Chapter 6

Stable Isotopes as Food-Web Tracers

Exxon Valdez Oil Spill
Restoration Project Annual Report

Sound Ecosystem Assessment: Confirming Fish Food Web Dependencies in the Prince William Sound Ecosystem Using Natural Stable Isotope Tracers (SEA-FOOD).

Restoration Project 98320I
Annual Report

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

Thomas C. Kline, Jr., Ph. D.

Prince William Sound Science Center, P. O. Box 705, Cordova, Alaska 99574

April 1998

Scales and Patterns of Temporal and Spatial Variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in Pelagic Biota

Thomas C. Kline, Jr. (Prince William Sound Science Center, P.O. Box 705, Cordova AK 99574; 907-424-5800 (tel), -5820 (fax); tkline@grizzly.pwssc.gen.ak.us)

In: Steve Brandt and Doran Mason (eds) Space, Time and Scale: New Perspectives in Fish Ecology and Management

Abstract

Stable isotope ratios of carbon and nitrogen are useful for reconstructing flow of biogenic materials in food webs when sources of production have contrasting isotopic signatures. Potential pelagic food sources of Prince William Sound (PWS), Alaska, were characterized isotopically at the secondary production level using two approaches, (1) bulk, 335 µ-mesh, net zooplankton samples, and (2) individuals of a single herbivorous copepod species, *Neocalanus cristatus*, at life-history stage copepodite IV to VI. The two approaches produced similar results in terms of correlation and graphical analyses. There was a strong ^{13}C gradient, but weak ^{15}N gradient within the PWS northern Gulf of Alaska (GOA) study area, suggesting a regional-scale spatial isotopic pattern. ^{15}N was positively correlated with ^{13}C only during the March to April phytoplankton bloom period. This is consistent with nutrient draw-down isotope effects and suggests a seasonal-scale temporal isotopic pattern. Little correlation of ^{15}N with ^{13}C during the May to June zooplankton bloom period was consistent with decoupling of N and C cycles, because N can be regenerated via zooplankton excretion whereas C is accumulated. Interannual isotopic patterns were suggested by relatively large differences in ^{13}C of juvenile herring, pollock, and diapausing copepods from 1994 and 1995. A consistency in the spatial distribution of plankton isotopic signatures suggests a diagnostic ^{13}C for GOA carbon. Large differences in ^{13}C of pelagic biota among years is ascribed to variation in cross-shelf transport of carbon from the GOA to PWS, which is postulated to effect recruitment and nutritional processes in fishes through their food base. The natural stable isotope tracer thus provides direct evidence of fluctuations in the transfer of carbon from the GOA to PWS.

Revised Draft, as of 29 March 1998
Incorporating changes suggested by the editor and two anonymous peer-reviewers

Scales and Patterns of Temporal and Spatial Variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in Pelagic Biota

Thomas C. Kline, Jr.
Prince William Sound Science Center
P.O. Box 705, Cordova AK 99574
907-424-5800 (tel.), -5820 (fax)
tkline@grizzly.pwssc.gen.ak.us

For:
Steve Brandt and Doran Mason (eds)
Space, Time and Scale: New Perspectives in Fish Ecology and Management,
Canadian Journal of Fisheries and Aquatic Sciences

Introduction

Prince William Sound (PWS), Southcentral Alaska, is a fjordlike inland sea that receives oceanic water from the Gulf of Alaska via the Alaska Coastal Current (Niebauer et al. 1994). In PWS, Pacific herring (*Clupea pallasi*) populations have supported important commercial and subsistence fisheries. However, since 1993, herring have not been abundant enough to harvest. An ecosystem level study called Sound Ecosystem Assessment (SEA) is examining trophic interactions to see if the flow of energy through the food web is impeding recovery of herring stocks in PWS. The principal SEA hypothesis, known as the river-lake hypothesis, states that spatial and temporal variability in regional oceanographic conditions control production in PWS. Conditions are postulated to vary from lentic (lakelike) to lotic (riverlike) in relation to the strength and influence of the Alaska Coastal Current (Niebauer et al. 1994) on PWS. Physical oceanographic processes are further hypothesized to affect both bottom-up and top-down biological processes that in turn affect recruitment of exploited fish stocks. Of concern here is the bottom-up effects on Pacific herring and other fishes in PWS that are seasonal feeders, building up fat stores to sustain them when food is scarce during the winter months (Blaxter and Holiday 1963). The advective regime connecting the northern Gulf of Alaska (GOA) with Prince William Sound (PWS) is postulated to control recruitment and nutritional processes in fishes. Of special interest is the role of interzonal copepods in the zooplankton advected from the Gulf of Alaska towards the bordering continental shelf (Cooney 1988). The concomitant transfer of carbon from the GOA to PWS being demonstrated by using natural stable isotope tracers is providing direct evidence of these links.

The natural abundance of nitrogen (N) and carbon (C) stable isotope ratios measured in aquatic biota is useful for reconstructing the flow of organic material in food webs. There may be considerable C and N isotopic variability in the supply of organic material for marine pelagic food webs that is passed on to higher trophic levels with consistent enrichment of ^{13}C and ^{15}N effecting $\delta^{13}C$ and $\delta^{15}N$ increases of ~ 1 and 3.4 ‰ per trophic level, respectively (DeNiro and Epstein 1978, 1981, McConnaughey and McRoy 1979, Rau et al. 1983, Minagawa and Wada 1984, Fry and Sherr 1984, Fry 1988, Wada et al. 1991, Hobson and Welch 1992, Kling et al. 1992, Cabana and Rasmussen 1994, Vander Zanden and Rasmussen 1996). Determination of temporal and spatial patterns of C and N stable isotope variability at the food web base in an ecosystem study provides a context for tracing material flow to higher trophic levels (Fry 1988, Dunton et al. 1989, Goering et al. 1990). Isotopic signatures are generated by primary producers which are then transferred to consumers such as microcrustacea (Fry and Sherr 1984, Stephenson et al. 1986, Peterson and Howarth 1987, Fry 1988, Goering et al. 1990, Vander Zanden et al. 1997) that are an important forage base for fishes. Isotopic characterization of the food web base using herbivores provides a good ecosystem baseline (Vander Zanden et al. 1997). For example, analysis of herbivorous zooplankton eliminates the compositional uncertainty associated with particulate organic material samples typically used as a proxy for phytoplankton and its consequential confounding effects on data (Owens 1987). Furthermore, an isotopic context based upon the temporal and spatial variability in zooplankton is appropriate for using isotope techniques to understand material flow in fish food webs that are dependent upon a zooplankton forage base.

The approach taken here was to examine net zooplankton collections made on research cruises before, during, and after the Spring zooplankton bloom (March through June) as well as late Summer (September), in order to characterize regional spatial and temporal variability in the isotopic composition of zooplankton, especially in relation to the spring bloom period. Although zooplankton sampling consisted principally of bulk net samples, single zooplankter species were supplemented when available, to assess effects of zooplankton species composition on isotopic signatures. Different zooplankter taxa were collected initially, later only a large interzonal (Miller and Terazaki 1989) copepod of the genus *Neocalanus*, an important taxon that dominates the zooplankton of the epipelagic North Pacific (Miller et al. 1984). These data were then compared with juvenile herring and pollock broadly sampled within the same geographical area to assess their linkages with carbon sources represented by zooplankton. The goal of this study was to assess the nature of temporal and spatial variability of ^{13}C and ^{15}N in the pelagic ecosystem given a broadscale sampling capability. This provided a context for assessing secondary production source dependencies by rapidly growing juvenile pelagic fishes, herring and pollock in Prince William Sound.

Materials and Methods

Field sampling

Zooplankton

Zooplankton were collected in 1994 (April, May, September, November) for western Prince William Sound, Alaska (PWS) and in 1995 (March, April, May, June, September, October) for PWS and adjacent Gulf of Alaska (Fig. 1) from the F/V *Alaska Beauty* and R/V *Bering Explorer*. Sampling techniques varied according to month, year, and target taxa. A 335 μ-mesh 0.5 m diameter ring was towed from 50m to the surface at 1 m s^{-1} (at various times of day throughout each cruise, Appendix 1) to collect composite (bulk) zooplankton samples. Deep vertical tows (~20m above the bottom to the surface) were made during March to June 1995 immediately after, using the same net as, the 50m tows. Bulk samples collected from March to June 1995 were immediately inspected for *Neocalanus cristatus* and other large (length > ~7 mm) zooplankters for isotopic analysis of individuals. A deep beam trawl (~ 200 m depth, 5 mm mesh) was used at station SEA4 (Fig. 1) in April 1994 and deep horizontal tucker trawls (400 m depth; 1 mm mesh) were used at two locations (SEA22 and SEA27, Fig 1) in November 1994 to collect macrozooplankters. In September 1995, a closing "Puget Sound" net (Miller et al. 1984) was towed from ~ 20 above bottom to 200 m below surface to collect diapausing *N. cristatus*. Macrozooplankters were removed by forceps in the laboratory from the collections made in 1994.

Following removal of macrozooplankters, bulk zooplankton samples were frozen in shipboard freezers (-20 °C) in 125 mL polyethelene jars (VWR "Trace-clean"). *Neocalanus* and other macrozooplanter samples, that were individually removed from tows described above, were placed into polyethylene "Omni-vials" (Wheaton) and frozen in shipboard freezers (-20 °C). In the laboratory, frozen bulk samples were thawed, then rinsed in tap water while holding the sample in a 223 μ-mesh nitex sieve to remove salts. Rinsed samples were returned to their jars, frozen and then freeze-dried open, in a Labconco "Shelf Drier - 6 Liter Freeze Drier" unit. Bulk freeze-dried samples were ground to a fine powder using a dental amalgamator (Crescent Dental "Wig-L-Bug") and returned to their jars. Omni-vial samples were placed directly into the freeze-drier without rinsing. Freeze-dried samples were shipped to the University of Alaska Fairbanks stable isotope facility for isotopic analysis.

Juvenile Pacific herring and walleye pollock

Juvenile Pacific herring (*Clupea pallasi*) and walleye pollock (*Theragra chalcograma*) were collected throughout PWS during a multi-vessel broadscale survey conducted from October to November 1995 (Fig. 1). Additionally, opportunistic samples were obtained in 1994 (Table 6). During the broadscale survey, the lead acoustic vessel located concentrations of fishes which were sampled with a variety of gear. From seine (50 m diameter by 4 m deep with 3 mm mesh (stretched)) samplings, a random sample of 200 herring up to 150 mm in length (age 0 and 1) and a random sample of 200 pollock up to 100 mm in length (age 0) were saved for energetic (Paul et al. In Press) and isotopic analysis (this study) at each study site. Fish were immediately frozen (-20 °C) in seawater after capture and kept frozen until processing. Details of how the fish were handled in the laboratory is described in Paul et al. (In Press). Following energetic analysis (Paul et al. In Press), dried fish samples were sent from Seward to Cordova for isotopic analysis preparation that included additional grinding and homogenization. From each sampling area, 25 herring and 25 pollock were randomly selected, sealed in polyethylene LSC (Wheaton) vials, and shipped to the University of Alaska Fairbanks Stable Isotope Facility for isotopic analysis. In 1994, fish samples were obtained using similar gear and analysis techniques.

Isotopic analysis and data modeling

Replicate sub-samples of ~1.5 mg were made from all samples except individual macrozooplankters since the entire organism was required for one analysis. Sub-samples or whole zooplankters, as appropriate, were weighed to the nearest µg and loaded into combustion boats for mass spectrometric analysis at the Stable Isotope Facility at the University of Alaska Fairbanks. Isotopic analyses were performed using a semi-automated stable isotope analyzer (Europa Scientific 20/20 equipped with Roboprep sample combustion and purification unit). A single analysis produced $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios in standard delta units, $\delta^{13}C$ and $\delta^{15}N$, respectively, and %C and %N. The conventional delta notation used to express stable isotope ratios are reported relative to international standards (air for N and Vienna Peedee belemnite (VPDB) for C) and defined by the following expression:

$$(1) \qquad \delta^{15}N \text{ or } \delta^{13}C = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000 ‰$$

where R = $^{15}N/^{14}N$ or $^{13}C/^{12}C$ (Craig 1957). The isotope standards have delta values of zero by definition, i.e. $\delta^{15}N = 0$ for atmospheric N_2. Typically, replication is < 0.2 ‰. The %C and %N data were used to calculate C/N atomic ratios. The data presented here consist of mean $\delta^{13}C$, $\delta^{15}N$ and C/N in the case of bulk zooplankton and fish samples, since they were replicated.

Removal of lipid (DeNiro and Epstein 1977) and trophic level (Rau et al. 1983) isotope effects from $\delta^{13}C$ values of nekton makes it possible to assess carbon source (Kline 1997). Kline (1997) found that PWS nekton ^{13}C content was correlated with C/N (a proxy for lipid content) unless lipid-normalized. The method of McConnaughey and McRoy (1979) was used to calculate lipid-normalized $^{13}C/^{12}C$ while $\delta^{15}N$ values were used to normalize for trophic level (Kline 1997). The McConnaughey and McRoy (1979) normalization is based upon the C/N ratio using a C/N = 4 as the base level. Kline (1997) used the herbivore, *Neocalanus*, as the trophic level baseline (Vander Zanden et al. 1997) for PWS nekton. The trophic level normalization converts $^{13}C/^{12}C$ of all samples as if they were at the same trophic level as *Neocalanus*. Thus $^{13}C/^{12}C$ values of fishes can be compared directly with herbivores.

The expressions $\delta^{13}C$, $\delta^{13}C'$, $\delta^{13}C_{TL}$, or $\delta^{13}C'_{TL}$ are used to denote ^{13}C abundance in relation to the international standard, normalized for lipid content, normalized for trophic level, and normalized for lipid content and trophic level, respectively. The normalizations are used according to the context of a particular data analysis. "^{13}C" is used to reflect generic $^{13}C/^{12}C$ isotopic trends irrespective of normalization.

Data mapping

Areal distribution of isotopic data were mapped and contoured using the Generic Mapping Tools computer program (Smith and Wessel 1990, Wessel and Smith 1995).

Results

Zooplankton species- and within-station variability

Bulk Plankton
The within-station variability $\delta^{15}N$, $\delta^{13}C$, and $\delta^{13}C'$ measured in upper 50 m net zooplankton (1994-5) suggested by the standard deviation (*SD)* value for each station was on the order of 1 to 2 ‰ while annual mean isotopic value differences (Table 1) ranged up to 3.4 ‰ at individual stations. The values and ranges of the isotopic composition of net zooplankton sampled over the water column were comparable to upper 50 m samples (Appendix 1). The collective bloom period (March through June) water column and upper 50m zooplankton data were compared statistically. The water column net zooplankton $\delta^{15}N$ values were not significantly correlated ($r^2 = 0.1$) with 50 m tows from the same station and date. Correlations between $\delta^{13}C$ and $\delta^{13}C'$ were significant, however ($r^2 = 0.3$ and 0.5, respectively, Table 2).

Macrozooplankton
Macrozooplankton consisting of various taxa extracted from plankton tows made in 1994 and individually isotopically analyzed are shown in Table 3. These macrozooplankters consisted largely of diel migrators, as they were found in 50 m tows when conducted at night, as well as tows made over the water column. Macrozooplankters other than interzonal copepods had $\delta^{15}N$ values (Table 3) that were more positive than was typical of bulk net samples (Table 1). Interzonal copepods were consistently lower in $\delta^{15}N$ than other taxa, with a mean value slightly greater than +8. Euphausiids (*Euphausia pacifica* and several *Thysanoessa* spp.) had $\delta^{15}N$ of about + 10, whereas amphipods (principally *Cyphocaris challengeri*) and decapods (principally unspecified larval stages) were about + 11. Carnivorous copepods (*Euchaeta elongata*) had the most positive macrozooplankter $\delta^{15}N$ value of about +12.

Unlike $\delta^{15}N$ values, macrozooplankter $\delta^{13}C$ and $\delta^{13}C'$ values were similar to bulk sample means. $\delta^{13}C$ values, which ranged from about -19 to -23, were reduced in range to -18 to -21, when normalized to $\delta^{13}C'$. The only macrozooplankters with mean $\delta^{13}C'$ values less than -20 were interzonal copepods. Differences in trophic level (note that carnivorous copepods had the highest $\delta^{15}N$ values) and lipid storage abilities (note that lipid normalization changed ^{13}C values of copepods more than other taxa; Table 3) among the taxa comprising bulk zooplankton samples probably contributed to much of their isotopic variability. Trophic level differences among species found in bulk samples (e.g., Table 3) is conjectured to explain the poor correlation of 50 m and water column zooplankton $\delta^{15}N$ values since higher trophic level taxa were more commonly collected in deep tows.

Neocalanus cristatus

To eliminate confounding effects of higher trophic level macrozooplankton taxa (Table 3), expanded isotopic analysis of macrozooplankters focused on the large interzonal copepod *Neocalanus cristatus. N. cristatus* were found in both water column and 50 m net plankton tows (Tables 4 and 5). These data are presented separately due to the fact that those sampled from the upper 50m were limited to those actively feeding, whereas those found in the water column included copepods undergoing diapause at depth as well as those actively feeding near the surface (the later principally in May, Table 4).

Copepodite IV and V stage *Neocalanus cristatus* were most abundant in the upper 50m in May (Table 4). The isotopic values of *N. cristatus* from 50 m tows were compared statistically with the bulk net samples from which they were collected (Table 2). Although, the monthly mean $\delta^{13}C$ and $\delta^{13}C'$ values of net zooplankton and *N. cristatus* collected from March through June 1995 were correlated ($r^2 = 0.4$ and 0.5, respectively), the $\delta^{15}N$ were not significant ($r^2 < 0.1$). Restricting the data to mean $\delta^{15}N$, $\delta^{13}C$ and $\delta^{13}C'$ values of net zooplankton and *N. cristatus* collected in May 1995 altered the correlations to $r^2 = 0.3$, 0.7 and 0.7, respectively. The correlation of $\delta^{15}N$, $\delta^{13}C$ and $\delta^{13}C'$ of *N. cristatus* with bulk samples was thus strongest during the peak zooplankton bloom. Varying trophic level composition of bulk samples (herbivore contribution peaked in May) probably contributed to the reduced $\delta^{15}N$ correlations. Four tows of collections made for *N. cristatus* from the upper 50 m produced large samples ($N \geq 12$, Table 4). The SD of these samples were small; 0.5 to 0.7 for $\delta^{15}N$, 0.3 to 1.4 for $\delta^{13}C$, and 0.4 to 1.3 for $\delta^{13}C'$.

Unlike the 50 m samples, the $\delta^{15}N$ values of *N. cristatus* from the water column were similar to the bulk net samples from which they were collected. The mean $\delta^{15}N$ value of *N. cristatus* and net plankton samples collected at each station were used to make X,Y pairs and regressed (Table 2). However when the same approach was used for $\delta^{13}C$ and $\delta^{13}C'$, the regressions were weak (Table 2). Furthermore, unlike upper 50m samples, the $\delta^{15}N$ and $\delta^{13}C$ values of *N. cristatus* from the water column were not significantly correlated (Table 2). A number of the deep *N. cristatus* tows had large N (Table 5). The SD of these were greater than from 50 m samples with $N \geq 12$, ranging in SD up to 4.3.

Mean values (1994-5) of upper 50 m *N. cristatus*, upper 50 m bulk zooplankton, and water column bulk zooplankton collected at each station yielded very similar plots (Fig. 5). Taxonomic variation (and hence trophic level) as well as temporal effects on isotopic variability of bulk samples were reduced by integrating over time. Correlations among sample types were better during the peak *Neocalanus* abundance when bulk samples consisted of mainly interzonal copepods. Seasonally, diapausing interzonal copepods form a large portion of the deep bulk zooplankton in PWS and thus should have been correlated at time of sampling. However, only $\delta^{15}N$ was correlated. Poor correlation in ^{13}C could only be explained when the bimodal nature of the variability was revealed in dual-isotope plots (Fig. 4) discussed in the Gulf of Alaska signature section, below. That is, a portion of the diapausing samples had ^{13}C inconsistent with other zooplankton from the same location. This was probably the case for the Fall 1994 interzonal copepod sample as well (Table 3). Bimodality also explains the greater SD values obtained for deep *N. cristatus* compared with 50 m if the deep tows reflected a mixture of the two modes while 50 m samples consisted of only one mode.

