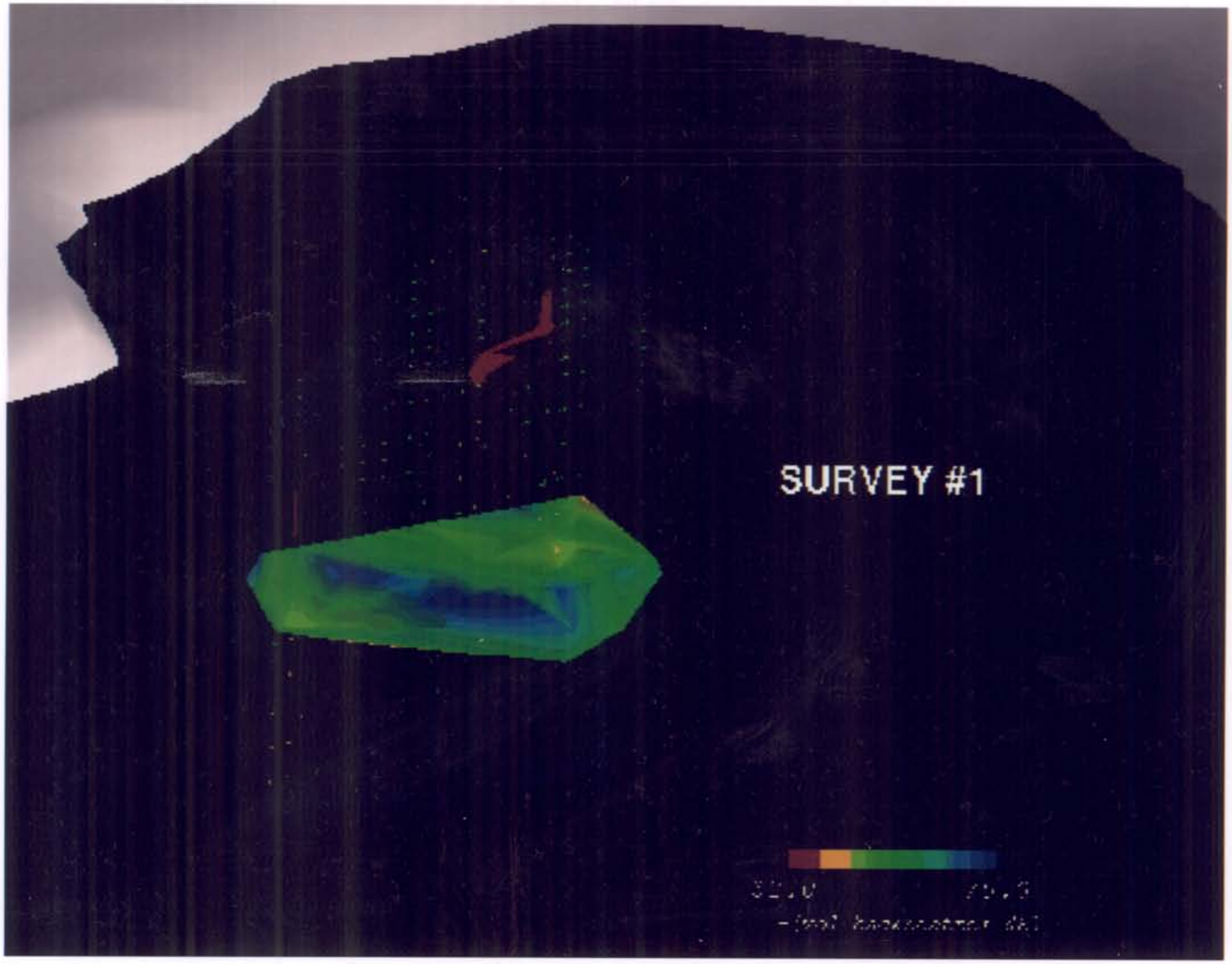
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