Exxon Valdez Oil Spill
Restoration Project Final Report

Pacific Herring Productivity Dependencies in the Prince William Sound Ecosystem Determined With Natural Stable Isotope Tracers

Restoration Project 98311
Final Report

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Study History: Project 311 was funded to expand upon the isotopic data series available from project 320I (SEA) so as to provide a total four-year time period, 1994-1998, corresponding to one period in the cyclicity of herring population abundance in Prince William Sound. The SEA isotopic data ran from April 1994 through early spring 1996 but did not include any data between fall, 1994 and fall, 1995. However, a few samples from early 1995 collected by E. Brown, University of Alaska Fairbanks (UAF), were made available to project 311 for analysis in 1998. Thus new data derived from this project included that from the 1996 to 1998 period as well as early 1995 samples.

Abstract: A surprising finding of the Sound Ecosystem Assessment (SEA) Project was that Prince William Sound (PWS) herring and other fishes have significant dependence upon organic carbon, generated in the Gulf of Alaska (GOA) rather than PWS. The advective regime connecting the northern GOA with PWS may affect recruitment and nutritional processes in Pacific herring. This project was the first step to better understanding of this fundamental environmental process by analyzing isotopically a time series of herring. Objective 1: to analyze archived samples that had been collected from spring 1996 onwards at fours bays selected by Dr. Brenda Norcross (UAF). Objective 2: to analyze new samples as they become available following energetic content determination by Dr. A.J. Paul (Seward Marine Center) eventually to complete a 1995-1998 time series. Objective 3: synthesize data; objective 4: disseminate results. Analysis of samples from May 1995 enabling a partial filling in of the data gap between fall 1994 and fall 1995 was added as objective 5 during the course of the project. Isotope data was contributed to the SEA herring synthesis paper (Norcross et al.) and was used for calculation of protein and lipid content in the SEA herring over-winter modeling paper (Patrick et al.).

Key Words: Carbon sources, *Clupea pallasi*, Gulf of Alaska, herring, oceanography, Prince William Sound, stable isotopes.

Project Data: *Description of data* - Data consist of natural carbon and nitrogen stable isotope abundance measurements expressed in intentionally recognized delta units. *Format* - Data are published in various scientific manuscripts in the form of tables, figures, and an appendix. *Custodian* - Contact Dr. Thomas C. Kline, Jr., Prince William Sound Science Center, P. O. Box 705, Cordova, AK 99754. e-mail: tkline@pwssc.gen.ak.us. *Availability* - See literature citations or contact Dr. Kline for specific data which can be e-mailed.

Citation:

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Summary of Results:

A summary and documentation of the results through the final sampling, March 1998, are included in this report in the following paragraphs.

The premise for using natural stable isotope abundance in ecological studies is the conservative nature of trophic transfer of $^{13}C/^{12}C$ and $^{15}N/^{14}N$; basically, 'you are what you eat'. Herring reflect the isotopic ratios of organisms making up their diet that in turn are derived from their diet's diet and so forth to the bottom of the food chain, i.e., the phytoplankton. Phytoplankton vary in their discrimination of $^{13}C/^{12}C$ in accordance with physical processes that affect their access to inorganic chemical building blocks. Therefore, organic carbon which is about 1.1 % ^{13}C can be relatively enriched or depleted in this isotope. Kline (1999B) established in the SEA project (320I) that the isotopic composition of copepods were a good proxy for the isotopic composition of organic carbon generated for planktonic food webs. Kline (1997 and 1999B) also established protocols for normalizing data to eliminate lipid and trophic level effects in $^{13}C/^{12}C$ data that are used here. The prime symbol (e.g., Delta C-13' in the figures) denotes lipid normalization while 'trophic level normalized' values are thus indicated. Copepod isotopic data were used for 'isotopic matching' whereby herring isotopic data which were normalized to the same trophic level of copepods could be compared directly with copepod isotope data to show their affiliation for either PWS or GOA carbon sources. Thus the isotopic signatures for PWS or GOA carbon sources had to be ascertained first from data pertaining to copepods.

Carbon isotope signatures for PWS and the GOA were found to vary (Figure 1). However, the PWS carbon isotope signature varied only slightly, ranging from -20.5 to -18. The symbol 'P' is placed on the ordinate in the figures to denote the PWS carbon isotopic signature. The most positive PWS carbon isotopic values occurred in May 1997 coinciding with the 1997-98 El Niño - Southern Oscillation (ENSO) event commencing at lower latitudes in the Pacific Ocean. It is unknown whether there was any significance to this apparent tele-connection. According to T. Weingartner (pers. comm., Univ. Alaska Fairbanks), ENSO signatures are detected in the water column at station GAK-1 near Seward, Alaska in the spring *following* ENSO events, i.e, the teleconnection should have occurred in 1998. Thus the isotopic variance observed during this project may reflect non-ENSO related variability and is thus more likely related to the large inter-annual differences observed in water column salinity and temperature patterns (S. Vaughan, pers. comm. Prince William Sound Science Center, Cordova). In May 1997, PWS followed the 1994-5 pattern of being ^{13}C-enriched relative to GOA, though not to the same extent since the GOA was also ^{13}C-enriched.