Zooplankton temporal variability

Bulk zooplankton

Isotopic values of bulk net zooplankton samples from individual stations sampled from 1994-5 varied by as much as 3.4‰ (Table 1). Much of this variance can be ascribed to stations only sampled in Fall 1994 since those stations sampled both in the Spring and Fall of 1994 as well as in 1995 differed by less than 1 ‰ (Table 1). Fall 1994 zooplankton had an east-west $\delta^{15}N$ gradient with higher values to the east, suggesting that eastern samples consisted of a proportion of higher trophic level zooplankters. There were several locations where $\delta^{13}C'$ was isotopically higher, particularly in Montague Strait. The Fall samples reflected secondary production long after the Spring phytoplankton bloom that accounts for most of the pelagic productivity in PWS (Goering et al. 1973). Accordingly, the high variability may reflect where littoral carbon was pumped into the pelagic area by tidal action. This is a possibility in this tidally dominated system (Niebauer et al. 1994). Enriched ^{13}C is consistent with isotopic signature of littoral carbon sources such as eelgrass (Cooper 1989, McConnaughey and McRoy 1979) and macroalgae (Dunton and Schell 1987, Stephenson et al. 1986). A consistency in pelagic productivity isotopic signature, was thus more effectively assessed using only Spring bloom data as suggested by the similarity of isotopic data collected at stations CFOS13, SEA11, SEA25, SEA32, and SEA4 in early 1994 with data collected at these stations in 1995 (Appendix 1). During the PWS phytoplankton (April) and zooplankton (May) biomass peak periods the $\delta^{15}N$ within PWS was uniform (though higher in May than April) when compared with March and the previous Fall (Fig. 2) consistent with a composition principally of herbivores at this time.

Goering et al. (1990) found that during the Spring bloom period, zooplankton $\delta^{15}N$ shift to higher values following a similar shift in phytoplankton which was driven by NO_3^- depletion. Prince William Sound (PWS) zooplankton $\delta^{15}N$ values were similar to Auke Bay (Southeast Alaska near Juneau). Correlations in isotopic shifts occurring during the Spring bloom followed those by Goering et al. (1990) using $\delta^{13}C$ vs. $\delta^{15}N$ regressions. All 1995 data (Appendix 1) were regressed collectively and by month (Table 2). All $\delta^{13}C$ vs. $\delta^{15}N$ regressions were significant except May. Zooplankton $\delta^{13}C$ was correlated with $\delta^{15}N$ from April to May in Auke Bay (Goering et al. 1990) but only in March and April in PWS (Table 2) since May and June PWS zooplankton $\delta^{13}C$ and $\delta^{15}N$ values were poorly correlated. Goering et al. (1990) found the following relationship for Auke Bay zooplankton: $\delta^{13}C = 1.8\delta^{15}N - 34.2$ ($r^2 = 0.46$), which was comparable to that found here for PWS zooplankton: $\delta^{13}C = 0.8\delta^{15}N - 28.3$ ($r^2 = 0.49$) (collectively over the Spring bloom period). The reduced correlation in May and June suggests that phytoplankton isotopic fractionation effects on ^{15}N and ^{13}C become decoupled in zooplankton as the Spring bloom winds down. This may be due, in part, to recycling of N via the regenerated N pool (Dugdale and Goering 1967). Since zooplankton, and calanoid copepods in particular, build energy reserves by storing C, C and N turnover rates within the organisms must differ. Additionally, zooplankton regenerate the N pool (Dugdale and Goering 1967) with ^{15}N-depleted N (Checkley and Miller 1989) serving to counteract the N-uptake isotopic distillation process (e.g., Owens 1987). This N source became available as the zooplankton bloom developed, lagging approximately one month behind the phytoplankton.

Macrozooplankton

Variability (expressed as *SD*, Table 3) of macrozooplanton isotopic composition was greater in the Fall than Spring (except the $\delta^{15}N$ values of interzonal copepods, *Neocalanus* spp., which decreased slightly). The increase in *SD* of $\delta^{15}N$ values suggests a greater degree in omnivory (Kline and Pauly 1998) for zooplankton species during the late season.

Neocalanus cristatus

Neocalanus cristatus were more abundant in water column net tows than those made in the upper 50m (Tables 4 and 5). Abundance at particular stations varied with time (Table 5), with greatest springtime abundance in March at stations NWS4, PW1, SEA11, SEA22, and SEA27, which were deep enough to provide diapause habitat (Fig. 1). In May 1995, there were far fewer at station SEA22 with only 18 sampled compared to > 100 sampled in March (only 33 of these were analyzed, while at other stations all were analyzed). In May however, *N. cristatus* were more broadly distributed than earlier, e.g., occurring in greater number at stations CS9, HE12, HE13, PV1, SEA25, where only few had been collected before. There was a gradual isotopic shift in water column collected *N. cristatus* to more positive $\delta^{13}C'$ values in May. The mean isotopic values of *N. cristatus* sampled in March to April throughout PWS as well as those from station SEA22 were comparable to the 20 *N. cristatus* sampled with the Tucker trawl at SEA 22 in the Fall of 1994 (Tables 3 and 5). However, *N. cristatus* sampled with a closing net in the Fall of 1995 differed considerably in $\delta^{13}C'$ value, from both the Fall 1994 and Spring 1995 water column samples. The variability, expressed as *SD*, was higher for the collective Fall 1995 sample compared with previous data as were the *SD* of each station. The mean $\delta^{13}C'$ of the Fall 1995 copepods of -22.4 fell between the -23.2 and -20.6 mean $\delta^{13}C'$ values of *N. cristatus* feeding (i.e., upper 50 m samples) in the GOA and PWS, respectively, during the March to June period (Tables 5 and 6).

Zooplankton Spatial variability

Data from stations that were sampled more than one time in the period, 1994 to 1995, were pooled by station (time-integrated) to reveal the average isotopic spatial pattern occurring in the region by method of sampling (bulk net zooplankton from upper 50m and entire water column and individual *N. cristatus* from the upper 50m) in Fig. 5. Fig. 5A suggests that zooplankton $\delta^{15}N$ values were relatively uniform at ~ +8 ± 1 ‰ while Fig. 5B suggests a ^{13}C isotopic gradient of ~ 3 to 4 ‰ between the GOA and PWS independent of sampling method, though more distinct for *N. cristatus* with more negative values occurring in the GOA.

The most ^{13}C-depleted signatures in bulk zooplankton occurred at station GOA6 in June when peak zooplankton abundance occurred in the Gulf (R. T. Cooney, Univ. Alaska, Fairbanks, pers. comm.) (Appendix 1). The June GOA values were also more depleted than any value obtained from the Fall of 1994. Furthermore, the $\delta^{13}C$ and $\delta^{13}C'$ throughout the 1995 Spring sampling series were consistently more depleted at GOA6 than at PWS stations (Fig. 2). Unlike the Spring, the spatial variability in September 1994, though considerable, suggests no definitive pattern in $\delta^{13}C$ or $\delta^{13}C'$ (Fig. 2). There was, however, a $\delta^{15}N$ gradient with more positive values to the east and south. In September 1994, the $\delta^{15}N$ of zooplankton was more positive than during the 1995 Spring period (Fig. 2) than suggested by the 0.6 ‰ difference of repeated stations (Table 1). The $\delta^{15}N$ values were lower in the GOA than PWS in the Spring of 1995 by ~ 1 ‰ (Fig. 2). This difference is much less than the ~ 3 for ^{13}C values. The greater ^{13}C gradient takes on more significance when trophic fractionation factors are taken into account, e.g., if the ^{13}C difference was due to trophic level differences (i.e., ~ 3 trophic levels), an ~ 10 ‰ δ^{15}N gradient would be expected. Therefore other processes are more relevant for explaining the ^{13}C spatial variation.

Neocalanus cristatus from upper 50m in PWS when compared with data from station GOA6 suggest differences in δ^{13}C' values of 3.5 and 3.6 ‰ seasonally, and in May, respectively, between PWS and GOA (Table 4). These same PWS vs. GOA comparisons when made for δ^{13}C were similar, 4.1 and 3.9 ‰. However, δ^{15}N differed by only 1.3 and 0.8 ‰, seasonally, and in May, respectively. The δ^{15}N is suggested to be relatively uniform in the region (PWS vs. adjacent GOA) in May since the difference was < 1 *SD* (Table 4). Thus *Neocalanus cristatus* reflected the same regional isotopic spatial variability observed in bulk samples though with a more distinctive δ^{13}C' gradient (Fig. 5A).

Zooplankton bloom period spatial and temporal variability model

The availability of a large isotopic dataset based upon bulk net zooplankton samples collected throughout the March-June period (Appendix 1) over the study area enabled a broad-scale assessment of Spring bloom spatial and temporal variability in PWS. A simple numerical model was devised to integrate spatial and temporal variability utilizing statistical data derived from third order polynomial regressions made of δ^{13}C, δ^{13}C' and δ^{15}N values of upper 50 m bulk zooplankton against time (in terms of Julian day) during the Spring of 1995 (Fig. 3). The shifts in values were similar, with peak values occurring in April (Fig. 3) while normalization of δ^{13}C to δ^{13}C' doubled the time-dependent correlation to 40%. The regression analyses correlation coefficients (r^2) were incorporated into a simple variability model:

(2) $V_s + V_t + V_o = V_b$

where V_s is the spatial variability, V_t is the temporal variability, V_o are sources of variability not otherwise accounted for (e.g., isotopic variability due to species composition), and V_b is the total bloom period (broadscale) variability. The similarity in the correlations of both δ^{15}N and δ^{13}C' (Fig. 3A and C; both r^2 ~ 0.4) suggested that temporal variability was 0.4. The remaining variability is unknown. Based on eq. (2), spatial variability could be as high as 60% of V_b, given $V_0 = 0$. This 60/40 split should differ among annual Spring blooms depending upon the relative strengths of the processes affecting isotopic composition such as the strength of physical processes controlling horizontal and vertical mixing. A lack of horizontal mixing may have contributed to the observed spatial variability whereas the vertical mixing indirectly affected zooplankton isotopic composition by controlling photic zone nutrient fluxes affecting fractionation by phytoplankton. The lower correlation of $\delta^{13}C$ with time (compared with $\delta^{13}C'$), which implied a V_t of about 20% (Fig. 3B.), suggested that lipid (carbon storage) effects accounted for about 20% of V_b.

Diagnostic signatures for GOA and PWS production

The variability model analysis suggests that spatial variability in the isotopic composition of upper 50m net zooplankton may have accounted for as much as 60% of the total bloom period variability in bulk plankton samples. Spatial variability assessed by contouring the mapped data from each cruise (Fig 2) as well as time-integrated from 1994-5 (Fig. 5) suggested an isotope gradient occurring between PWS and the adjacent GOA. Figure 2 also indicated a temporal shift to more positive isotopic values from March to May and a return to lower values in June 1995 while maintaining the isotopic gradient. This gradient was evident in single species as well as mixed species bulk net samples (Fig. 5), but was particularly well-defined for the former.

Combination scatterplots with histograms (Fig. 4) suggested that $\delta^{13}C'$ values were bimodal, whereas $\delta^{15}N$ were unimodal, but slightly skewed to more positive values. These plots are distinguished by sampling method and inferred life history stage (Fig. 4). March and April 1995 water column samples consisted principally of copepods in diapause phase from the 1994 year class (the calendar year when they were actively feeding), as very few *N. cristatus* were found in the upper 50m during that period (Table 4). Since the May 1995 water column sample was more similar to the upper 50 m sample than the March or April sample, these copepods were from the 1995 year class, either feeding or just entering diapause (Fig. 4). The Fall 1995 sample (Fig. 4) was taken at depth and at the time of year when the population is in diapause. Reference lines at $\delta^{15}N = 8$, $\delta^{13}C' = -23$ and -19 are shown in each panel of Fig. 5 which aided in comparisons, suggest a consistency in occurrence of values near the intersections of the lines. These "cross-hairs" fall near the centers of the two clusters of diapausing copepods from the 1994 year class and the single dominant cluster of diapausing copepods from the 1995 year class. This latter cluster departs significantly from both the upper 50m copepods sampled throughout the Spring of 1995 as well as the May, 1995 water column data that were dominated by the $\delta^{13}C'$ values near -19. Based on the $\delta^{13}C'$ values copepods during their feeding phase stages in Spring in the GOA and PWS (Table 4), it is conjectured that the crosshairs in Fig. 5 approximate centers of the isotopic value distribution for GOA copepods on the left and PWS copepods on the right of each plot.

Juvenile herring and pollock

Age-0 and -1 herring (*Clupea pallasi*) and age-0 walleye pollock (*Theragra chalcograma*) were found in abundance at 10 and 7 sites (Table 7), respectively, during the Fall 1995 broad-scale fish survey (Norcross et al. 1996). Pollock were consistently elevated in $\delta^{15}N$ values when compared with herring, with a difference of 0.4 ‰ corresponding to an approximately 0.1 trophic level difference. Normalization reduced ^{13}C variability enabling comparisons among species without the confounding effects of trophic level and lipid content (Kline 1997). Trophic level normalization reduced the difference in $\delta^{13}C'_{TL}$ between the species in 1995 to 0.7 ‰, a value twice the *SD* and thus significant. Note that the $\delta^{13}C'_{TL}$ values of juvenile fishes in 1995 were quite different than those obtained in 1994 (Table 6). Interannual differences of 1.4 ‰ for pollock and 2.0 ‰ for herring were greater than the species differences each year.

Juvenile fishes change isotopic composition rapidly, reflecting isotopic changes in diet at temporal scales only slightly longer than zooplankton (Hesslein 1993). Isotopic spatial variability of fish may differ from large zooplankton, since they have the potential to integrate food sources of varying isotopic composition from different locations in proportion to their foraging range. This was revealed in the data (Table 6) as the differences in mean values among locations were small compared to bulk plankton samples during any one sampling period.

Discussion

The $\delta^{13}C'$ values of GOA bulk net zooplankton and *Neocalanus cristatus* sampled from the upper 50 m and bulk net zooplankton sampled from the entire water column consistently demonstrated higher levels of depletion than those in PWS, whether based on time-averaged data or based on monthly Spring bloom data. This consistency suggests that during the period of this study, 1994-5, that $\delta^{13}C'$ values less than -22, when measured at the herbivore trophic level, were diagnostic of GOA carbon. PWS production in the form of herbivore carbon, had $\delta^{13}C'$ values greater than ~ -21. This dichotomy in pelagic carbon source ^{13}C is not unlike that observed in Atlantic Ocean mesopelagic shrimp (Rau et al. 1989). Pelagic ^{13}C gradients have also been observed across the continental shelf of New England (Fry 1988), across Drake Passage (Rau et al. 1991), near Cape Hope (Rau 1989), and between the Beaufort, Chukchi, and Bering Seas off Alaska (Saupe et al. 1989). The PWS zooplankton carbon isotope range observed here confirms an isotope source effect postulated on $\delta^{13}C'_{TL}$ of ~ 1700 fish collected from PWS (Kline 1997).

The variability and distinct patterns of isotopic data that when identified with an underlying process can be used to trace variability of that process in the ecosystem. Of particular interest here is the connection of isotopic signatures with oceanographic processes that have been postulated to control the strength of secondary production which is important as fish forage within Prince William Sound (Cooney 1993, 1997). Lateral movement of interzonal copepods from the GOA continental shelf adjacent to PWS (Cooney 1986), is postulated to drive PWS zooplankton abundance (Cooney 1997), is conjectured to cause a mixture of zooplankton populations in PWS with bimodal $\delta^{13}C'$(Fig. 4).

The 1995 low $\delta^{13}C'$ value mode of *Neocalanus cristatus* diapausing in PWS were inconsistent with those sampled when they were feeding earlier in the year (Spring) within PWS. Instead, these values were very similar to those sampled in the Spring from the GOA. In comparison, those copepods sampled in the Spring in PWS were predominantly affiliated with the high $\delta^{13}C'$ value mode, particularly in May during their peak abundance. Thus many of the diapausing copepods found in PWS were affiliated with the low $\delta^{13}C'$ value mode of GOA origin copepods. It is also apparent that 1995 had a higher representation of GOA-origin copepods than diapausing copepods from the 1994 cohort. Most copepods collected in diapause during the Fall of 1995 were from the GOA, whereas only about half of the 1994 cohort originated there. The few ($N = 20$) diapaused *N. cristatus* that were collected in 1994 were similar to those sampled in Spring of 1995. Though not enough to histogram, their low mean $\delta^{13}C'$ value of -21 and large SD of 1.8 is consistent with the Spring 1995 sample shown in Fig. 4A. The timing of the collection early in the diapause period was therefore not important (the bottom row of Table 3 compares favorably with Fig. 4A), confirming the differences between the 1994 and 1995 cohorts diapausing within PWS.

The differences to the contribution of the diapaused copepod populations from the GOA mirrors differences seen in PWS juvenile herring and pollock in 1994 and 1995. In 1995, these fishes reflected the GOA isotopic signature to a much greater extent than in 1994 - - much like the copepods. A probable explanation for the observed phenomenon of coincident isotopic shift is that of variable horizontal transport of production from the GOA affecting each species each year to a similar extent. Ekman transport of zooplankton is estimated to deliver 10 million metric tons per year over the 1000 km northern GOA continental shelf;

and into the Alaska Coastal Current and coastal waters during periods of relaxed downwelling in the late Spring and Summer (Cooney 1986, 1988). The late Spring to Summer period is also the period of deep water renewal of PWS (Niebauer et al. 1994) and large tidal fluctuations. The isotopic shift suggests that these processes may vary markedly from year to year.

An alternative explanation is that the fishes carried the GOA signature into PWS. This may seem plausible but is inconsistent with what is known of herring populations in the NE Pacific (E. Brown, Univ. Alaska, Fairbanks, pers. comm.). The nearest upstream (Alaska Coastal Current) source of herring is in southeastern Alaska. This source of herring would have acquired their Gulf signature enroute to PWS. Another alternative would be to have virtually all juvenile herring and pollock leave PWS, feed in the Gulf, then each species return as a group to explain the 1995 within-species isotopic uniformity. Such a mass migration has never been noted. These scenarios seem less likely than fishes acquiring the GOA signature from their plankton diet. Since plankton are by definition drifters, their inflow into PWS is passive and thus dependent on physical processes as were the diapausing copepods. Thus, year-to-year differences in advection provides the most consistent explanation for the isotopic shifts observed in this study (Table 7).

Sample effects

Bulk zooplankton samples typically consist of a mixture of different species and life-history stages, each with potentially different trophic levels. The complex nature of bulk net plankton samples may confound interpretations because of multiple processes with attendant isotopic effects (e.g., mixing due to lateral movement and nutrient depletion related to bloom dynamics) are involved. Extensive stable isotope analysis was performed on individuals of a single copepod species as an alternative approach to reduce the confounding effects of multiple factors associated with bulk net zooplankton samples. Analysis of individual copepods was directed at copepodite - IV and - V *Neocalanus cristatus* for the following reasons: 1) they are large in size at ~7 to 10 mm in length, ~ 1 to 5 mg in weight, thus large enough for one animal per analysis, 2) they are easy to identify while fresh and at sea, 3) they have a described life history pattern (Miller et al. 1984), and 4) they are principally herbivorous (Gifford 1993), giving them a well-defined trophic level (herbivore, TL = 2). Although these copepods are consumed by herring less than 150 mm in length (B. Foy, Univ. Alaska, Fairbanks, pers. comm., including age-1 fish) and other fishes (Willette, et al. 1997) in PWS, they are probably not the prey of age-0 fishes because of gape-size limitations.