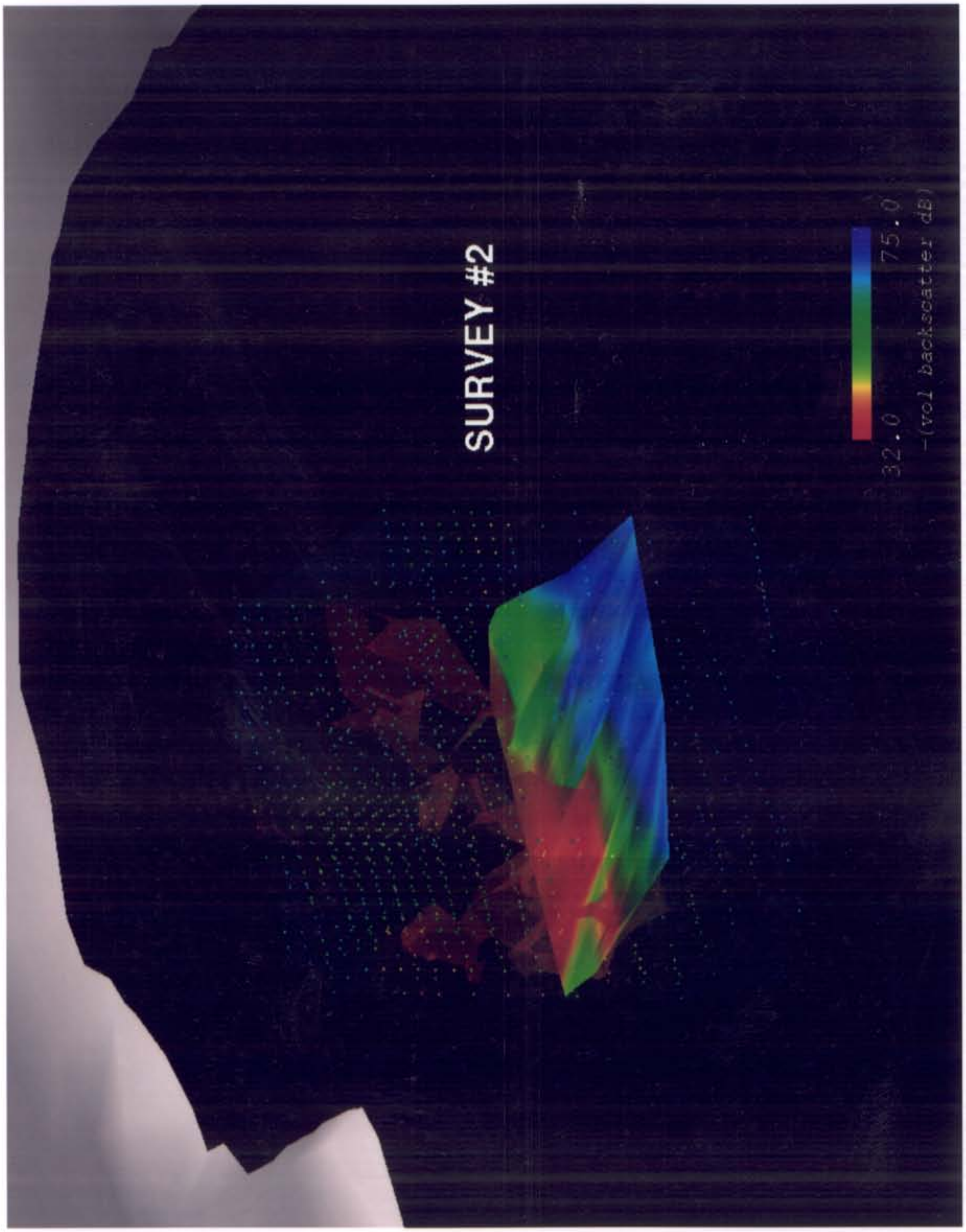
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