The carbon isotope shifts occurring in the GOA were substantial (Fig. 1). GOA carbon was depleted in ^{13}C in 1994-5 (Kline 1999B); this signature is represented by the symbol 'G' in the figures. However in spring 1996, GOA carbon became substantially enriched in ^{13}C, shifting ~ 4.5 units compared to $^{13}C/^{12}C$ values previously observed (symbol 'G*' in the figures). In spring 1997, GOA carbon was also ^{13}C-enriched but not to the same extent as in 1996 (symbol 'G"). Except for spring 1996, GOA carbon was ^{13}C-depleted relative to PWS carbon.

Although spring 1996 zooplankton carbon was ^{13}C-enriched area-wide, there was evidence of a ^{13}C-depleted carbon source similar to that seen in 1994-5. The first line of evidence were the diapausing *Neocalanus cristatus* sampled during fall 1996. Approximately half the diapausing *Neocalanus* from fall 1996 had ^{13}C values outside the range of any sampled during the spring. Since the only other previously observed *Neocalanus* values in this range were from the GOA, it was conjectured that these too came from the GOA (Kline 1999A). Thus there were *Neocalanus* from the GOA but from outside the temporal and spatial scope of the May oceanographic sampling conducted by SEA, which contributed significantly (about half) to the diapausing population. Another line of evidence can be found in the herring data. In 1996 nearly all herring had carbon that was more ^{13}C-depleted than that observed in the zooplankton in May (note that most 1996 points are positioned lower than P or G* in Fig. 2). Therefore, there had to be a source of ^{13}C-depleted carbon in 1996 similar to that seen in 1994-5. A third line of evidence comes from the on-going GLOBEC investigation of Weingartner et al. (Univ. Alaska Fairbanks). Preliminary GLOBEC results are posted on the internet at http://www.ims.uaf.edu:8000/globec/results/. GLOBEC has found that *Neocalanus* copepods are most abundant near the continental shelf break. Furthermore, there were still substantial *Neocalanus* in July beyond the continental shelf break when the zooplankton bloom in PWS and on the shelf was long past. GLOBEC observations confirm the conjecture for substantial *Neocalanus* numbers outside the spatio-temporal scope of SEA project sampling. If isotopic analysis of *Neocalanus* samples collected at the outer Seward Line stations during GLOBEC consistently have depleted ^{13}C carbon, it would provide further proof for the conjecture that the substantial post-spring bloom ^{13}C-depleted carbon input into PWS came from the GOA. Furthermore the process of GOA carbon flux into PWS may be related to deep-water renewal processes (Kline 1999B) which occurs during summer months (Niebauer et al. 1994).

A synthesis using $^{13}C/^{12}C$ data in the context of the SEA herring synthesis paper (Norcross et al., manuscript 2 in the products section) is provided by Fig. 2. Figure 2 incorporates all juvenile herring data collected in projects 311 and 320I. Noteworthy points are indicated by annotations. There was a consistent increase in ^{13}C among the four over-wintering periods of the study which are shown as dashed lines in Fig. 2. The overwintering ^{13}C shift suggests that herring were not 'fasting' but consuming enough to effect a ^{13}C shift. The positive shift is consistent with an autochthonous carbon source being important rather than GOA carbon during winter. Stomach content analyses by B. Foy confirm that herring are feeding during the winter (reported in Norcross et al., manuscript 2). Nevertheless, herring loose whole body energetic content during winter (Paul et al. 1998). The arrows indicate increased diversity of carbon source-isotopic range during the summer. However, summer isotopic diversification did not take place in 1997. Possibly, a reason for this not occurring in 1997 were the highly atypical climatic conditions - possibly related to the El Niño-Southern Oscillation event of that year - with much warmer sea surface temperatures suggesting that the water column was more stratified than usual preventing intrusion of allochthonous carbon.

The most ^{13}C-depleted herring carbon was found in the fall of 1995. Since the $^{13}C/^{12}C$ values were relatively high in May 1995, the large magnitude change to low ^{13}C content had to have taken place later, therefore during the summer. Note that although there was a large spread in the data, there was no systematic spatial gradient as all fall 1995 sites were ^{13}C-depleted (Kline 1999B). Effects of the great 1995 ^{13}C-depletion continued into March 1996. However, ^{13}C increased sharply with the commencement of the 1996 production cycle with ^{13}C values peaking in June. It cannot be determined whether the shift to more positive values in spring 1996 was due to GOA or PWS as both carbon sources were ^{13}C-enriched (Fig. 1). By August of 1996 there was a recurrence of ^{13}C-depleted carbon as seen in previous years. The source of ^{13}C-depleted carbon for herring and that of copepods found in diapause that fall (see above) was outside the time-space scale of spring zooplankton samples, which in 1996 included samples as far away as the shelf edge near Middleton Is. Depleted carbon that is suggested to enter PWS from the Gulf during the summer thus represents either carbon generated in the near-Gulf late in the season or spring production from further out in the Gulf.