However, since *N. cristatus* and bulk net zooplankton sample $\delta^{13}C$' were strongly correlated (Table 2) and had a similar ^{13}C spatial distribution (Fig. 5B), they appear to be a good proxy for each other and for carbon source. There was no relation between $\delta^{15}N$ of *N. cristatus* and bulk net zooplankton. This may have been due, in part, to the mixed species assemblage, and therefore mixed trophic level nature of bulk samples with consequential isotope effects. *N. cristatus* ^{13}C was more strongly correlated to $\delta^{15}N$ in May than bulk samples and also had y-intercept values more similar to earlier net plankton (Table 2), possibly because *N. cristatus* reflected a greater proportion of carbon that was previously assimilated. This is consistent with their storage of carbon integrating longer time scales. Their values may reflect an averaging of the carbon isotopic variation of phytoplankton to a greater extent than nitrogen, providing further evidence of N and C decoupling in zooplankton.

N. cristatus isotopic data shown as scatterplots with frequency histograms revealed the bimodal distribution of ^{13}C in a way that was not available in the bulk net zooplankton sample analysis. The latter yielded a homogenized effect. The analyses of a large number of individual zooplankters, particularly during diapause when a large number of individuals were obtainable, revealed the bimodality. However, since bulk net zooplankton sample analysis provided a single datum for each time and place, it was more practical for assessment of spatio-temporal factors.

Scales of Variability

The data presented in this paper suggest that mesoscale spatial (e.g., ~ 100 km, the length dimension of PWS) and mesoscale temporal (seasonal to annual) scales predominated; were thus effectively the predominant isotopic variability modes (Fig. 6). Zooplankton had both spatial and temporal variability. Although there was a moderate seasonal shift in ^{15}N and ^{13}C, the spatial gradient occurring between the GOA and PWS was the principal source of ^{13}C variability and was the predominant isotopic variability mode (Fig. 6). The variability in the physical processes that drives the advection mediating the transfer of carbon in the form of zooplankton between the GOA and PWS, resulting in interannual differences in ^{13}C abundance in juvenile fishes and diapausing copepods in PWS, forms second and third variability modes. Spatial variability in fishes was negligible when the GOA transfer was great, but was present when the GOA and PWS carbon were in near balance in 1994, thus forming a weak fourth mode in ^{13}C variability (Fig. 6).

Proxy Sampling

The large interannual differences in ^{13}C measured in diapausing copepods and juvenile fishes ascribed to oceanographic processes that transfer carbon in the form of zooplankton from the GOA to PWS suggests the use of this tool as a proxy for carbon transport in long-term studies. An isotopic time series (when compared with upwelling indices and fishery statistics) could resolve a hypothetical relationship of oceanographic processes with fluctuations in fisheries, which in the northern GOA region appear to undergo regime shifts (Brodeur and Ware 1992, Francis and Hare 1994). Such sampling would require a confirmation of the isotopic gradient as well as sampling of diapaused copepods and fishes. The simplicity of single zooplankter species analysis appears to yield clearer results than bulk net sampling and may be the best sampling approach for long-term studies. *Neocalanus cristatus* consistently had low mean $\delta^{15}N$ values of ~ 8, confirming their herbivorous ecological role (Gifford 1993) and making them an ideal candidate as a carbon proxy. Although the bulk net zooplankton samples are more likely to include the small zooplankton prey of early-stage juvenile herring and pollock, the use of *N. cristatus*, an herbivorous species, in the analysis, eliminates species composition, life history stage, and trophic level as sources of variability. The PWS setting includes an area of deep water to (> 700 m depths) that provides an isolated and well-defined diapausing habitat for *Neocalanus* sp. that could be easily sampled on a consistent basis to determine if changes in source of diapausing copepods occurred in cycles like those postulated for zooplankton abundance in the subarctic Pacific ocean (Brodeur and Ware 1992).

Fishes dependent on GOA carbon would be subject to vagaries of carbon flow that fall under the domain of physical oceanographic processes connecting the GOA with PWS. If fishes were wholly dependent on PWS carbon, they would be more directly affected by internal PWS processes. However, increased competition for PWS carbon by all species could occur if GOA carbon was less available to those that normally use it. Shifting to increased dependency on PWS carbon by species with normal affinity for GOA carbon during years of poor GOA carbon availability would provide evidence of competition for a limited carbon supply by the increasing overlap in their ^{13}C. Decadal cyclity in fish populations in the Northeast Pacific is postulated to results from decadal changes in the ring of zooplankton around the Gulf of Alaska (Francis and Hare 1994). This study suggests that zooplankton stocks are further transported, into PWS, being detectable by changes in ^{13}C abundance. Time series measurements of natural stable isotopes in zooplankton and fishes in conjunction with population indices and physical oceanographic measurements could thus enable a new understanding of how climatically-driven bottom-up processes affect fish recruitment and interaction.

Acknowledgments: This project was funded by the *Exxon Valdez* Oil Spill Trustee Council through the Sound Ecosystem Assessment project. However, the findings presented by the author are his own and not necessarily the Trustee Council's position. SEA colleagues collected fish specimens. Evelyn Brown oversaw aging of the fish. J. M. Paul and P. Shoemaker did the initial fish sample preparation. Captain Mike Gaegel, the crew of the *R/V Bering Explorer*, E. Stockmar, J. Murphy, B. Barnett, and T. Cooney assisted with *Neocalanus cristatus* sampling. Kim Antonucci did the laboratory processing of samples for stable isotope analysis. Bruce Barnett at the University of Alaska Fairbanks Stable Isotope Facility performed the stable isotope analysis. John Williams made the station map and contour plots. We thank Paul Wessel and others in the GMT discussion group for assisting with Fig. 1. Kate Williams assisted with editing the first draft.

Literature Cited

Blaxter J. H. and F. G. Holiday. 1963. The behavior and physiology of herring and other clupeids. Adv. Mar. Biol. 1: 261-393.

Brodeur, R.D. and D.M. Ware. 1994. Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. Fish. Oceanogr. 1:32-38.

Cabana, G. and J. B. Rasmussen. 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372:255-257.

Checkley, D. M., Jr. and C. A. Miller. 1989. Nitrogen isotopic fractionation by oceanic zooplankton. Deep-Sea Res. 36:1449-1456.

Cooney, R.T. 1986. The seasonal occurrence of *Neocalanus cristatus*, *Neocalanus plumchrus*, and *Eucalanus bungii* over the shelf of the northern Gulf of Alaska. Cont. Shelf Res. 5:541-553.

Cooney, R. T. 1988. Distribution and ecology of zooplankton in the Gulf of Alaska: a synopsis. *In:* (Nemoto, T. and W.G. Pearcy (eds.) *The biology of the subarctic Pacific, proceedings of the Japan-United States of America seminar on the biology of micronekton of the subarctic Pacific, Part I*. Bull. Ocean Res. Inst., University of Tokyo. p. 27-41.

Cooney, R. T. 1993. A theoretical evaluation of the carrying capacity of Prince William Sound, Alaska, for juvenile Pacific salmon. Fish. Res. 18:77-87.

Cooney, R. T. and K. O. Coyle. 1996. Sound Ecosystem Assessment: The role of zooplankton in the Prince William Sound Ecosystem. *Exxon Valdez* Oil Spill Restoration Project Annual Report

(Restoration Project 95320-H), Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99775-1080.

Cooney, R. T. 1997. Sound Ecosystem Assessment (SEA): A science plan for the restoration of injured species in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 96320), Institute of Marine Science, University of Alaska Fairbanks, Fairbanks, Alaska 99775-7220.

Cooper, L. W. 1989. Patterns of carbon isotopic variability in eelgrass, *Zostera marina* L., from Izembek Lagoon, Alaska. Aquat. Bot. 34:329-339.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochim. Cosmochim. Acta 12:133-149.

DeNiro, M. J. and S. Epstein. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. Science. 197:261-263.

DeNiro, M. J. and S. Epstein. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochim. Cosmochim. Acta 42:495-506.

DeNiro, M. J. and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta . 45:341-353.

Dugdale, R. C. and J. J. Goering. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. Limnol. Oceanogr. 9:507-510.

Dunton, K. H. and D. M. Schell. 1987. Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an Arctic kelp community: $\delta^{13}C$ evidence. Mar. Biol. 93:615-625.

Dunton, K. H., S. M. Saupe, A. N. Golikov, D. M. Schell, and S. V. Schonberg. 1989. Trophic relationships and isotopic gradients among Arctic and subarctic marine fauna. Mar. Ecol. Progr. Ser. 56:89-97.

Francis, R.C. and S.R. Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the northeast Pacific: a case for historical science. Fish. Oceanogr. 3:279-291.

Fry, B. and E. B. Sherr. 1984. δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contr. Mar. Sci. 27:13-47.

Fry, B. 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. 33:1182-1190.

Gifford, D. J. 1993. Protozoa in the diets of *Neocalanus* spp. in the oceanic subarctic Pacific. Prog. Oceanogr. 32:223-237.

Goering, J. V. Alexander, and N. Haubenstock. 1990. Seasonal variability of stable carbon and nitrogen isotope ratios of organisms in a north Pacific bay. Estuar. Coast. Shelf Sci. 30:239-260.

Goering , J. J., C. J. Patton and W. E. Shiels. 1973. Primary Production *In:* D. W. Hood, W. E. Shiels, and E. . Kelley (eds), *Environmental Studies of Port Valdez*. Inst. Mar. Sci. Occ. Pub. No. 3. University of Alaska Fairbanks. P. 253-279.

Hesslein, R. H., K. A. Hallard, and P. Ramlal. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by δ^{34}S, δ^{13}C, and δ^{15}N. Can. J. Fish. Aquat. Sci. 50:2071-2076.

Hobson, K. A. and H. E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using δ^{13}C and δ^{15}N analysis. Mar. Ecol. Prog. Ser. 84:9-18.

Kline, T. C. 1997. Confirming forage fish food web dependencies in the Prince William Sound ecosystem using natural stable isotope tracers. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 9701. University of Alaska Fairbanks. P. 257 - 269.

Kline, T.C. and D. Pauly. 1998. Cross-validation of trophic level estimates from a mass-balance model of, and ^{15}N/^{14}N data from, Prince William Sound. Proceedings of the International Symposium on Fishery Stock Assessment Models for the 21st Century -- Combining Multiple Data Sources. Alaska Sea Grant College Program Report. University of Alaska Fairbanks. In Press.

Kling, G. W., B. Fry, and W. J. O'Brien. 1992. Stable isotopes and planktonic trophic structure in Arctic lakes. Ecology 73:561-566.

McConnaughey, T. and C. P. McRoy. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Mar. Biol. 53:257-262.

Miller, C. B., B. W. Frost, H. P. Batchelder, M. J. Clemons, and R. E. Conway. 1984. Life histories of large, grazing copepods in a subarctic ocean gyre: *Neocalanus plumchrus*, *Neocalanus cristatus*, and *Eucalanus bungii*. Progr. Oceanogr., 13:201-243.

Miller, C. B. and M. Terazaki. 1989. The life histories of *Neocalanus flemingeri* and *Neocalanus plumchrus* in the Sea of Japan. Bull. Plankton Soc. Japan 36:27-41.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta 48:1135-1140.

Niebauer, H.J., T.C. Royer, and T.J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. J. Geophys. Res. 99:113-126.

Norcross, B. L., E. D. Brown, K. D. E. Stokesbury, and M. Frandsen. 1996. Juvenile herring growth and habitat, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 95320T), University of Alaska Fairbanks, Institute of Marine Science, Fairbanks, Alaska.

Owens, N. J. P. 1987. Natural variations in ^{15}N in the marine environment. Advances in Marine Biology 24:389-451.

Patrick, V. et al. 1997. Sound Ecosystem Assessment: information systems and model development. *Exxon Valdez* oil spill restoration project annual report (Restoration project 96320J), Prince William Sound Science Center, Cordova, Alaska.

Paul, A. J., J. M. Paul and E. Brown. Fall and Spring somatic energy content for Alaskan Pacific herring (*Clupea pallasi* Valenciennes 1847) relative to age, size and sex. J.Exp. Mar. Biol. Ecol. In Press.

Peterson, B. J. and R. W. Howarth. 1987. Sulfur, carbon and nitrogen isotopes used to trace organic matter flow in the salt-marsh estuaries of Sapelo Island, Georgia. Limnol. Oceanogr. 32:1195-1213.

Rau, G.H. 1989. AMERIEZ 1986: Carbon-13 and Nitrogen-15 natural abundances in Southern Ocean biota collected during AMERIEZ 1986. Antarct. J. of the U.S. 24:168-169.

Rau, G.H., M. Heyraud, and R.D. Cherry. 1989. $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in mesopelagic shrimp from the northeast Atlantic Ocean: evidence for differences in diet. Deep-Sea Res. 36:1103-1110.

Rau, G.H., T. Takahasi, D.J. Des Marais, and C.W. Sullivan. 1991. Particulate organic matter $\delta^{13}C$ variations across the Drake Passage. J. Geophys. Res. 96:131-135.

Rau, G.H., A.J. Mearns, D.R. Young, R.J. Olson, H.A. Schafer, and I.R. Kaplan. 1983. Animal $^{13}C/^{12}C$ correlates with trophic level in epipelagic food webs. Ecol. 64:1314-1318.

Saupe,S.M., D.M. Schell, and E.W. Griffiths. 1989. Carbon isotope ratio gradients in western Arctic zooplankton. Mar. Biol. 103:427-433.

Smith, W. H. F., and P. Wessel. 1990. Gridding with continuous curvature splines in tension. Geophys. 55:293-305.

Stephenson, R. L., F. C. Tan, and K. H. Mann. 1986. Use of stable carbon isotope ratios to compare plant material and potential consumers in a seagrass bed and kelp bed in Nova Scotia, Canada. Mar. Ecol. Progr. Ser. 30:1-7.

Vander Zanden, M.J. and J.B. Rasmussen. 1996. A trophic position model of pelagic food webs: impact on contaminant bioaccumulation in lake trout. Ecol. Monogr. 66:451-477.

Vander Zanden, M.J., G. Cabana, and J.B. Rasmussen. 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}N$) and literature dietary data. Can. J. Fish. Aquat. Sci. 54:1142-1158.

Wada, E., H. Mizutani, and M. Minagawa. 1991. The use of stable isotopes for food web analysis. Crit. Rev. Food Sci. Nutr. 30:361-371.

Wessel, P. and W.H.F. Smith. 1995. New version of the Generic Mapping Tools released. EOS Trans. Amer. Geophys. U. 72:441, 445-446.

Willette, M., M. Clapsadl, P. Saddler, M. Powell. 1997. Sound ecosystem assessment: salmon and herring integration. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 96320E), Alaska Department of Fish and Game, Cordova, Alaska.

Wu, J. S.E. Calvert, and C.S. Wong. 1997. Nitrogen isotope variations in the subarctic Pacific: relationships to nitrate utilization and trophic structure. Deep Sea Res 44:287-314.

Table 1. Interannual differences of Prince William Sound, Alaska net zooplankton isotopic composition by oceanographic station; 1994 vs. 1995.

	1994			1995				(1994-1995)		
Station	$\delta^{15}N$	$\delta^{13}C$	$\delta^{13}C'$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{13}C'$		$\delta^{15}N$	$\delta^{13}C$	$\delta^{13}C'$
CFOS13	8.2	-21.2	-19.6	7.6	-22.1	-19.5		0.5	0.9	-0.1
CS3	9.4	-21.2	-17.2	8.4	-21.7	-19.1		1.0	0.6	1.8
HE12	9.6	-21.0	-17.5	7.5	-23.0	-20.9		2.1	2.0	3.4
MS3	9.1	-22.3	-19.4	7.5	-22.3	-19.7		1.5	0.0	0.3
MS6	8.6	-21.6	-18.8	8.6	-21.5	-19.0		0.0	-0.1	0.2
NS1	9.6	-23.2	-20.1	8.4	-22.2	-19.7		1.1	-1.0	-0.4
NWS4	10.0	-22.8	-20.1	8.5	-21.7	-19.1		1.5	-1.1	-1.1
SEA11	8.7	-22.0	-19.6	8.9	-22.0	-19.3		-0.1	0.0	-0.2
SEA22	5.6	-23.2	-20.6	8.3	-21.0	-18.6		-2.7	-2.2	-2.0
SEA25	9.0	-22.4	-20.4	8.4	-21.9	-19.5		0.6	-0.5	-0.9
SEA27	9.1	-22.4	-20.4	8.4	-21.7	-18.9		0.8	-0.7	-1.5
SEA32	9.3	-22.0	-20.0	8.1	-22.2	-19.8		1.2	0.2	-0.2
SEA37	9.1	-21.3	-17.5	7.9	-22.9	-20.8		1.2	1.6	3.3
SEA4	7.7	-22.7	-20.0	8.4	-22.3	-19.4		-0.7	-0.4	-0.6
							mean	0.6	-0.1	0.1

Table 2. Regression analyses: their correlation, intercept and slope values with probabilities.

Data	Fixed Parameter	Variable 1	Variable 2	r^2	P	Intercept	P	Slope	P	N
Net Zooplankton										
Spring 95	Upper 50m	$\delta^{15}N$	$\delta^{13}C$	0.4420	<.0001	-28.2920	<.0001	0.7770	<.0001	79
Mar-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C$	0.5690	0.0070	-29.8010	<.0001	0.9880	0.0007	16
Apr-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C$	0.7440	<.0001	-28.4750	<.0001	0.8410	<.0001	22
May-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C$	0.1290	0.1314	-25.0520	<.0001	0.4310	0.1314	19
Jun-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C$	0.1770	0.0291	-29.6230	<.0001	0.8870	0.0291	22
Spring 95	Upper 50m	$\delta^{15}N$	$\delta^{13}C'$	0.4870	<.0001	-27.2490	<.0001	0.9480	<.0001	79
Mar-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C'$	0.5420	0.0011	-28.3880	<.0001	1.0580	0.0011	16
Apr-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C'$	0.5480	<.0001	-25.2310	<.0001	0.7440	<.0001	22
May-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C'$	0.1880	0.0639	-22.4440	<.0001	0.4720	0.0639	19
Jun-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C'$	0.1680	0.0582	-26.1440	<.0001	0.7290	0.0582	22
Temporal comparisons										
	Upper 50m	Julian Date (Apr & May)	Auke $\delta^{15}N$	0.8670	0.0069	4.5980	0.0019	0.0250	0.0069	6
	Upper 50m	Julian Date (Apr & May)	PWS $\delta^{15}N$	0.5860	<.0001	0.4490	0.5473	0.0690	<.0001	82
	Upper 50m	Julian Date (Apr & May)	Auke $\delta^{13}C$	0.7290	0.0304	-26.8740	0.0002	0.0530	0.0304	6
	Upper 50m	Julian Date (Apr & May)	PWS $\delta^{13}C$	0.3570	<.0001	-26.7640	<.0001	0.0450	<.0001	82
Net zooplankton, Spring 1995										
	$\delta^{15}N$	Water column	Upper 50m	0.1040	0.0330	5.5020	<.0001	0.2990	0.0330	44
	$\delta^{13}C$	Water column	Upper 50m	0.3290	<.0001	-10.2450	0.0004	0.5440	<.0001	43
	$\delta^{13}C'$	Water column	Upper 50m	0.5100	0.0003	-6.3630	0.0520	0.7200	0.0003	43
Neocalanus vs. Net Zooplankton		Upper 50m	Upper 50m							
Spring 95	$\delta^{15}N$	Net zooplankton	*Neocalanus cristatus*	0.0030	0.8220	7.9440	0.0117	0.0730	0.8220	18
Spring 95	$\delta^{13}C$	Net zooplankton	*Neocalanus cristatus*	0.4260	0.0013	-1.6160	0.7564	0.8910	0.0013	21
Spring 95	$\delta^{13}C'$	Net zooplankton	*Neocalanus cristatus*	0.5100	0.0003	-6.3630	0.0520	0.7200	0.0003	21
May-95	$\delta^{15}N$	Net zooplankton	*Neocalanus cristatus*	0.0300	0.6118	6.9980	0.0175	0.1360	0.6118	11
May-95	$\delta^{13}C$	Net zooplankton	*Neocalanus cristatus*	0.2040	0.1408	-6.1190	0.5128	0.6790	0.1408	12
May-95	$\delta^{13}C'$	Net zooplankton	*Neocalanus cristatus*	0.5240	0.0078	-0.6840	0.9074	1.0400	0.0078	12
		Water column	Upper 50m							
Spring 95	$\delta^{15}N$	Net zooplankton	*Neocalanus cristatus*	0.1100	0.0688	5.7160	0.0002	0.2790	0.0688	31
Spring 95	$\delta^{13}C$	Net zooplankton	*Neocalanus cristatus*	0.1160	0.0564	-15.5910	<.0001	0.2650	0.0564	32
Spring 95	$\delta^{13}C'$	Net zooplankton	*Neocalanus cristatus*	0.0360	0.2983	-16.7420	<.0001	0.1690	0.2983	32
Neocalanus cristatus										
Spring 95	Upper 50m	$\delta^{15}N$	$\delta^{13}C$	0.2620	<.0001	-29.3380	<.0001	0.9890	<.0001	124
May-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C$	0.2060	<.0001	-29.6210	<.0001	1.0670	<.0001	72
Spring 95	Upper 50m	$\delta^{15}N$	$\delta^{13}C'$	0.3510	<.0001	-28.0150	<.0001	0.9050	<.0001	124
May-95	Upper 50m	$\delta^{15}N$	$\delta^{13}C'$	0.3380	<.0001	-29.9510	<.0001	1.1760	<.0001	72
Spring 95	Water column	$\delta^{15}N$	$\delta^{13}C$	0.0790	<.0001	-24.3770	<.0001	0.3640	<.0001	420
Spring 95	Water column	$\delta^{15}N$	$\delta^{13}C'$	0.0060	0.1003	-20.9130	<.0001	0.0920	0.1003	420

Table 3. Macro-zooplankton: isotopic data of individual zooplankters by taxon collected in Prince William Sound, Alaska in 1994. Copepods were distinguished as carnivorous (C) or interzonal (I). Fall 1994 interzonal copepods consisted of *Neocalanus cristatus* in diapause.