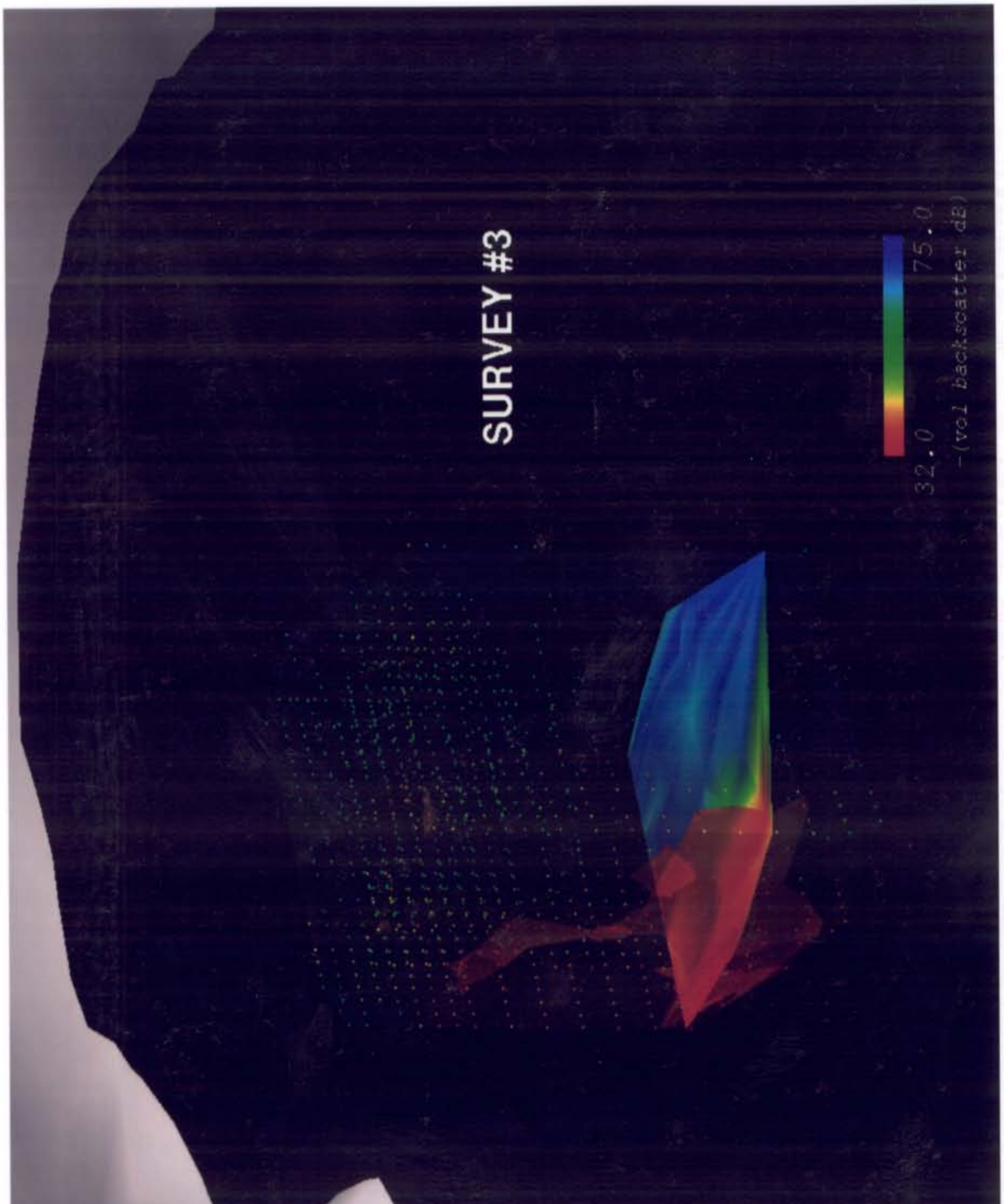
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