The data for the four bays including the samples from early 1995 through to the end of sampling in 1998 are shown in Fig. 3. The large ^{13}C shift occurring in 1995-6 differed slightly among the bays in terms of slope or rate of change. Note that each bay shifted systematically ,e.g., Eaglek was consistently the most negative of the four bays during the shift. This pattern suggests that fish in each bay functioned as a unit and were not mixing. Zaikof Bay shifted to the most positive value of ~ -20 then retained this values through August unlike the other three bays that became more negative. A possible reason is the shallowness of Zaikof. Although located near the Gulf, its depth prevents inflow of the deep water that is conjectured to contain Gulf-origin plankton. Furthermore, the Zaikof Bay water column did not contain higher density layers of seawater that were found in the other three bays during August 1996 (S. Gay, pers. comm.). Simpson Bay received the highest proportion of very low ^{13}C carbon in 1996. However, this was not the case in 1997-8 when it tended to more positive ^{13}C sources. Eaglek shifted the most in 1997-8 although it underwent the least change between November 1995 and June 1996. Thus there can be large variability in carbon exchange within a bay among years as well as differences in carbon exchange among bays within years. Given the variability among the four bays investigated here, continued use of at least four sites, possibly more, is warranted in future PWS herring studies. Certainly using fewer sites would reduce any chance for acquiring a representative sample of the overall PWS herring population.

A surprising and significant finding of these studies (320I and 311) is that much of the carbon in herring is allocthonous, i.e., derived from production generated outside PWS. The SEA sampling premise was that in PWS, secondary production (zooplankton, principally large herbivorous copepods) peaks during the month of May (Cooney 1997). However, within the northern GOA, plankton blooms are known to be delayed and protracted in time relative to PWS (Cooney 1986), which has been confirmed by recent GLOBEC cruises. Noteworthy are the *Neocalanus cristatus* in diapause (Kline 1999A) with consistent negative carbon isotope signatures even when those from the adjacent GOA to PWS in May had more positive signatures, as in 1996. These copepods influxed from outside PWS, originating outside the time and space scale sampled by SEA (Most extensive in May 1996; June 1996 GOA sampling was restricted to one station compared to four in May). Furthermore herring had more negative carbon isotope signatures in 1996 compared to copepods sampled in May within PWS or nearby GOA stations.

A limitation of the SEA study was the nearly exclusive focus on PWS oceanography. The importance of GOA carbon for herring demonstrated here as well as large-scale anomalous climatic conditions occurring during the course of these studies make it difficult to generalize further about herring ecology within a four-year time-frame. However, future research question recommendations are suggested based on what has been learned.

Future Research:

This study suggested that the advective regime connecting the northern GOA with PWS may be important for recruitment and nutritional processes in Pacific herring (*Clupea pallasi*). PWS herring can have significant dependence on GOA carbon. It is suggested that the advective environment introduces production from a distance away into PWS. Therefore it is important to integrate over greater spatial scales than simply PWS or even the adjacent shelf area plus PWS when assessing effects of long-term shifts in primary and secondary production on fishes (Cooney 1993).

PWS herring consistently acquired carbon from a source that was ^{13}C-depleted during the summer months. GLOBEC observations of post-spring production near the continental shelf break suggest that this may be the carbon source. A confirmation of this conjecture would therefore be made if these plankters had consistently low ^{13}C-content carbon isotope signatures.

The observations made here provide a challenge for circulation models presently in development for PWS. In particular, can models predict the large inferred year to year variability in strength of cross-shelf transport and influx into PWS? The inter-annual variability in cross-shelf flow assessed using stable isotope abundance could then be compared to model predictions of the same process once they are able to do so. A greater understanding of this meso-scale process will come about from the ability the measure interannual variability and from modeling exercises testing "what if?" scenarios.

Herring are subject to changes in carbon flow occurring between GOA and PWS. What about long term changes suggested by the recently recognized regime shift phenomenon (Frances and Hare 1994 Ingraham et al. 1998)? Isotopic analysis is suggested as a tool for unraveling this question since the role of GOA carbon in PWS may fluctuate according to long-terms change the "ring of zooplankton" undergoes as described by Broduer and ware (1992).