Taxon/Season	$\delta^{15}N$	SD	$\delta^{13}C$	SD	$\delta^{13}C'$	SD	*N*
Amphipods							
Spring	11.58	0.79	-20.25	1.10	-18.46	0.81	23
Fall	10.58	2.02	-21.55	1.19	-18.94	1.14	85
Decapods							
Spring	11.39	1.52	-20.42	0.46	-19.53	0.28	38
Fall	11.22	1.92	-20.56	0.88	-19.04	0.67	20
Euphausiids							
Spring	10.53	0.57	-19.36	0.56	-18.71	0.53	55
Summer	9.36	0.28	-19.76	0.63	-19.34	0.62	20
Fall	10.72	1.90	-21.24	1.13	-19.70	0.81	95
Copepods(C)							
Spring	12.00	0.24	-21.38	0.40	-19.98	0.39	6
Fall	11.91	0.62	-22.43	0.67	-19.92	0.33	23
Copepods(I)							
Spring	8.64	1.20	-22.96	0.96	-19.81	1.18	59
Fall	8.33	1.07	-22.89	2.12	-20.95	1.75	20

Table 4. Isotopic composition of copepodite IV and V *Neocalanus cristatus* sampled from upper 50 m at indicated oceanographic stations in Prince William Sound and northern Gulf of Alaska where at least one individual was found in March to June, 1995, except no monthly table is given for March since only 8 were found in total. Zeros indicate that none were found while NS indicate that station was not sampled. Mean $\delta^{13}C'$, $\delta^{15}N$, and $\delta^{13}C$, their *SD*, and *N* of total sample collected from each station given. The *N* for some $\delta^{15}N$ analyses are less than the station sample total when copepods contained too little N for the analysis (B. Barnett, mass. spec. technician, pers. comm.). The total means for only Prince William Sound (PWS) stations just above Gulf of Alaska station GOA6 to facilitate comparison of mean PWS values with GOA values.

	April									**May**								
Station	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	SD	N	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N
CFOS 13			0			0			0	8.7		1	-19.8		1	-19.3		1
CFOSBY			0			0			0	8.3	0.5	21	-19.7	0.3	21	-19.7	0.4	21
CS3			0			0			0	7.8	0.8	11	-20.0	0.3	11	-19.9	0.6	11
CS9			0			0			0			0			0			0
HE12			0			0			0	8.2	0.3	2	-19.7	0.0	2	-19.4	0.5	2
NS1	7.9		1	-23.1		1	-20.8		1	8.6	0.2	2	-19.2	0.8	2	-18.8	0.7	2
NWS4			0			0			0	9.3	0.6	4	-20.2	0.5	4	-18.6	0.5	4
OB1	7.1		1	-20.8		1	-18.7		1			0			0			0
OB2	9.1		1	-22.9		1	-20.9		1			0			0			0
PV1			0			0			0	8.7	0.2	2	-19.2	0.9	2	-18.9	0.9	2
PW1			0	-20.2		1	-20.3		1			0			0			0
SEA11			0			0			0	8.4	1.1	10	-20.4	1.1	10	-19.4	0.6	10
SEA22	9.1		0	-20.3	1.5	3	-19.3	1.6	3			0			0			0
SEA25	8.8	1.5	8	-21.7	1.4	8	-19.4	1.3	8			0			0			0
SEA4			0			0			0	8.3	0.6	3	-20.5	0.5	3	-19.4	0.9	3
all PWS	8.6	1.4	12	-21.5	1.4	15	-19.6	1.2	15	8.3	0.8	56	-19.9	0.7	56	-19.5	0.6	56
GOA6			NS			NS			NS	7.5	0.7	20	-23.8	1.4	20	-23.1	1.3	20

	June									**Mar-Jun**								
	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N
CFOS 13			0			0			0	8.7		1	-19.8		1	-19.3		1
CFOSBY			0			0			0	8.3	0.5	21	-19.7	0.3	21	-19.7	0.4	21
CS3			0			0			0	7.8	0.8	9	-20.0	0.3	11	-19.9	0.6	11
CS9	8.7	0.5	14	-20.1	0.6	14	-20.3	0.6	14	8.7	0.5	14	-20.1	0.6	14	-20.3	0.6	14
HE12			0			0			0	8.2	0.3	2	-19.7	0.0	2	-19.4	0.5	2
NS1			0			0			0	8.4	0.4	3	-20.5	2.3	3	-19.5	1.3	3
NWS4			0			0			0	9.3	0.6	4	-20.7	1.1	5	-19.1	1.1	5
OB1			0			0			0			0	-20.8		1	-18.7		1
OB2	8.3	1.2	8	-19.4	0.6	8	-19.9	0.8	8	8.2	1.2	9	-19.8	1.3	9	-20.0	0.8	9
PV1			0			0			0	8.7	0.2	2	-19.2	0.9	2	-18.9	0.9	2
PW1			0			0			0	9.5	1.5	6	-20.3	2.1	7	-19.8	1.5	7
SEA11			0			0			0	8.8	1.9	11	-20.3	1.2	11	-19.4	0.6	11
SEA22			0			0			0	9.1		1	-20.3	1.5	3	-19.3	1.6	3
SEA25			0			0			0	8.8	1.5	8	-21.7	1.4	8	-19.4	1.3	8
SEA4			0			0			0	8.3	0.6	3	-20.5	0.5	3	-19.4	0.9	3
all PWS	8.6	0.8	22	-19.8	0.7	22	-20.2	0.7	22	8.6	1.1	94	-20.2	1.1	101	-19.7	0.9	101
GOA6	7.0	0.5	12	-25.1	0.9	12	-23.5	0.6	12	7.3	0.7	30	-24.3	1.4	32	-23.2	1.1	32

Table 5. Isotopic composition of copepodite V and VI *Neocalanus cristatus* sampled from the water column at indicated oceanographic stations in Prince William Sound and northern Gulf of Alaska where at least one individual was found in March to June, 1995. Number of copepods collected at each station each month are given. Zeros indicate that none were found while NS indicates that the station was not sampled. ND indicates "no data" while an N less than the station sample total reflect copepods containing too little nitrogen for the analysis (B. Barnett, mass. spec. technician, pers. comm.). Data for the Fall cruise which started in September and ended in October are given in the Sept-Oct block. Means for the March to April and March to May period are given at the bottom.

	March									**April**								
Station	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N
CFOS 13	10.6	0.8	7	-20.7	2.0	7	-20.0	1.9	7			ND	-20.0	1.0	2	-17.6	0.4	2
CS4			NS			NS			NS			NS			NS			NS
CS9			ND	-21.1	2.4	4	-19.6	2.4	4	8.1	0.6	2	-21.4	0.4	3	-20.0	1.1	3
HE11	6.8		1	-23.2		1	-21.4		1			NS			NS			NS
HE12			0			0			0			0			0			0
HE13	8.6	1.8	9	-20.3	1.4	9	-20.0	1.6	9	6.8		1			ND			ND
NS2			NS			NS			NS			NS			NS			NS
NWS4	9.0	1.5	20	-21.5	2.3	20	-20.7	1.8	20	9.5	1.1	16	-21.6	1.8	16	-20.5	1.6	16
PB1			NS			NS			NS	7.1	0.7	2	-21.2	1.2	3	-19.8	1.1	3
PV1			NS			NS			NS	9.0		1	-22.1	1.2	3	-20.4	1.0	3
PW1	8.8	2.3	21	-22.0	2.3	21	-21.1	1.9	21	9.1	1.7	17	-21.4	2.1	17	-20.8	1.9	17
SEA11	8.9	1.5	20	-21.5	2.1	20	-20.6	1.9	20	8.0	0.9	15	-22.5	1.8	18	-20.5	1.8	18
SEA22	8.0	0.9	31	-21.6	2.4	33	-20.4	2.1	33	7.8	1.4	30	-22.2	2.4	33	-20.2	2.0	33
SEA25			NS			NS			NS	8.7	2.3	8	-23.1	1.1	8	-21.6	1.2	8
SEA27	9.3	2.1	22	-22.1	2.1	26	-21.2	1.7	26	8.9	1.0	12	-21.2	1.6	17	-20.0	1.4	17
SEA4	9.4		1	-21.4	0.8	2	-21.2	1.9	2	8.3	1.0	11	-21.2	1.5	14	-19.7	1.3	14
all PWS	8.8	1.7	132	-21.6	2.2	143	-20.7	1.9	143	8.5	1.5	115	-21.8	1.9	134	-20.3	1.7	134

	May									**Sept-Oct**								
	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N
CFOS 13	8.2	0.1	3	-20.9	0.1	3	-18.5	0.3	3	7.1	1.9	24	-24.4	1.6	24	-22.4	1.6	24
CS4	8.6	0.7	19	-20.2	0.5	20	-19.4	1.0	20			NS			NS			NS
CS9	8.9	1.0	12	-20.6	0.8	13	-19.6	0.8	13			NS			NS			NS
HE11			NS			NS			NS			NS			NS			NS
HE12	8.0	0.5	20	-20.1	0.3	21	-19.7	0.6	21			NS			NS			NS
HE13	8.0	0.9	18	-21.3	1.2	20	-21.1	1.2	20	8.5	2.6	12	-23.0	1.7	12	-21.7	1.7	12
NS2			NS			NS			NS	8.9	3.0	25	-24.3	1.7	25	-22.6	1.7	25
NWS4	8.3	0.9	8	-20.8	1.2	12	-19.4	0.9	12	6.9	1.7	26	-23.6	1.1	26	-22.3	1.1	26
PB1			NS			NS			NS			NS			NS			NS
PV1	8.2	0.7	19	-20.4	1.1	19	-19.3	0.9	19			NS			NS			NS
PW1	7.5	1.2	13	-21.2	1.2	13	-19.5	0.8	13			NS			NS			NS
SEA11	7.6	1.1	13	-20.5	0.8	18	-19.0	0.4	18	7.9	1.7	25	-24.3	1.3	25	-22.5	1.3	25
SEA22	6.8	0.9	17	-22.0	1.8	18	-19.7	1.7	18	6.8	1.8	50	-24.5	1.2	50	-22.5	1.2	50
SEA25	7.6	1.0	10	-21.0	2.2	12	-19.7	1.8	12	7.1	1.9	25	-24.0	1.2	25	-22.3	1.2	25
SEA27	7.8	1.3	11	-20.9	0.5	11	-19.1	0.8	11	11.5	4.3	22	-23.0	1.2	22	-22.3	1.2	22
SEA4	8.0	0.7	11	-20.9	1.0	12	-19.6	0.6	12			NS			NS			NS
all PWS	7.9	1.0	174	-20.8	1.8	192	-19.6	1.1	192	7.8	2.8	209	-24.0	1.6	209	-22.4	1.4	209

	Mar-Apr									**Mar-May**								
	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N	$\delta^{15}N$	*SD*	N	$\delta^{13}C$	*SD*	N	$\delta^{13}C'$	*SD*	N
all PWS	8.7	1.6	247	-21.7	2.1	277	-20.5	1.8	277	8.4	1.4	421	-21.3	1.8	469	-20.1	1.6	469

Table 6. Juvenile herring (Age 0 and 1) and pollock (age 0) isotopic data from indicated Prince William Sound sampling sites (Map codes refer to site location symbols in Fig. 1) sampled from 1994 to 1995. Annual means are given for each species on top line of their respective data blocks.

1994

Age 0 and 1 Herring	Map code	$\delta^{15}N$ Mean	SD	$\delta^{13}C$ Mean	SD	$\delta^{13}C'_{TL}$ Mean	SD	N
Total		12.3	0.93	-20.9	1.12	-20.8	0.80	110
Apr-Wells Passage	H	12.1	1.86	-20.5	0.69	-19.9	0.54	20
Jun-Knight Is. Pass.	I	13.1	0.21	-19.8	0.57	-20.8	0.50	9
Oct-Port Gravina	C	12.0	0.49	-22.0	0.76	-21.5	0.49	31
Oct-Knowles Head	D	13.1	0.18	-19.5	0.34	-20.8	0.35	13
Oct- Windy Bay	B	12.2	0.26	-20.9	0.90	-20.8	0.74	37

Age 0 Pollock		$\delta^{15}N$ Mean	SD	$\delta^{13}C$ Mean	SD	$\delta^{13}C'_{TL}$ Mean	SD	N
Total		11.3	0.88	-20.3	1.00	-20.7	0.51	116
Jul-Knight Is.Pass.	I	10.6	0.20	-21.1	0.23	-20.8	0.15	59
Sep-Redhead/Gravina	C	11.4	0.15	-19.4	0.23	-20.3	0.22	20
Oct-Redhead/Gravina	C	12.4	0.64	-18.9	1.49	-20.3	1.33	11
Oct-Windy Bay	B	12.5	0.20	-19.7	0.41	-20.6	0.43	26

Fall 1995

Age 0 and 1 Herring		$\delta^{15}N$ Mean	SD	$\delta^{13}C$ Mean	SD	$\delta^{13}C'_{TL}$ Mean	SD	N
Total		12.7	0.34	-22.7	0.62	-22.8	0.37	250
Eaglek Bay	G	12.7	0.35	-22.9	0.73	-22.8	0.52	25
Green Island	M	12.7	0.22	-22.5	0.40	-22.6	0.23	25
Hogg Bay	K	12.7	0.32	-22.3	0.46	-22.7	0.18	25
Jack Bay	F	12.6	0.33	-22.5	0.51	-22.7	0.29	25
Knowles Head	D	12.7	0.36	-23.4	0.71	-22.9	0.58	25
Sawmill Bay	L	12.8	0.27	-22.9	0.39	-22.9	0.26	25
Simpson Bay	A	12.7	0.24	-22.6	0.67	-22.8	0.43	25
Snug Corner Cove	E	12.8	0.35	-22.5	0.59	-22.9	0.37	25
Whale Bay	J	12.3	0.22	-23.0	0.34	-23.2	0.20	25
Zaikof Bay	N	12.8	0.35	-22.3	0.40	-22.7	0.19	25

Age 0 Pollock		$\delta^{15}N$ Mean	SD	$\delta^{13}C$ Mean	SD	$\delta^{13}C'_{TL}$ Mean	SD	N
Total		13.1	0.32	-20.9	0.45	-22.1	0.37	171
Eaglek Bay	G	12.9	0.20	-21.2	0.59	-22.0	0.48	25
Hogg Bay	K	13.0	0.25	-20.9	0.31	-22.1	0.26	25
Knowles Head	D	13.4	0.27	-20.6	0.38	-22.0	0.33	25
Sawmill Bay	L	13.1	0.36	-21.1	0.34	-22.2	0.30	25
Simpson Bay	A	13.2	0.35	-20.9	0.43	-22.1	0.41	25
Whale Bay	J	12.9	0.26	-20.9	0.44	-22.0	0.41	25
Zaikof Bay	N	13.1	0.28	-20.6	0.40	-22.1	0.33	21

Table7

	1994	1995
<u>Observations</u>		
Source of diapaused copepods in PWS	GOA & PWS	GOA
Carbon source in PWS juvenile fishes	GOA & PWS	GOA
Advection deduced to be:	Moderate	Strong

FIGURE CAPTIONS

1. Sampling Stations and potential copepod diapause habitat in Prince William Sound Alaska. Zooplankton were sampled at designated oceanographic stations which had alphanumeric names (listed in Appendix 1). Fishes were sampled near map symbols consisting of single Roman characters (A - N). Names of these sites are given in Table 5. Potential diapause habitat is the area of Prince William Sound deeper than 400 m as indicated by shading.

2. Areal distribution of net zooplankton $\delta^{15}N$ and $\delta^{13}C$ (columns) in the PWS study area during September 1994, March, April, May, and June 1995 (rows), from upper 50 m in the PWS study area.

3. Temporal shift in zooplankton $\delta^{15}N$ (A), $\delta^{13}C$ (B) and $\delta^{13}C'$ (C) in the PWS study area during March to June 1995. A. Regression is: $\delta^{15}N = -1.2249J + 0.011J^2 - 0.0000315J^3$, all P values < 0.0001, $r^2 = 0.412$, where J is the Julian date. B. Regression is: $\delta^{13}C = -0.638J + 0.006J^2 - 0.0000176J^3 - 0.453$, P values are 0.0068, 0.0029, 0.0013, and 0.959 for the J, J^2, J^3 coefficients and Y-intercept, respectively, $r^2 = 0.209$, where J is the Julian date. C. Regression is $\delta^{13}C' = -0.749J + 0.007J^2 - 0.0000228J^3 + 3.25$, P values are 0.0021, 0.0003, < 0.0001, and 0.720 for the J, J^2, J^3 coefficients and Y-intercept, respectively, $r^2 = 0.423$, where J is the Julian date.

4. Scatterplots with histograms of copepodite IV and V *Neocalanus cristatus* collected from the water column in March to April, 1995 (A), and May, 1995 (B), below 200m in Fall, 1995 (C), and from the upper 50m in the Spring, 1995 (D). "Cross-hairs" positioned near center of distribution of inferred GOA and PWS isotopic signatures to aid in comparisons of plots. Inferred life history stage shown in parentheses. A and C suggest large differences in source of copepods in diapause each year. Diapaused copepods in late 1995 differed considerably from those completing feeding and entering diapause phase in Spring (B), instead, resembling copepods sampled in the GOA (left cluster in D).

5. Mean areal distribution of (A) $\delta^{15}N$ and, (B) $\delta^{13}C$ and $\delta^{13}C'$ in: (1) feeding copepodite IV and V *Neocalanus cristatus* (top row); (2) upper 50m net zooplankton (second row); and (3) water column net zooplankton (bottom row) in the PWS study area in 1994-5.