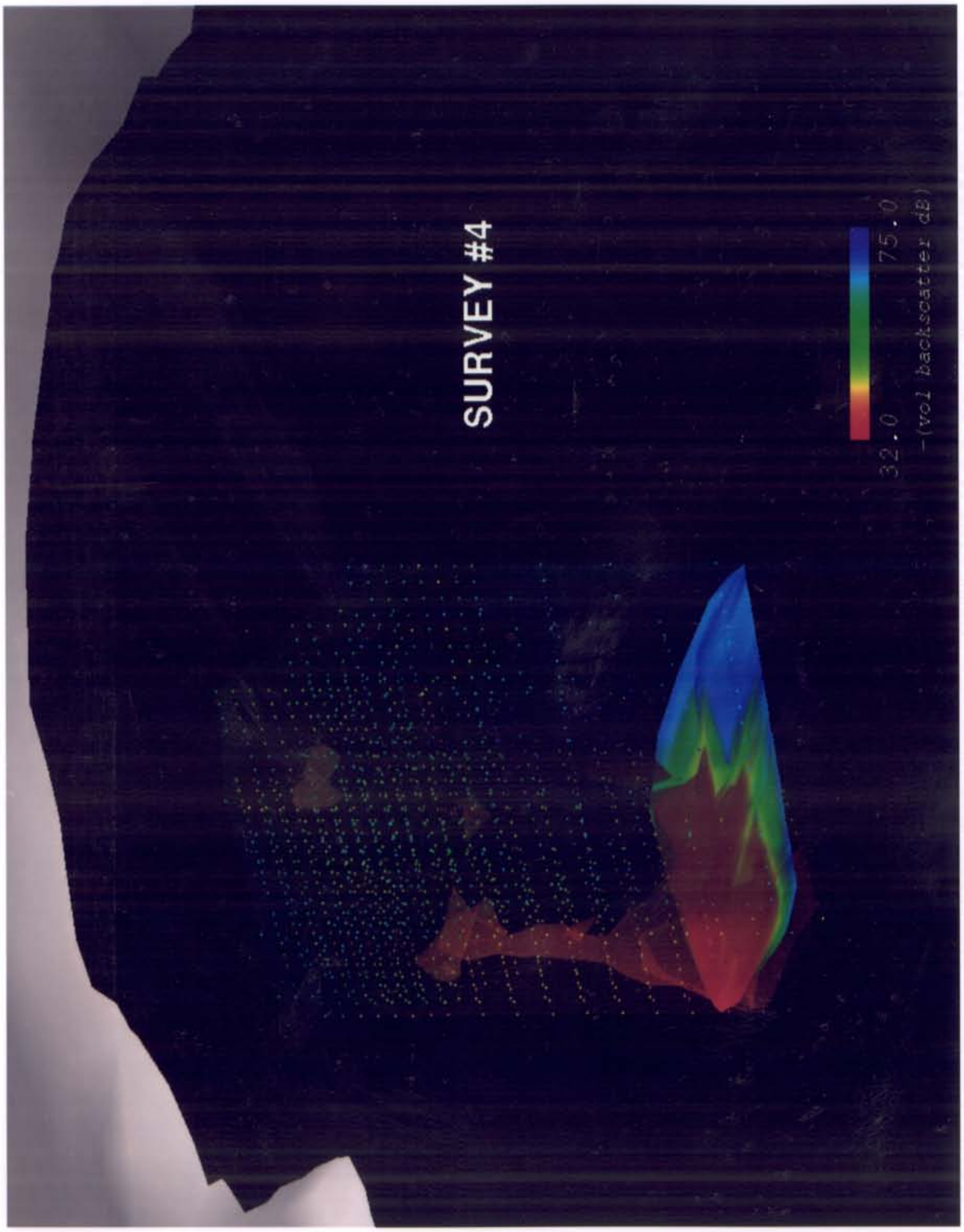
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