6. Scales of ^{13}C variability in the PWS pelagic system. Relative strength suggested by this study is ranked and reflected by the number of asterisks (greater number of asterisks, the higher the rank). Physical forcing mediates (lines) the transfer of spatial variability on biota at annual scaling.

Figure 1

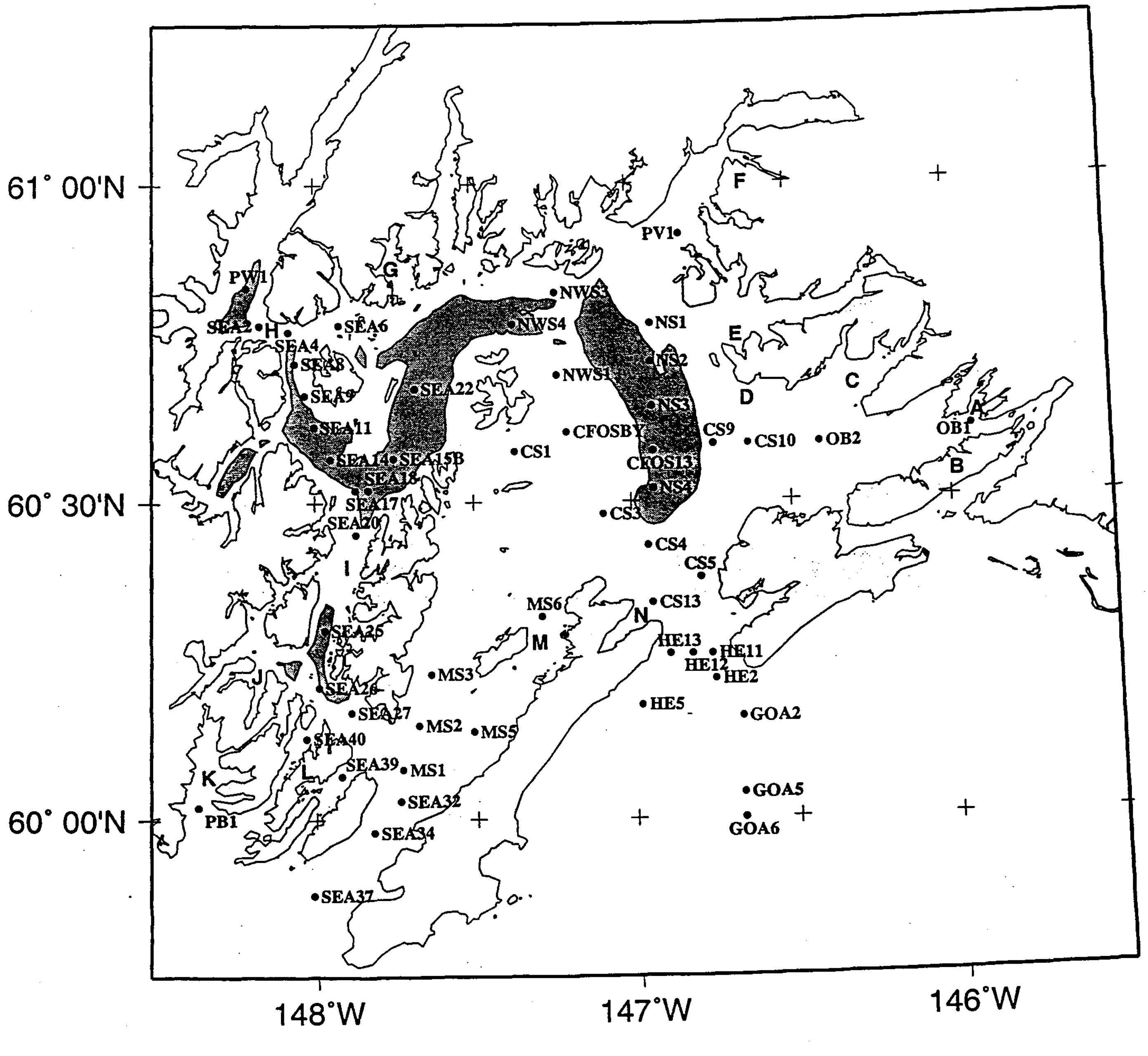

61° 00'N
60° 30'N
60° 00'N
148°W
147°W
146°W
A
B
C
D
E
F
G
H
I
J
K
L
M
N
PV1
PW1
SEA2
SEA4
SEA6
SEA8
SEA9
SEA11
SEA14
SEA15B
SEA18
SEA17
SEA20
SEA22
SEA25
SEA26
SEA27
SEA40
SEA39
SEA32
SEA34
SEA37
PB1
NWS3
NWS4
NWS1
NS1
NS2
NS3
NS4
CFOSBY
CFOS13
CS1
CS3
CS4
CS5
CS9
CS10
CS13
OB1
OB2
MS1
MS2
MS3
MS5
MS6
HE2
HE5
HE11
HE12
HE13
GOA2
GOA5
GOA6

Figure. 2

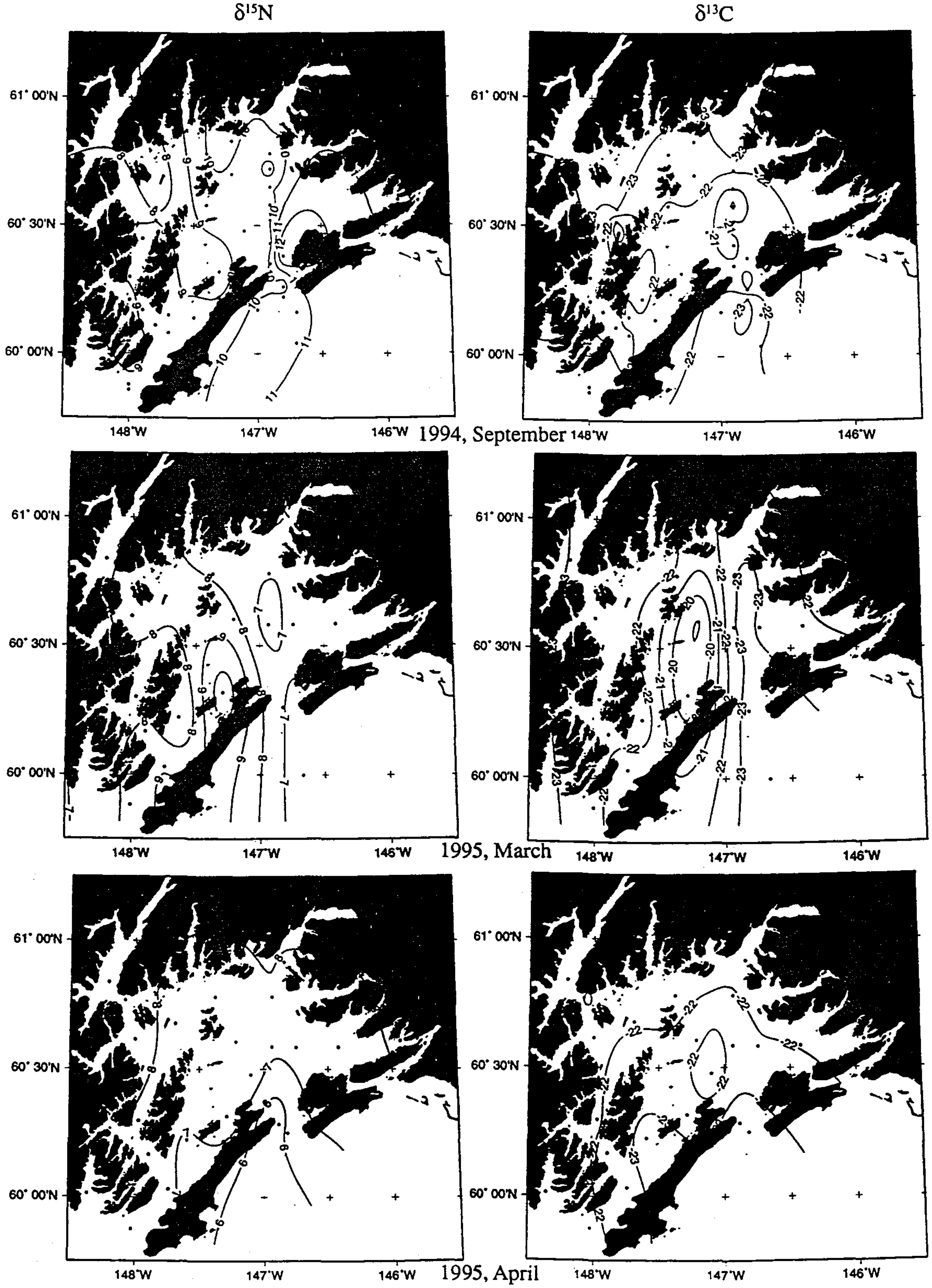
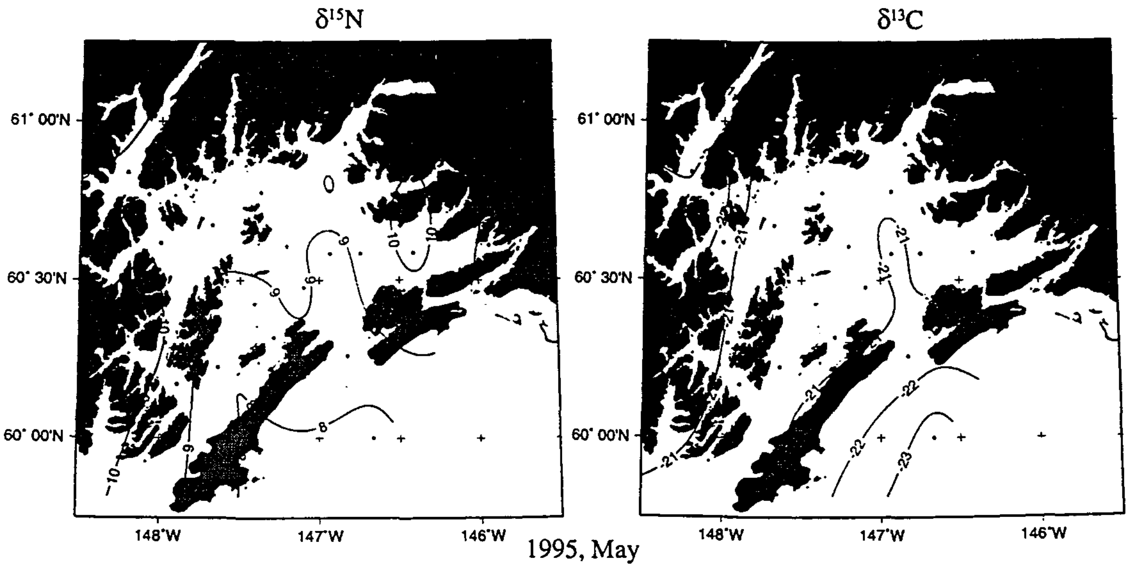
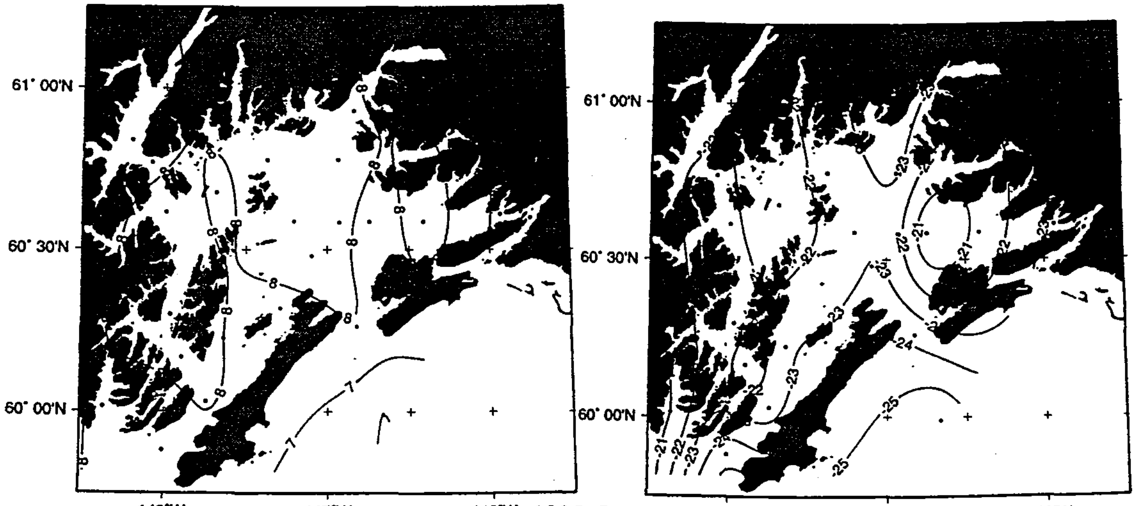

δ^{15}N
δ^{13}C
61° 00'N
60° 30'N
60° 00'N
148°W
147°W
146°W
1994, September
1995, March
1995, April

Figure. 2 continued



$\delta^{15}N$ $\delta^{13}C$

1995, May



1995, June

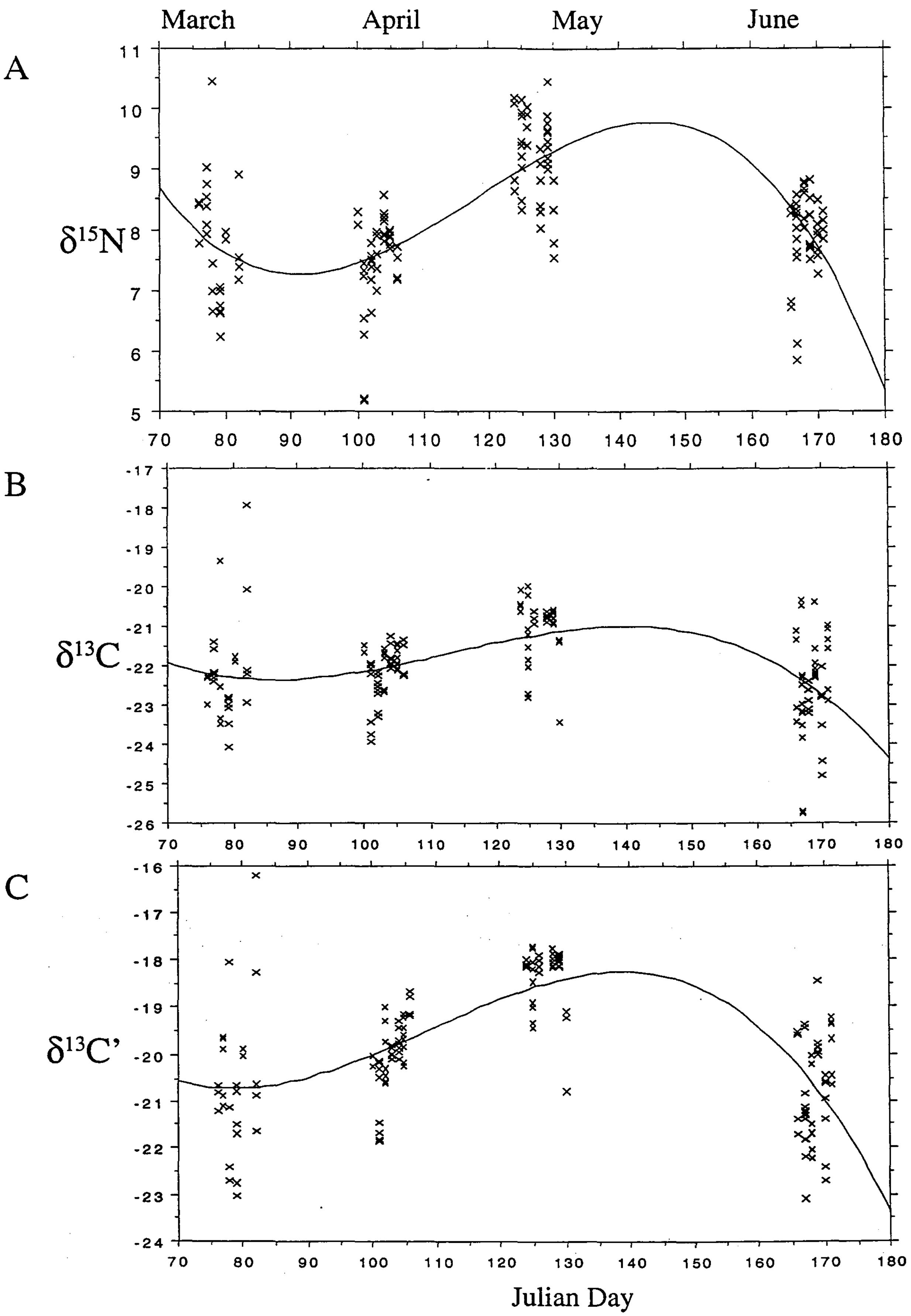
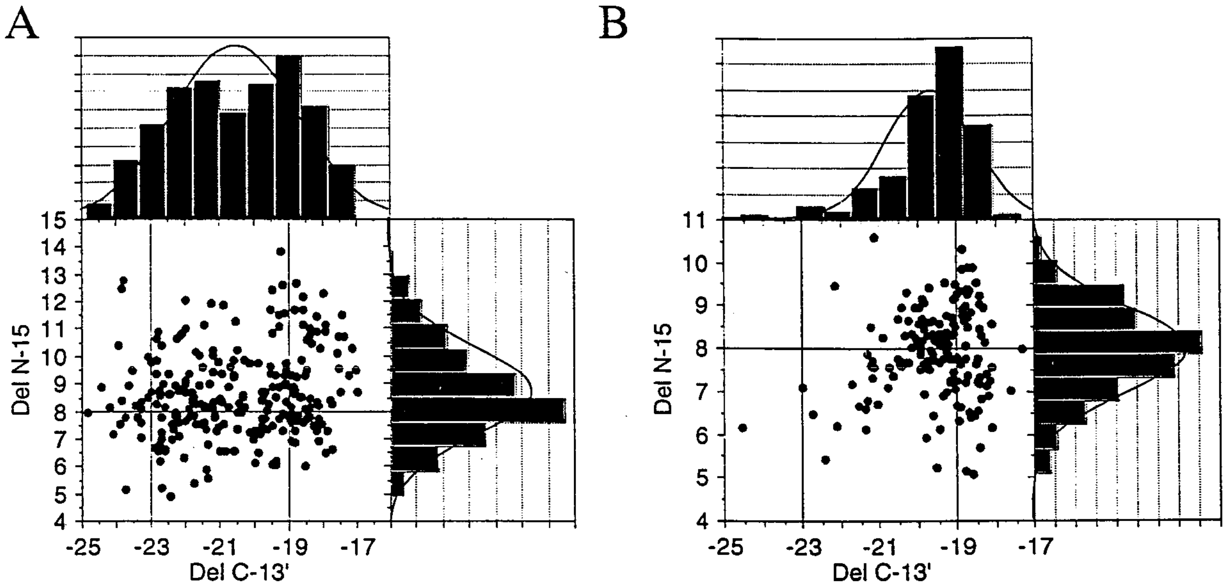
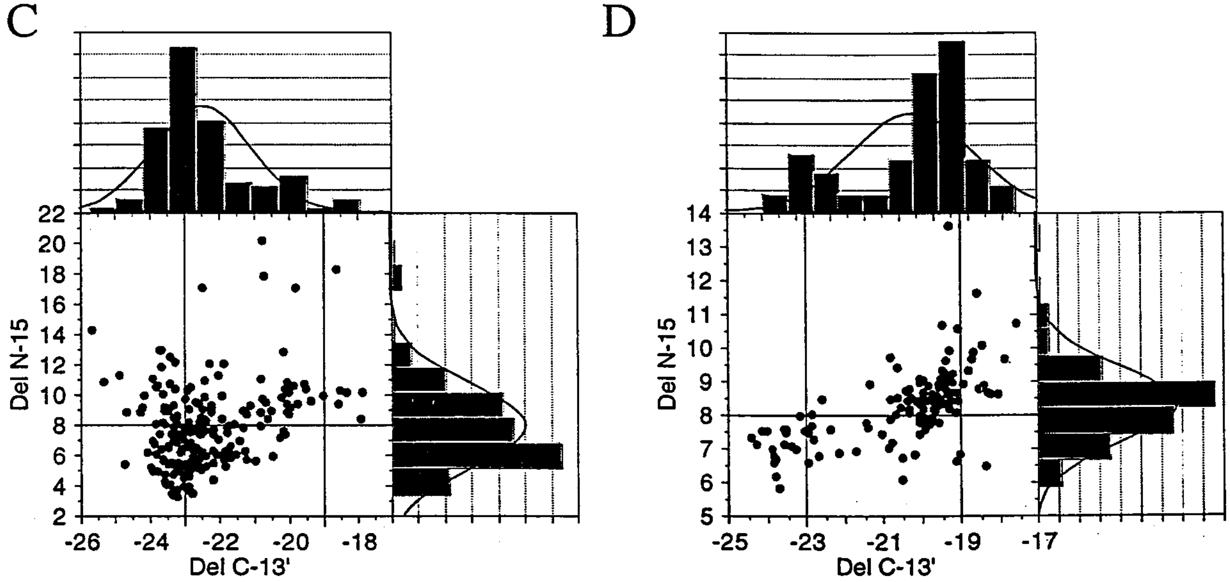

March
April
May
June
A
δ15N
11
10
9
8
7
6
5
70
80
90
100
110
120
130
140
150
160
170
180
B
δ13C
-17
-18
-19
-20
-21
-22
-23
-24
-25
-26
C
δ13C'
-16
-17
-18
-19
-20
-21
-22
-23
-24
Julian Day

Figure 3



March -April 1995 Water column
(Diapause)

May 1995 Water column
(Feeding-Diapause)



Fall 1995 Below 200m
(Diapause)

March - June 1995 Upper 50m
(Feeding)

Figure 4

Figure. 5A

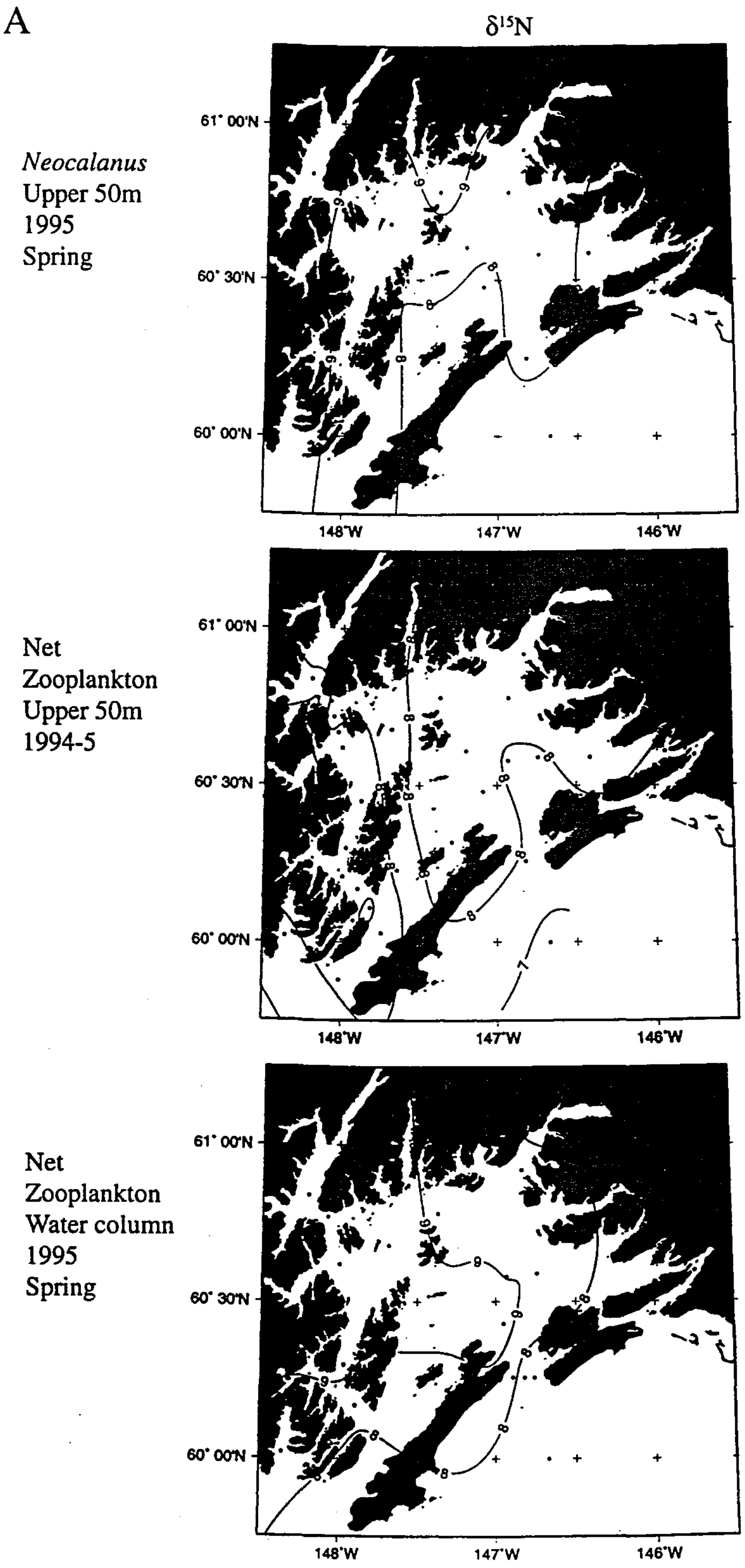
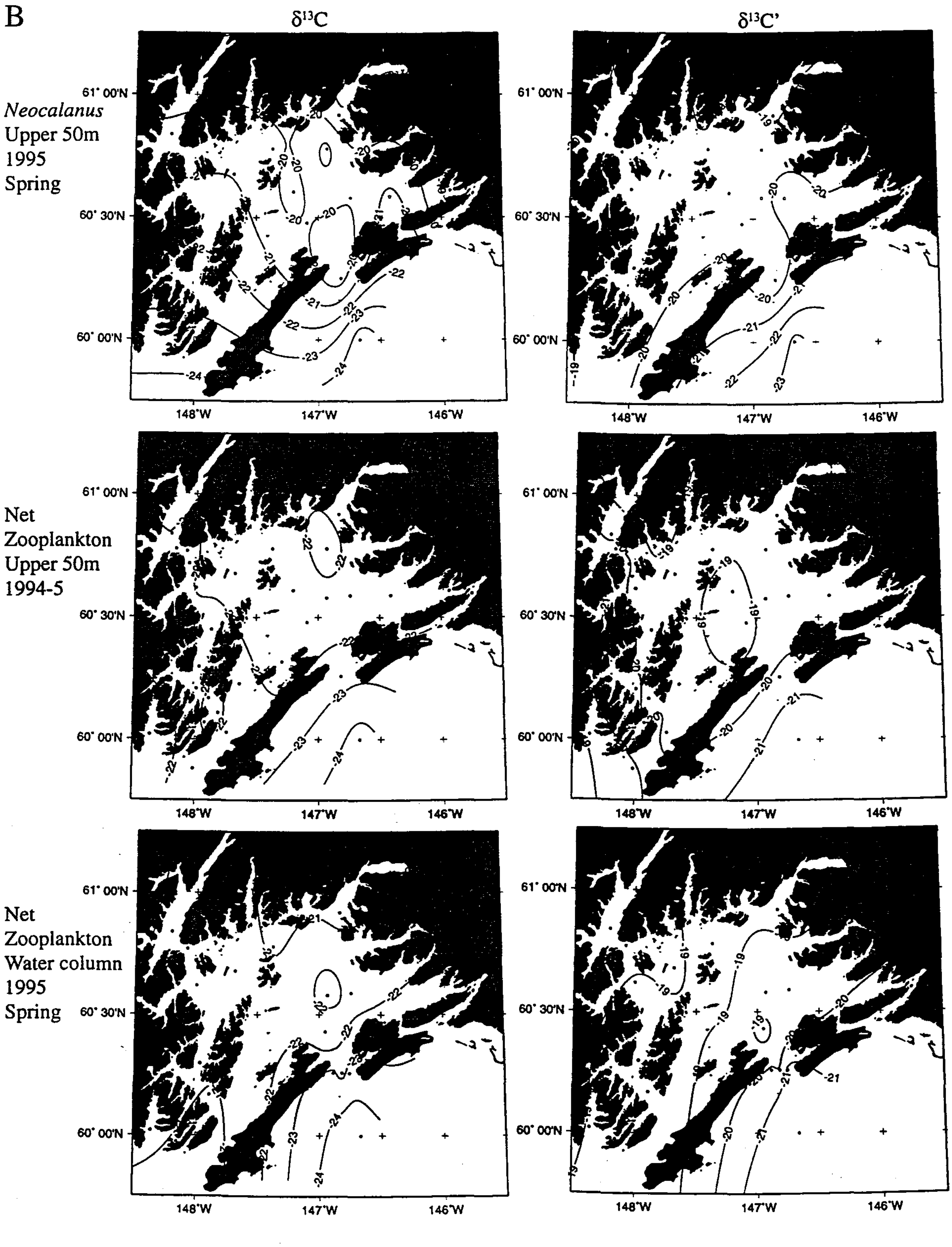
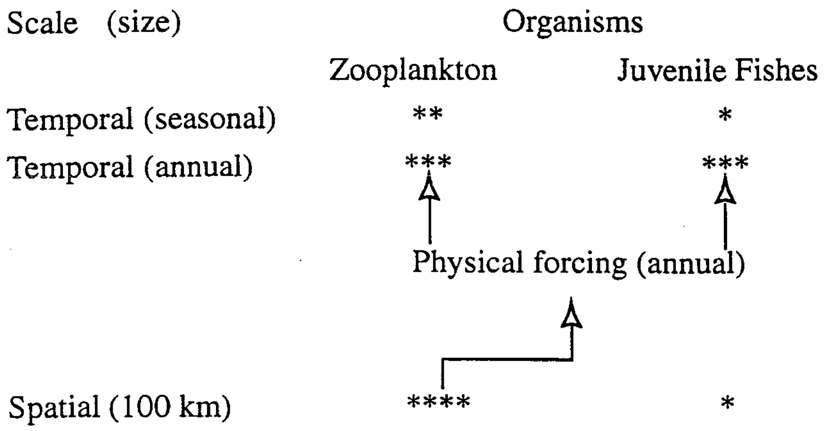

A
δ15N
Neocalanus
Upper 50m
1995
Spring
Net
Zooplankton
Upper 50m
1994-5
Net
Zooplankton
Water column
1995
Spring
61° 00'N
60° 30'N
60° 00'N
148°W
147°W
146°W
9
8
7

Figure. 5B


B
δ¹³C
δ¹³C'
Neocalanus
Upper 50m
1995
Spring
Net
Zooplankton
Upper 50m
1994-5
Net
Zooplankton
Water column
1995
Spring
61° 00'N
60° 30'N
60° 00'N
148°W
147°W
146°W



Scale (size)	Organisms Zooplankton	 Juvenile Fishes
Temporal (seasonal)	**	*
Temporal (annual)	***	***
Spatial (100 km)	****	*

Figure 6

Appendix 1. Bulk net (335μ-mesh, 0.5 m ring net) zooplankton isotopic and C/N data (replicate means) from indicated Prince William Sound and adjacent Gulf of Alaska oceanographic stations (Fig. 1) sampled from 1994 to 1995 by cast type (either upper 50 m or enire water column).

Date (YMD)	Time	Station	$\delta^{15}N$	$\delta^{13}C$	C/N (atoms)	$\delta^{13}C'$	Cast type
940421	19:58	CFOS13	6.42	-21.81	5.15	-20.79	Upper 50m
940623	13:45	CFOS13	8.66	-21.90	6.30	-20.24	Upper 50m
940927	17:08	CFOS13	9.42	-19.83	6.99	-17.89	Upper 50m
950320	14:00	CFOS13	6.66	-22.91	9.07	-20.38	Upper 50m
950416	13:38	CFOS13	7.20	-22.23	14.55	-18.96	Upper 50m
950505	23:57	CFOS13	8.42	-21.11	13.80	-17.91	Upper 50m
950616	4:13	CFOS13	8.33	-22.26	6.04	-20.72	Upper 50m
950323	10:05	CFOSBY	8.24	-18.97	7.52	-16.84	Upper 50m
950412	20:13	CFOSBY	7.58	-22.19	14.39	-18.93	Upper 50m
950509	1:00	CFOSBY	9.09	-20.82	11.87	-17.82	Upper 50m
950616	6:42	CFOSBY	8.51	-22.82	7.50	-20.70	Upper 50m
940924	22:01	CS1	9.44	-21.92	7.17	-19.91	Upper 50m
940623	11:26	CS10	7.66	-21.89	5.33	-20.76	Upper 50m
940925	23:29	CS13	10.20	-21.21	6.39	-19.51	Upper 50m
940924	18:05	CS3	9.40	-21.17	32.70	-17.22	Upper 50m
950416	17:43	CS3	7.65	-21.39	11.39	-18.46	Upper 50m
950508	21:50	CS3	9.22	-20.68	10.64	-17.86	Upper 50m
950616	9:19	CS3	8.24	-23.09	7.94	-20.84	Upper 50m
940927	13:51	CS4	9.78	-20.71	6.24	-19.08	Upper 50m
940925	21:52	CS5	12.81	-21.53	6.81	-19.65	Upper 50m
950323	14:15	CS9	7.40	-22.89	6.45	-21.17	Upper 50m
950411	5:45	CS9	7.35	-22.12	7.52	-19.99	Upper 50m
950509	18:10	CS9	9.37	-20.85	13.87	-17.64	Upper 50m
950616	1:40	CS9	7.60	-20.41	5.99	-18.90	Upper 50m
940926	23:41	GOA2	10.40	-22.27	9.99	-19.56	Upper 50m
940927	1:27	GOA5	10.84	-22.02	6.64	-20.21	Upper 50m
950320	5:45	GOA6	6.50	-23.75	5.77	-22.35	Upper 50m
950510	21:18	GOA6	7.67	-23.41	11.16	-20.51	Upper 50m
950616	21:46	GOA6	5.98	-25.72	11.16	-22.82	Upper 50m
940926	14:15	HE12	9.56	-21.02	17.70	-17.53	Upper 50m
950319	22:35	HE12	7.05	-23.39	5.75	-22.00	Upper 50m
950411	13:10	HE12	6.41	-23.56	8.12	-21.26	Upper 50m
950510	15:20	HE12	8.58	-21.36	9.13	-18.81	Upper 50m
950616	16:20	HE12	7.94	-23.68	7.40	-21.59	Upper 50m
950411		HE13	5.19	-23.80	8.48	-21.41	Upper 50m
940926	22:10	HE2	10.34	-23.03	8.06	-20.74	Upper 50m
940926	18:25	HE5	10.20	-22.46	7.29	-20.41	Upper 50m
940923	13:15	MS1	9.29	-22.11	7.43	-20.02	Upper 50m
940923	19:11	MS2	9.59	-21.74	7.76	-19.55	Upper 50m
940923	21:11	MS3	9.06	-22.35	11.34	-19.42	Upper 50m
950319	9:20	MS3	7.00	-22.51	6.68	-20.69	Upper 50m
950412	13:50	MS3	6.92	-23.23	12.72	-20.13	Upper 50m
950508	14:31	MS3	8.16	-20.75	12.17	-17.71	Upper 50m
950619	11:08	MS3	8.00	-22.75	9.19	-20.19	Upper 50m
940923	17:30	MS5	9.37	-21.16	17.47	-17.68	Upper 50m
940924	14:06	MS6	8.65	-21.57	10.08	-18.84	Upper 50m
950319	14:40	MS6	10.44	-19.36	6.55	-17.59	Upper 50m
950412	10:50	MS6	7.55	-22.66	8.63	-20.23	Upper 50m
950508	18:55	MS6	8.61	-20.77	13.09	-17.63	Upper 50m
950619	7:42	MS6	7.89	-23.13	8.90	-20.63	Upper 50m
940927	21:30	NS1	9.55	-23.24	12.98	-20.12	Upper 50m
950320	18:45	NS1	7.04	-22.93	6.67	-21.11	Upper 50m
950415	18:25	NS1	7.92	-22.07	13.08	-18.93	Upper 50m
950509	14:35	NS1	10.03	-20.87	12.72	-17.77	Upper 50m
950617	10:19	NS1	8.77	-23.11	7.00	-21.16	Upper 50m

940927	20:06	NS2	8.58	-22.08	7.63	-19.92	Upper 50m
940927	18:30	NS3	9.96	-21.08	6.21	-19.46	Upper 50m
940927	16:01	NS4	9.97	-21.15	6.47	-19.41	Upper 50m
940928	21:21	NWS1	9.86	-22.77	9.21	-20.21	Upper 50m
940928	23:52	NWS3	10.17	-22.71	9.20	-20.15	Upper 50m
940929	1:45	NWS4	10.00	-22.83	9.89	-20.13	Upper 50m
950321	0:15	NWS4	7.92	-21.82	7.90	-19.58	Upper 50m
950415	6:52	NWS4	7.73	-21.72	9.03	-19.19	Upper 50m
950509	4:45	NWS4	9.83	-20.74	12.51	-17.67	Upper 50m
950617	22:01	NWS4	8.63	-22.51	9.89	-19.81	Upper 50m
950410	21:40	OB1	8.19	-21.55	6.78	-19.69	Upper 50m
950504	14:40	OB1	8.73	-20.52	9.91	-17.82	Upper 50m
950615	18:37	OB1	6.78	-23.25	7.46	-21.15	Upper 50m
950323	16:45	OB2	7.17	-22.19	6.60	-20.40	Upper 50m
950411	2:30	OB2	7.39	-21.96	7.78	-19.75	Upper 50m
950504	19:02	OB2	10.14	-20.27	9.19	-17.71	Upper 50m
950615	22:01	OB2	8.33	-21.23	7.35	-19.16	Upper 50m
950413	0:00	PB1	7.62	-21.60	7.47	-19.49	Upper 50m
950620	23:59	PB1	7.92	-21.01	7.54	-18.88	Upper 50m
950415	15:26	PV1	7.96	-21.45	7.48	-19.34	Upper 50m
950509	12:00	PV1	9.41	-20.58	10.43	-17.79	Upper 50m
950617	13:07	PV1	8.11	-23.03	5.83	-21.60	Upper 50m
950317	16:40	PW1	7.78	-22.96	7.69	-20.79	Upper 50m
950414	16:50	PW1	8.24	-21.33	6.42	-19.62	Upper 50m
950505	17:05	PW1	9.21	-21.92	13.68	-18.73	Upper 50m
950618	14:03	PW1	7.74	-21.97	8.40	-19.59	Upper 50m
940423	17:18	SEA11	8.72	-21.98	8.55	-19.57	Upper 50m
950317	20:45	SEA11	8.44	-22.25	7.02	-20.30	Upper 50m
950414	9:55	SEA11	8.39	-21.82	10.21	-19.07	Upper 50m
950505	22:00	SEA11	9.92	-21.53	14.50	-18.26	Upper 50m
950618	7:55	SEA11	8.68	-22.21	9.22	-19.64	Upper 50m
940423	22:42	SEA14	7.52	-22.93	10.52	-20.12	Upper 50m
940920	16:39	SEA15B	7.53	-23.05	20.95	-19.41	Upper 50m
940424	8:55	SEA17	6.49	-22.60	12.55	-19.52	Upper 50m
940920	17:53	SEA18	8.93	-20.97	7.75	-18.78	Upper 50m
940422	14:27	SEA2	9.56	-23.39	9.35	-20.81	Upper 50m
940602	10:30	SEA2	8.56	-22.27	7.45	-20.17	Upper 50m
940424	12:55	SEA20	7.30	-22.30	10.47	-19.51	Upper 50m
940920	20:02	SEA20	9.43	-22.55	8.35	-20.19	Upper 50m
940421	23:46	SEA22	5.63	-23.18	9.28	-20.61	Upper 50m
950415	22:50	SEA22	7.70	-21.93	7.51	-19.81	Upper 50m
950505	9:00	SEA22	9.33	-20.10	9.79	-17.42	Upper 50m
950618	2:17	SEA22	7.97	-20.97	7.99	-18.71	Upper 50m
940613	12:32	SEA25	8.86	-21.80	5.84	-20.37	Upper 50m
940921	0:07	SEA25	9.09	-22.90	8.88	-20.41	Upper 50m
950323	14:00	SEA25	7.40	-22.10	6.90	-20.19	Upper 50m
950414	22:50	SEA25	7.89	-21.86	8.17	-19.54	Upper 50m
950506	15:34	SEA25	9.98	-20.90	11.67	-17.93	Upper 50m
950620	19:24	SEA25	8.23	-22.73	8.98	-20.21	Upper 50m
940613	17:37	SEA26	8.58	-22.36	6.19	-20.75	Upper 50m
940921	11:34	SEA26	8.85	-22.52	6.83	-20.63	Upper 50m
940921	14:54	SEA27	9.12	-22.40	7.17	-20.39	Upper 50m
950318	16:30	SEA27	8.24	-22.21	10.82	-19.36	Upper 50m
950412	18:00	SEA27	7.54	-22.46	11.72	-19.48	Upper 50m
950506	18:25	SEA27	9.55	-20.72	12.02	-17.71	Upper 50m
950620	15:31	SEA27	8.15	-21.43	8.17	-19.12	Upper 50m
940613	19:52	SEA29	9.16	-21.66	6.85	-19.77	Upper 50m
940921	17:02	SEA29	9.17	-22.18	6.79	-20.31	Upper 50m
940614	11:34	SEA32	9.29	-21.98	6.96	-20.05	Upper 50m
950318	19:10	SEA32	8.90	-21.47	7.53	-19.34	Upper 50m
950413	10:15	SEA32	7.19	-22.63	10.90	-19.77	Upper 50m
950619	14:06	SEA32	8.22	-22.39	7.28	-20.34	Upper 50m
940613	13:41	SEA34	7.89	-22.71	6.84	-20.83	Upper 50m