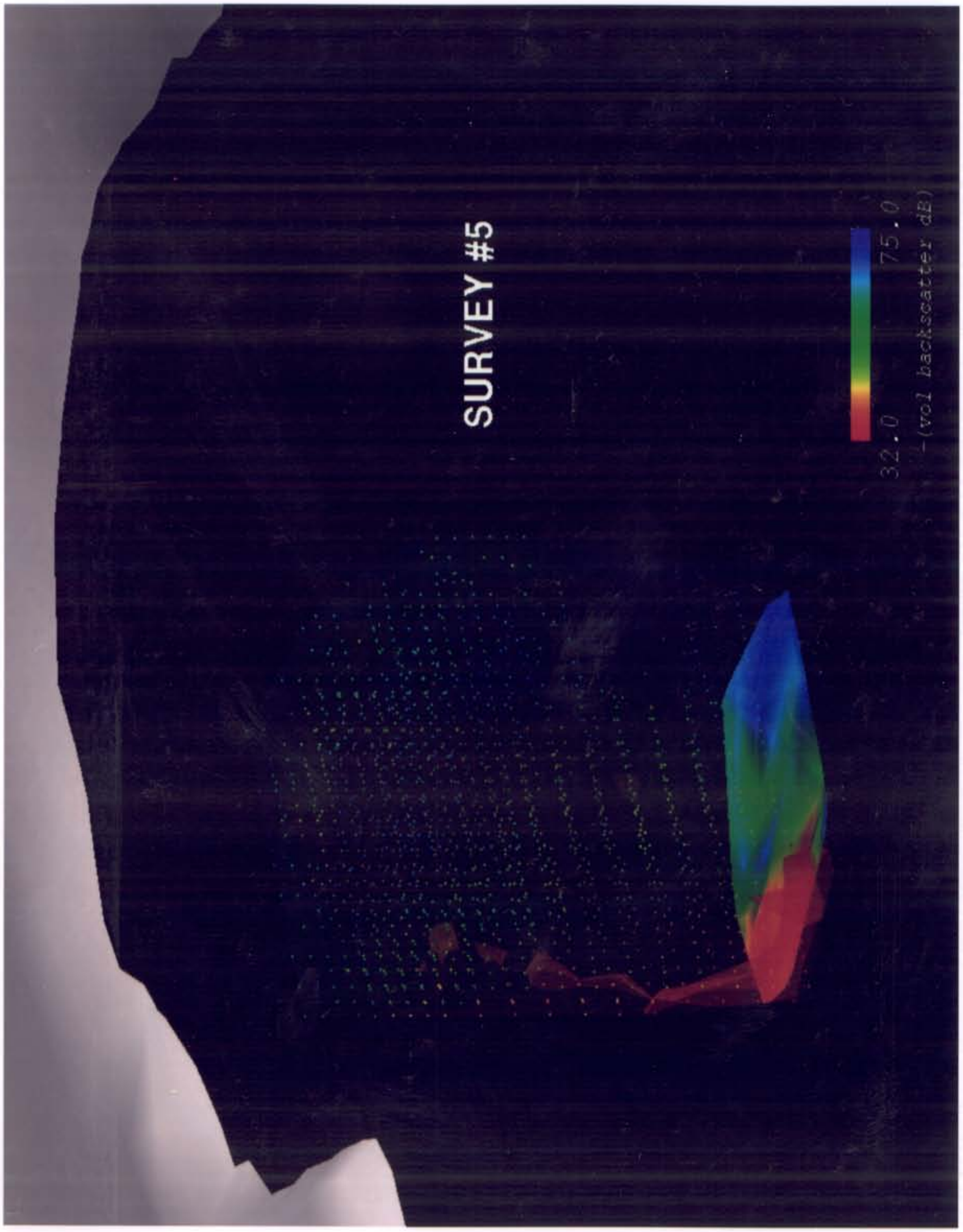
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