940922	16:22	SEA37	9.06	-21.28	26.38	-17.46	Upper 50m
950318	23:20	SEA37	8.24	-22.28	6.54	-20.51	Upper 50m
950413	5:20	SEA37	7.93	-21.74	7.80	-19.53	Upper 50m
950619	18:54	SEA37	7.43	-24.60	8.48	-22.21	Upper 50m
940614	9:45	SEA39	8.80	-22.23	6.86	-20.33	Upper 50m
940923	11:15	SEA39	9.10	-21.63	6.20	-20.01	Upper 50m
940422	17:00	SEA4	7.59	-22.79	8.52	-20.39	Upper 50m
940425	10:24	SEA4	6.40	-23.74	12.57	-20.66	Upper 50m
940425	14:43	SEA4	7.36	-22.94	11.02	-20.06	Upper 50m
940425	18:48	SEA4	5.73	-22.71	9.86	-20.02	Upper 50m
940425	22:43	SEA4	8.47	-22.42	9.45	-19.81	Upper 50m
940426	2:40	SEA4	8.89	-22.02	8.88	-19.53	Upper 50m
940426	7:26	SEA4	8.23	-22.93	11.82	-19.94	Upper 50m
940602	13:15	SEA4	8.85	-21.93	8.00	-19.66	Upper 50m
950414	14:35	SEA4	8.03	-22.01	9.36	-19.42	Upper 50m
950505	14:20	SEA4	9.59	-22.75	18.36	-19.23	Upper 50m
950618	11:44	SEA4	7.61	-22.22	9.87	-19.53	Upper 50m
940615	15:39	SEA40	7.98	-22.72	4.83	-21.93	Upper 50m
940422	20:43	SEA6	9.18	-22.07	6.90	-20.16	Upper 50m
940423	9:52	SEA8	6.00	-22.98	7.76	-20.78	Upper 50m
940604	9:39	SEA8	8.77	-21.71	7.50	-19.59	Upper 50m
940423	12:24	SEA9	8.07	-22.39	10.82	-19.54	Upper 50m
940604	11:58	SEA9	8.63	-21.77	6.94	-19.84	Upper 50m
950315		CFOS13	11.10	-21.20	6.29	-19.54	Water column
950416		CFOS13	8.61	-21.62	7.48	-19.51	Water column
950505		CFOS13	8.11	-25.22	13.65	-22.03	Water column
950616		CFOS13	8.11	-21.34	12.37	-18.29	Water column
950509		CS4	10.52	-20.29	6.93	-18.37	Water column
950617		CS4	8.08	-22.43	14.79	-19.14	Water column
950323		CS9	10.71	-21.57	6.20	-19.95	Water column
950411		CS9	8.08	-22.35	8.04	-20.07	Water column
950509		CS9	9.14	-20.76	10.35	-17.99	Water column
950616		CS9	7.87	-22.55	12.24	-19.51	Water column
950510		GOA6	8.50	-23.87	11.18	-20.97	Water column
950616		GOA6	5.94	-25.00	7.21	-22.98	Water column
950319		HE11	7.19	-23.45	8.05	-21.17	Water column
950319		HE12	7.08	-23.08	7.76	-20.89	Water column
950411		HE12	6.02	-23.28	7.51	-21.16	Water column
950510		HE12	8.97	-20.99	11.46	-18.05	Water column
950615		HE12	7.59	-23.16	12.45	-20.09	Water column
950419		HE13	6.59	-24.76	13.96	-21.54	Water column
950510		HE13	10.15	-22.05	11.72	-19.07	Water column
950616		HE13	8.19	-22.70	11.15	-19.80	Water column
950321		NWS4	9.09	-21.50	7.42	-19.41	Water column
950415		NWS4	8.34	-21.19	7.29	-19.14	Water column
950509		NWS4	8.82	-20.02	8.12	-17.72	Water column
950617		NWS4	8.68	-21.01	10.67	-18.18	Water column
950413		PB1	8.71	-21.96	9.33	-19.37	Water column
950413		PB1	9.03	-20.33	5.10	-19.34	Water column
950620		PB1	7.71	-21.22	12.53	-18.14	Water column
950415		PV1	7.90	-21.15	6.46	-19.42	Water column
950509		PV1	9.05	-19.86	7.08	-17.89	Water column
950617		PV1	7.66	-21.23	8.91	-18.74	Water column
950317		PW1	10.47	-21.68	8.62	-19.25	Water column
950414		PW1	8.84	-21.70	6.19	-20.09	Water column
950505		PW1	10.32	-21.61	10.26	-18.85	Water column
950618		PW1	8.49	-22.50	9.98	-19.79	Water column
950317		SEA11	8.92	-21.74	7.30	-19.69	Water column
950414		SEA11	9.64	-21.81	8.58	-19.39	Water column
950505		SEA11	9.57	-21.10	10.55	-18.29	Water column
950618		SEA11	7.95	-21.16	10.37	-18.38	Water column
950317		SEA22	10.97	-20.97	6.50	-19.22	Water column
950414		SEA23	9.44	-21.87	8.11	-19.59	Water column

950505	SEA22	9.11	-21.15	12.58	-18.07	Water column
950618	SEA22	9.74		8.91		Water column
950414	SEA25	9.62	-21.60	8.22	-19.27	Water column
950506	SEA25	9.76	-21.06	11.15	-18.16	Water column
950620	SEA25	8.37	-21.21	12.98	-18.09	Water column
950412	SEA27	8.36	-21.74	7.76	-19.54	Water column
950506	SEA27	8.65	-20.45	8.04	-18.17	Water column
950620	SEA27	7.76	-20.62	10.06	-17.90	Water column
950317	SEA4	9.77	-21.65	8.26	-19.31	Water column
950414	SEA4	8.76	-21.85	7.79	-19.64	Water column
950505	SEA4	9.70	-22.27	14.73	-18.99	Water column
950618	SEA4	8.10	-21.55	7.76	-19.36	Water column

Cross-validation of trophic level estimates from a mass-balance model of, and $^{15}N/^{14}N$ data from, Prince William Sound

by

Thomas C. Kline Jr.$_1$ and Daniel Pauly$_2$

(1)
Prince Willliam Sound Science Center
P. O. Box 705
Cordova, AK 99574, USA
(corresponding author)
907-424-5800 (phone)
907-424-5820 (fax)
tkline@grizzly.pwssc.gen.ak.us

(2)
Fisheries Centre
2204 Main Mall
University of British Columbia
Vancouver, B.C., Canada V6T 1Z4

Proceedings of the International Symposium on Fishery Stock Assessment Models for the 21st Century -- Combining Multiple Data Sources. Alaska Sea Grant College Program Report. University of Alaska Fairbanks. (In Press)

Cross-validation of trophic level estimates from a mass-balance model of, and $^{15}N/^{14}N$ data from, Prince William Sound

Thomas C. Kline Jr. and Daniel Pauly

*Abstract

Trophic mass-balance models of ecosystems constructed using the Ecopath approach and software include the diet composition of functional groups as model inputs, and trophic level estimates for these same groups as a model outputs. The well-documented 0.34% enrichment of $^{15}N/^{14}N$ that occurs at each feeding step in food webs can be used to determine trophic level as well. This contribution is the first to ever examine the relation between trophic levels estimated by these two independent methods. This was achieved by using a published Ecopath model of Prince William Sound (PWS) as reference, i.e., estimating $^{15}N/^{14}N$ ratios for each of the model's functional groups. Re-expression of theses ratios as absolute estimate of trophic levels (TL) was done following calibration using the herbivorous copepods *Neocalanus cristatus*, for which TL = 2. The correlation between both sets of TL values (n= 7) was extremely high (r = 0.986), with the points evenly distributed about the 1:1 line. Also, the magnitude of the standard errors of the TL estimates based on $^{15}N/^{14}N$ data was similar to those of the Ecopath estimates. Applying $^{15}N/^{14}N$ data from PWS to an Ecopath model of the Alaska Gyre System resulted in a reduced correlation (r = 0.755, for n = 16), suggesting that TL estimates may be transferred between ecosystems, though at the cost of reduced precision. These encouraging results warrant further exploration.

*Introduction

While the trophic level concept existed since the beginning of ecosystem research (Golley 1993), controversy has raged as to its operational validity. Particularly, some ecologists could not reconcile this concept, articulated in form of integers (primary producers = 1; first order consumers = 2, etc.), with the observation that many organisms derive their food from widely different parts of food webs (see e.g., Rigler 1975). This problem was overcome by the introduction, through Odum and Heald (1975), of fractional trophic levels (TLs). These are computed as weighted means from disparate diet compositions, and their variance can be interpreted as an omnivory index (OI), in agreement with Pimm (1982), who defined omnivory as "feeding on more than one trophic level" (Pauly et al. 1993, Pauly and Christensen 1995). Until the late 1980's, however, estimation of trophic levels continued to be largely definitional for lower levels (see above), or based on crude, and often grossly erroneous guesses for higher levels. (See Pauly 1996 for the a discussion of such guesses by Ryther 1972 and other authors).

In recent years, two methods have emerged that are capable of reliably estimating TL and related statistics: (1) the $^{15}N/^{14}N$ method (DeNiro and Epstein 1981, Fry 1988, Wada et al. 1991, and see below), and (2) the construction of mass-balance trophic models of ecosystems (Christensen and Pauly 1992, and see below). The former estimates are identified as TL_N, the latter as TL_E. In this study, we present a first comparison of results obtained by these two approaches, using a preliminary mass balance model of the Prince William Sound (PWS) ecosystem (Dalsgaard and Pauly 1997) as a starting point. Another model, describing the Alaska Gyre System (AGS; Pauly and Christensen 1996) is then used to test whether estimates of TL and OI may be transferred from one ecosystem to the other.

*Materials and Methods

The trophic mass-balance models of PWS used here was constructed using the Ecopath approach of Polovina (1984) and Christensen and Pauly (1992); this are based on the system of linear equations

(1) $$B_i \times (P/B)_i \times EE_i = Y_i + \sum B_j \times (Q/B)_j \times DC_{ij}$$

where, for any conventional period without massive change of system structure: B_i is the mean biomass of functional group i (e.g., a group species with similar vital statistics, diet compositions and consumers); B_j is the mean biomass of the consumers of i; $(P/B)_i$ is the production/biomass ratio of i (equivalent to its instantaneous rate of mortality; Allen 1971); EE_i is the fraction of production $\{P_i = B_i \times (P/B)_i\}$ that is consumed within the system; Y_i is the catch of i by the fishery, if any; $(Q/B)_j$ the consumption per unit biomass of j; and DC_{ij} is the contribution of i to the diet of j.

The Ecopath software (Christensen and Pauly 1992) was used to solve this system of equations, after estimation of values of B, P/B, etc, from the literature on PWS and related systems. The assumptions made when estimating the inputs, and for their subsequent adjustment when establishing mass-balance, are documented in Dalgaard and Pauly (1997). The other trophic mass-balance model used here, representing the Alaska Gyre system was constructed in similar fashion, and is documented in Pauly and Christensen (1996).

For both models, estimation of the TL values was performed by Ecopath, based on

(2) $$TL_{Ei} = (1 + \text{mean trophic level of prey})$$

Omnivory indices (OI_{Ei}) were computed as the variance of the TL_{Ei} estimates (Christensen and Pauly 1992); the square root of the OI_{Ei} values was then treated as standard error of the TL_{Ei} estimates ($S.E._{Ei}$).

Further details on Ecopath, including its ability to account for uncertainty in input values through a Monte-Carlo resampling scheme interpreted in a Bayesian context, are provided in Walters (1996) and other contributions in Pauly and Christensen (1996).

Stable isotope measurements are unique in that they trace assimilated material. Nitrogen stable isotope ratios provide excellent definition of relative trophic level (Fry 1988, Wada et al. 1991, Hobson and Welch 1992, Kiriluk et al. 1995). The heavy isotope of nitrogen, ^{15}N, is enriched by about 0.34 % (or 3.4 ‰ in conventional delta units with each trophic level (DeNiro and Epstein 1981, Minagawa and Wada 1984) and has been shown to accurately indicate the "realized" trophic level of species within an ecosystem (Kling et al. 1992, Cabana and Rasmussen 1994). Thus, the set of TL_N values used for comparison was derived from samples collected in 1994-1995 in PWS (Kline 1997), and based upon the trophic bioconcentration of ^{15}N.

The conventional delta notation used to express a stable isotope ratio is reported relative to international standards (air for N) and defined by the following expression:

$$\delta^{15}N = (R_{sample} / R_{standard} - 1) \times 1000 ‰ \tag{3}$$

where $R = {}^{15}N/{}^{14}N$. The isotope standard has a delta value of zero by definition, i.e., $\delta^{15}N = 0$ for atmospheric N_2. Naturally occurring $\delta^{15}N$ values observed in biota range from ~0 to ~ +20.

TL_N are estimated by relating observed $\delta^{15}N$ values to a reference value (TL_{ref}), and to the trophic enrichment factor, 3.4 (Minagawa and Wada 1984, Kline 1997), via:

(4) $$TL_{Ni} = 1 + (\delta^{15}N_i - \delta^{15}N_{ref}) / 3.4$$

Where TL_{Ni} is the trophic level of group i, $\delta^{15}N_i$ is the mean $\delta^{15}N$ of group i, and $\delta^{15}N_{ref}$ is the mean $\delta^{15}N$ value of the herbivorous copepod (with TL = 2, by definition) used as reference, here *Neocalanus cristatus* (Kline 1997). The standard deviations of the $\delta^{15}N_i$, $S.D._{Ni}$ were multiplied by the trophic enrichment factor, 3.4 (Minagawa and Wada 1984, Kline 1997), to estimate $\delta^{15}N$-based omnivory indices, OI_{Ni}. Given their relative magnitudes, we compared the OI_{Ni} estimates with the $S.E._{Ei}$, rather than with the OI_{Ei}.

Isotope sampling and data acquisition procedures were described elsewhere (Kline et al. 1993, Kline 1997). To account for the different definitions of the functional groups in the two ecosystem models (PWS and AGS), the available isotopic database were arranged differently for each comparison. For example, in the PWS model, herring are considered separately (Table 1), while they are included in the small pelagics group of the AGS (Table 2).

*Results and Discussion

Table 1 presents our results for PWS, i.e., the estimates of TL and S.E. derived by the two methods under comparison. As might be seen, the fit between the estimates of TL_E and TL_N is very tight, even if one omits the reference data point, pertaining to *Neocalanus,* and for which $TL_E = TL_N = 2$ by definition (see arrow in Figure 1A). Moreover, the data points are close to the 1:1 line, as they should if TL_E and TL_N measure the same underlying quantity. Figure 1B shows that the magnitude of the omnivory index estimates are similar for both methods compared here, except for the reference group (see arrow), which cannot, by definition, take a value of $S.E._E$ other that zero, while the estimate of OI_N can be quite large. This feature precludes correlation analysis.

The good match between the two types of TL estimates for functional groups in the PWS model is due, we believe, to the taxonomic correspondence between the Ecopath groups and the groups for which $\delta^{15}N$ were available. Another factor is scope of the sampling for stable isotope data, which involved numerous samples (Table 1) and which was very broad for all groups except birds. (Bird isotopic data were collected within a limited spatial and temporal range and included few of the common duck-like shorebirds; M.A. Bishop, U.S.F.S., pers. comm.).

The Ecopath model of PWS was based almost exclusively on data collected prior to the 1989 *Exxon Valdez* oil spill, while the $\delta^{15}N$ data were collected after the spill. The good match between the two data sets implies that the basic structure of the food web has not been modified by the spill, at least as far as can be detected within the scope of this comparison. On the other hand, $\delta^{15}N$ data are not available for marine mammals and many bird species that experienced large mortalities, and this conclusion may thus change when the issue is revisited.

Table 2 and Figure 1C show that using $\delta^{15}N$ data from one system (PWS) to estimate trophic levels in another, adjacent system (AGS), leads to predictions that are less precise than when inferences are drawn within the same system. Moreover, the omnivory index values become completely uncorrelated (Figure 1D), partly because of overaggregation of functional prey groups, which leads to predators that appear to feed at only one trophic level.

A likely reason for the differences between TL_E in AGS and TL_N estimates from PWS is the shoe-horning of taxa with $\delta^{15}N$ data into the "boxes" of the AGS model. For example, the TLN estimate for demersal fish in PWS is compared with a TL_E estimate for "large fish" in the AGS, though these consist of large pelagic fish (Pauly and Christensen 1996).

The $\delta^{15}N$ data on salmonids in Table 2 refer to adult specimens collected during their return migration through PWS and/or the Copper River, of which all would have done most of their feeding on the Gulf of Alaska shelf and/or in the AGS. However, having broadly similar life histories may not be sufficient for their TL values to be similar: the iteroparous salmonid, Dolly Varden (*Salvelinus malma*) had an estimated TL_N much lower than another iteroparous salmonid, steelhead (*Oncorhynchus mykiss*; Table 2), but close to the value of $TL_N = 3.54 \pm 0.21$ estimated for semelparous coho salmon (*O. kisutch*; n = 12). Thus, caution needs to be used when selecting "analog" species for cross-validation.

Still, we view the cross-validation exercise presented here as encouraging, in that the data we assembled led to coherent results, fully validating the independent, within-system estimates of TL. We also think that the lower correlation between the TL values from PWS and AGS were largely due to the lack of correspondence between the species included in the functional groups that were compared.

The next step is to refine our analyses, based on ecosystem models that are more detailed, thus requiring less "shoehorning", making better use of the available $\delta^{15}N$ data, and reducing the occurrence of misleadingly low estimates of $S.E._E$. Also, an important test will be to verify the high trophic level ($TL_E \sim 5$; Pauly and Christensen 1996) estimated for transient killer whales. Future work by both authors will be devoted to these and related issues, important in view of the recent demonstration (Pauly et al. 1998) that the trophic levels of global fisheries catches have been steadily declining in the last decades.

**Acknowledgments

This project was funded by the Exxon Valdez Oil Spill Trustee Council through the Sound Ecosystem Assessment (SEA) and the Mass Balance Modeling (MBM) projects. However the findings presented by the authors are their own and do not necessarily represent the Trustee Council's position. John Williams assisted with the translation of incompatible computer files between DP and TCK. Two anonymous reviewers provided useful improvements to our first draft.

* References Cited

Allen, K.R. 1971. Relation between production and biomass. J. Fish. Res. Board Can. 28:1573-1581.

Cabana, G. and J. B. Rasmussen, 1994. Modeling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. Nature 372:255-257.

Christensen, V. and D. Pauly 1992. Ecopath II: a system for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Model. 61: 169-185.

Christensen, V. and D. Pauly 1995. Primary production required to sustain global fisheries. Nature 374:255-257.

Dalgaard and Pauly. 1997. A tentative mass-balance trophic model of Prince William Sound, Alaska, for the period 1980-1989, prior to the Exxon Valdez Oil Spill. University of British Columbia. Fisheries Centre Research Reports. Vol. 5(2). 33 pp.

DeNiro, M. J. and S. Epstein. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochim. Cosmochim. Acta. 45:341-353.

Fry, B. 1988. Food web structure on the Georges Bank from stable C, N, and S isotopic compositions. Limnol. Oceanogr. 33:1182-1190.

Golley, F.B. 1993. A history of the ecosystem concept in ecology: more than the sum of its part. Yale University Press. New Haven, 254 pp.

Hobson, K. A. and H. E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. Mar. Ecol. Progr. Ser. 84:9-18.

Hobson, K.A., J.L. Sease, R.L. Merrick, and J.F. Piatt. 1997. Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. Mar. Mammal Sci. 13:114-13.

Kiriluk, R. M., M. R. Servos, D. M. Whittle, G. Cabana, J. B. Rasmussen. 1995. Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, mirex, and PCB in a Lake Ontario pelagic food web. Can. J. Fish. Aquat. Sci. 52:2660-2674.

Kline, T.C. Jr., J.J. Goering, O.A. Mathisen, P.H. Poe, P.L. Parker, and R.S. Scalan. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}N$ and $\delta^{13}C$ evidence in the Kvichak River watershed, southwestern Alaska. Can. J. Fish. Aquat. Sci. 50:2350-2365.

Kline, T. C. 1997. Confirming forage fish food web dependencies in the Prince William Sound ecosystem using natural stable isotope tracers. In: Forage Fishes in Marine Ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No. 97-01. University of Alaska Fairbanks. pp.257-269.

Kline, T.C. Scales and Patterns of Temporal and Spatial Variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in Pelagic Biota. In: S. Brandt and D. Mason (eds.) Space, Time and Scale: New Perspectives in Fish Ecology and Management. Can. J. Fish. Aquat. Sci. (in review)]

Kling, G.W., B. Fry, and W.J. O'Brien. 1992. Stable isotopes and plankton trophic structure in arctic lakes. Ecology 73:561-566.

Minagawa, M., and E. Wada. 1984. Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim. Cosmochim. Acta 48:1135-1140.

Odum, W.E. and Heald, 1975. The detritus-based food web of an estuarine mangrove community. In: L.E. Cronin (ed.) Estuarine Research. Vol. 1. Academic Press, New York. pp. 265-286.

Pauly, D. 1996. One million tonnes of fish and fisheries research. Fisheries Research 25(1):25-38.

Pauly, D. and V. Christensen, 1995. Primary production required to sustain global fish catches. Nature 374:255-257.

Pauly, D. and V. Christensen (editors). 1996. Mass-balance models of north-eastern Pacific ecosystems. Univ. British Columbia. Fisheries Centre Reports 4(1). 131pp.

Pauly, D., M. Soriano-Bartz and M.L. Palomares. 1993. Improved construction, parameterization and interpretation of steady-state ecosystem models. In: D. Pauly and V. Christensen (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26. pp. 1-13.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese and F.C. Torres Jr. 1998. Fishing down marine food webs. Science 279: 860-863.

Pimm, S.L. 1982. Food Webs. Chapman and Hall, London. 219 pp.

Polovina, J.J. 1984. Model of a coral reef system. I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3:1-11.

Rigler, F.H. 1975. The concepts of energy flow and nutrient flow between trophic levels. In: W.H. Van Dobben and R.H. Lowe-McConnel (eds.) Unifying concepts in ecology. Dr. W. Junk Publishers, The Hague. pp. 15-26.

Ryther, J.H. 1972. Photosynthesis and fish production in the sea. Science 166: 72-76.

Wada, E., H. Mizutani, and M. Minagawa. 1991. The use of stable isotopes for food web analysis. Crit. Rev. Food Sci. Nutr. 30:361-371.

Walters, C. 1996. Suggested improvements for the Ecopath model. In: D. Pauly and V. Christensen (eds.). 1996. Mass-balance models of north-eastern Pacific ecosystems. Univ. British Columbia. Fisheries Centre Reports 4(1). pp. 82-87.

Table 1. Comparison of trophic level (TL) and omnivory index ($S.E._E$ and OI_N) estimates for seven functional groups in the Prince William Sound ecosystem.

Ecopath group [a]	Corresponding taxa with $\delta^{15}N$ data	data source [b]	n [c]	TL_E [d]	TL_N	$S.E._E$ [e]	OI_N
Mesozooplankton	*Neocalanus cristatus* [f]	1	938	2	2	0	0.54
Macrozooplankton	Euphausiids, amphipods, chaetognaths, etc.	1,2	329	2.8	2.81	0.43	0.49
Salmon fry	Young-of the year chum, sockeye and pink salmon	3	285	3.2	3.18	0.32	0.31
Herring	*Clupea pallasi* (Pacific herring)	1,3	385	3.3	3.33	0.37	0.21
Small pelagics	Smelts, juvenile gadids	3	273	3.3	3.08	0.34	0.32
Demersal fishes	Flatfish, rockfishes, greelings, gadids, cottids.	3	459	3.9	3.88	0.53	0.40
Birds	Seabirds	4	191	4.1	3.81	0.45	0.44

a. model is described in Dalgaard and Pauly (1997), including details of species included in each functional group; b. numbers in this column indicate sources of $\delta^{15}N$ data, viz. 1 = Kline (in press?); 2 = Kline (unpublished data) ; 3 = Kline (1997); 4 = M.A. Bishop (U.S.F.S., Cordova, unpublished data); c. number of $\delta^{15}N$ measurements; d. as given on Table 23 of Dalsgaard and Pauly (1997); e. from Ecopath file of PWS, available from second author; f. reference group for $^{15}N/^{14}N$ as discussed in text.

Table 2. Comparison of estimates of TL_E and $S.E._E$ for functional groups in the Alaska Gyre system with TL_N and OI_N estimates derived from Prince William Sound organisms.

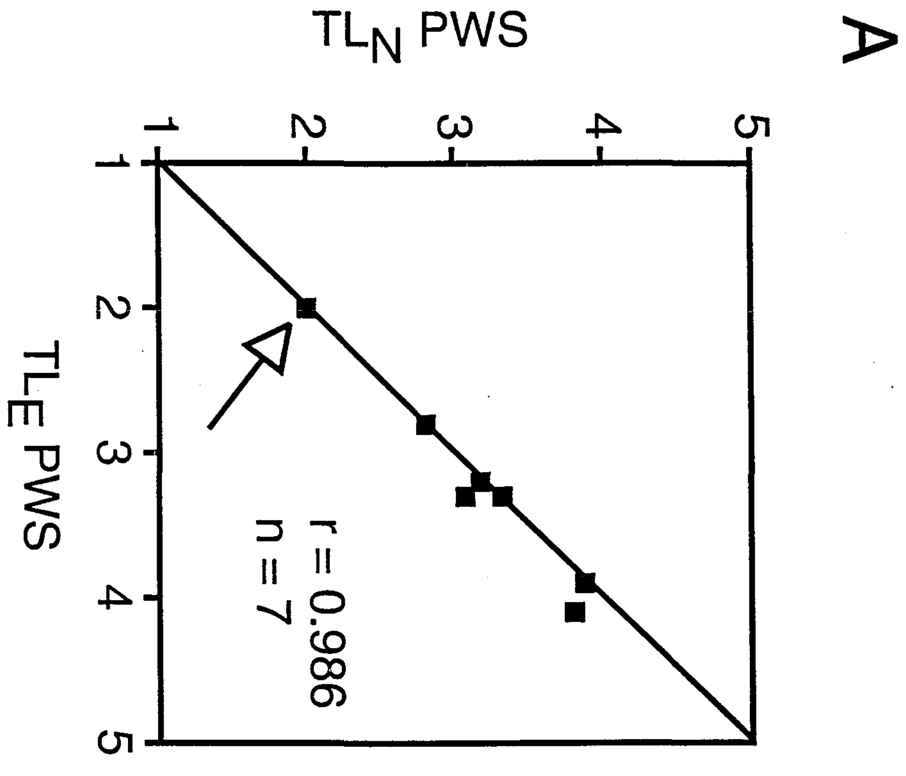
Ecopath group [a]	Corresponding taxa with $\delta^{15}N$ data	data source [b]	n [c]	TL_E	TL_N	$S.E._E$	OI_N
Small herb. zoopl.	*Neocalanus cristatus* [e]	1	938	2	2	0	0.54
Microzooplankton	Bulk net samples	1	195	2	2.17	0	0.34
Carnivorous zoopl.	Amphipods, chaetognaths, decapod larvae, etc.	1,2	159	3	2.89	0	0.52
Jellies[f]	Gelatinous zooplankton	2	4	3	2.35	0	0.35
Krill	Euphausids	1	170	2.05	2.74	0.22	0.45
Squids	Squids	3	104	3.15	3.44	0.37	0.25
Smallpelagics	Herring, smelts, juvenile gadids	1,3	545	3.16	3.24	0.36	0.27
Sockeye salmon	Sockeye salmon	4	118	3.91	2.88	0.45	0.13
Chum salmon	Chum salmon	2	1	4	3.05	0	
Pink salmon	Pink salmon	2	4	3.99	2.94	0.38	0.18
Steelhead	Dolly Varden[g]	2	6	4.12	3.46	0.2	0.31
Mesopelagics	Myctophids, smoothtongue, glass shrimp, snailfish	3	73	3.04	3.12	0.05	0.39
Large fish	Flatfishes, rockfishes, greenlings,	2	459	4.04	3.88	0.3	0.4

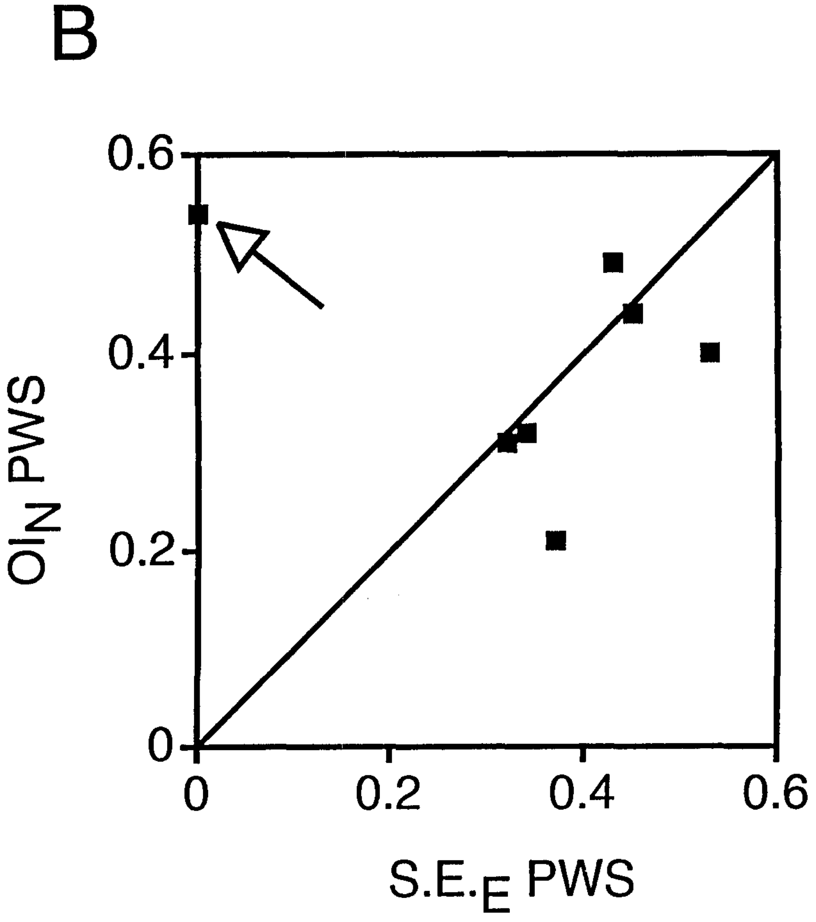
	gadids, etc.						
Sharks	Dogfish, salmon shark	2	5	4.49	3.66	0.45	0.4
Pinnipeds	Copper R. Delta Harbor seals & Steller Sea lions	5	22	4.33	4.92	0.36	0.08
Marine birds	Seabirds	6	191	4.08	3.81	0.28	0.44

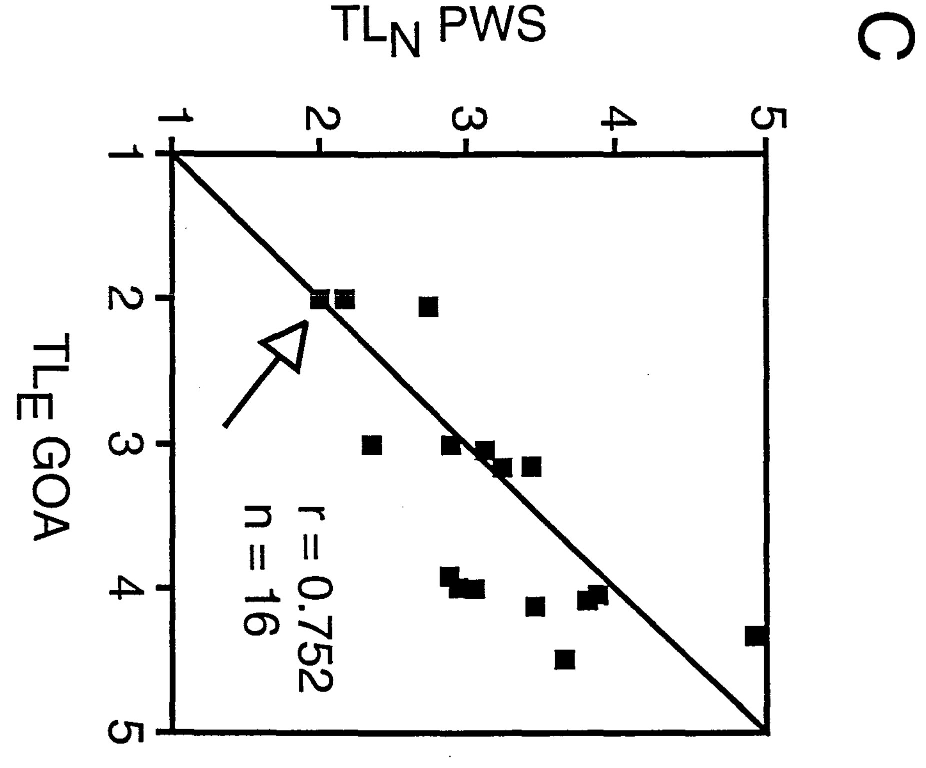
a. model described in Pauly and Christensen (1996), including details of species included in each functional group; b. numbers in this column indicate sources of $\delta^{15}N$ data, viz. 1 = Kline (in press?); 2 = Kline (unpublished data) ; 3 = Kline (1997); 4 = Kline and Ewald (unpublished data); 5 = Hobson et al. (1997); 6 = M.A. Bishop (U.S.F.S., Cordova, unpublished data); c. number of $\delta^{15}N$ measurements; d. from Ecopath file of Alaska gyre, available from the second author; e. reference group for $\delta^{15}N$; f. diet composition, omitted in Pauly and Christensen (1996), consisted of 88 % herbivorous zooplanton, and 12 % microzooplanton; g. presumed analogous to steelhead because both are iteroparous salmonids; see text.

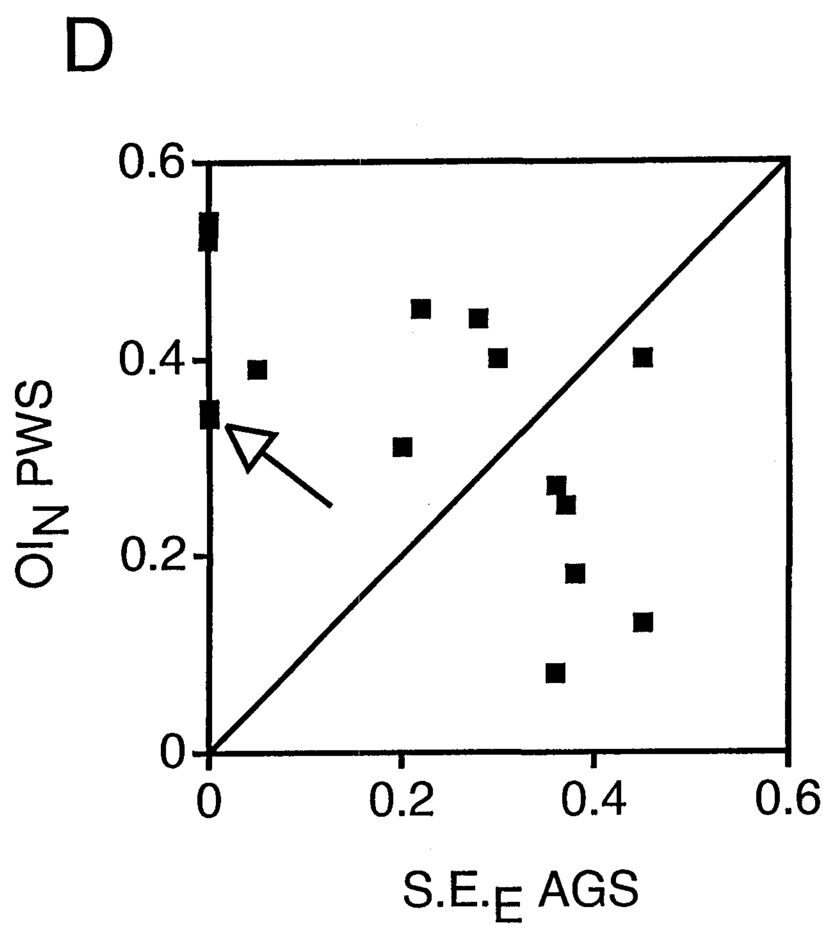
FIGURE CAPTIONS:

Figure 1. Relationships between estimates of trophic level derived from $\delta^{15}N$ data (TL_N) and Ecopath modeling (TL_E), and between the corresponding standard errors, for functional groups in Prince William Sound (PWS) and the Alaska Gyre System (AGS). [Arrows indicate reference group (*Neocalanus cristatus*); see Table 1 and 2 for details] A: Correlation between TL_N and TL_E estimates from PWS; B: Relationship between OE_N and $S.E._E$ estimates from PWS; C: Correlation between TL_N estimates from PWS and TL_E estimates from AGS; D: Lack of relationship between OE_N estimates from PWS and $S.E._E$ estimates from AGS.


A
TL_N PWS
TL_E PWS
1
2
3
4
5
1
2
3
4
5
r = 0.986
n = 7


B
0.6
0.4
0.2
0
OI_N PWS
0
0.2
0.4
0.6
S.E.$_E$ PWS


C
TL_N PWS
TL_E GOA
r = 0.752
n = 16
1
2
3
4
5
1
2
3
4
5


D
OI$_N$ PWS
0.6
0.4
0.2
0
0
0.2
0.4
0.6
S.E.$_E$ AGS

Chapter 7

Information Systems and Model Development