An important result of this project is the apparent spatial and temporal heterogeneity of carbon sources detected within herring. This has important implications for long-term sampling programs such as GEM that will need to sample a representative portion of the herring population in space and time. Carbon turnover was quick enough in juvenile herring to effect large isotopic changes in the ~2 month sampling interval of the four-bay study and there was significant differences in carbon source among bays within sampling time-frames. Undesirable biases could be introduced if long-term sampling was either temporally (e.g., sampling at one time of year) or spatially limited (e.g., sampling at limited sites). Therefore a systematic sampling scheme that addresses the temporal and spatial variability found here will need to be developed.

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Products:

Project 311 products were whole manuscripts or contributions to manuscripts:

1. Kline, Thomas C. Jr. 1999. Monitoring Changes in Oceanographic Forcing Using the Carbon and Nitrogen Isotopic Composition of Prince William Sound Pelagic Biota. *In:* Ecosystem Approaches for Fisheries Management. University of Alaska Sea Grant, AK-SG-99-01, Fairbanks. p. 87-95

2. Norcross, B. L., E. D. Brown, S. Gay, R. J. Foy, M. Jin, T. Kline, J. Kirsch, D. Mason, C. N. K. Mooers, V. Patrick, A. J. Paul, K. D. E. Stokesbury, S. J. Thornton, S. Vaughan, J. Wang. Biological and Physical Effects on the Early Life History of Herring in Prince William Sound, Alaska. (in review for Fisheries Oceanography,

3. E. V. Patrick, D. M. Mason, R. J. Foy, B. L. Norcross, A.J. Paul, K. D. E. Stokesbury, and T. C. Kline, Jr. Effects of physiological condition and water temperature on over-winter survival of age-0 Pacific herring: A modeling synthesis. (to be submitted to Fisheries Oceanography)

Manuscript 1 is included as part of this final report
Manuscripts 2 and 3 are included in project 320 SEA-Synthesis (Cooney et al.) final report.

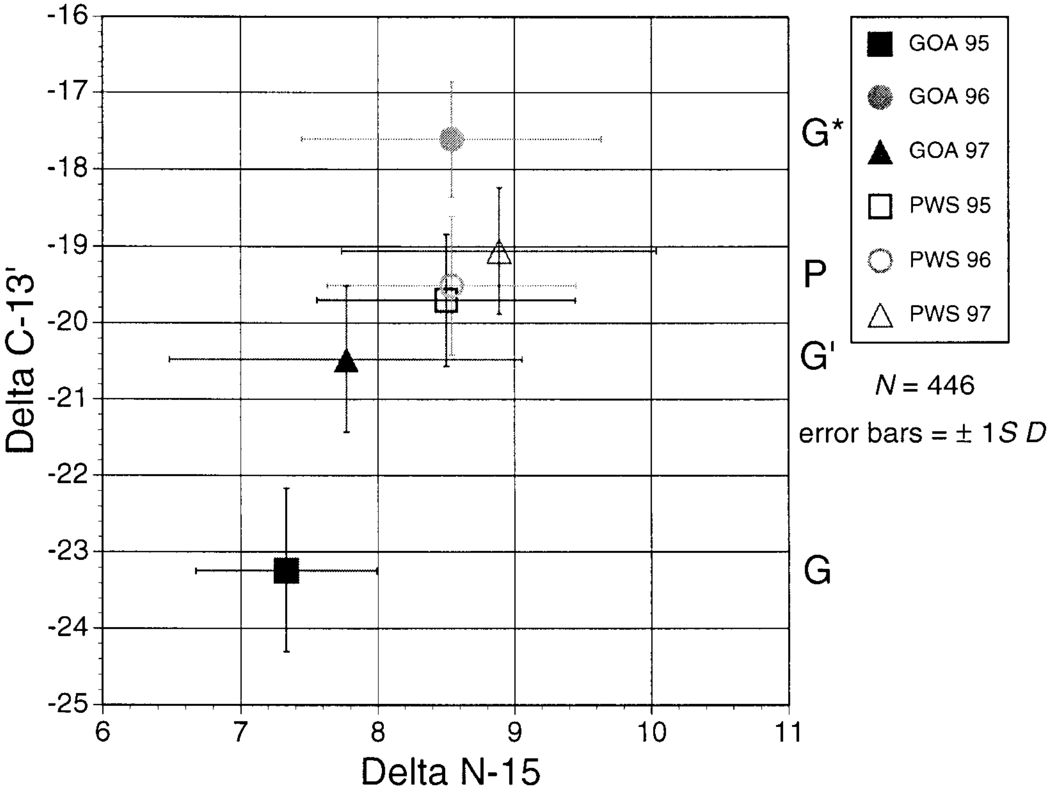


Figure 1. *Neocalanus cristatus* terminal feeding stages in upper 50m during spring

Figure 2. Juvenile (age 0 - 1) Pacific herring (*Clupea pallasi*) from Prince William Sound

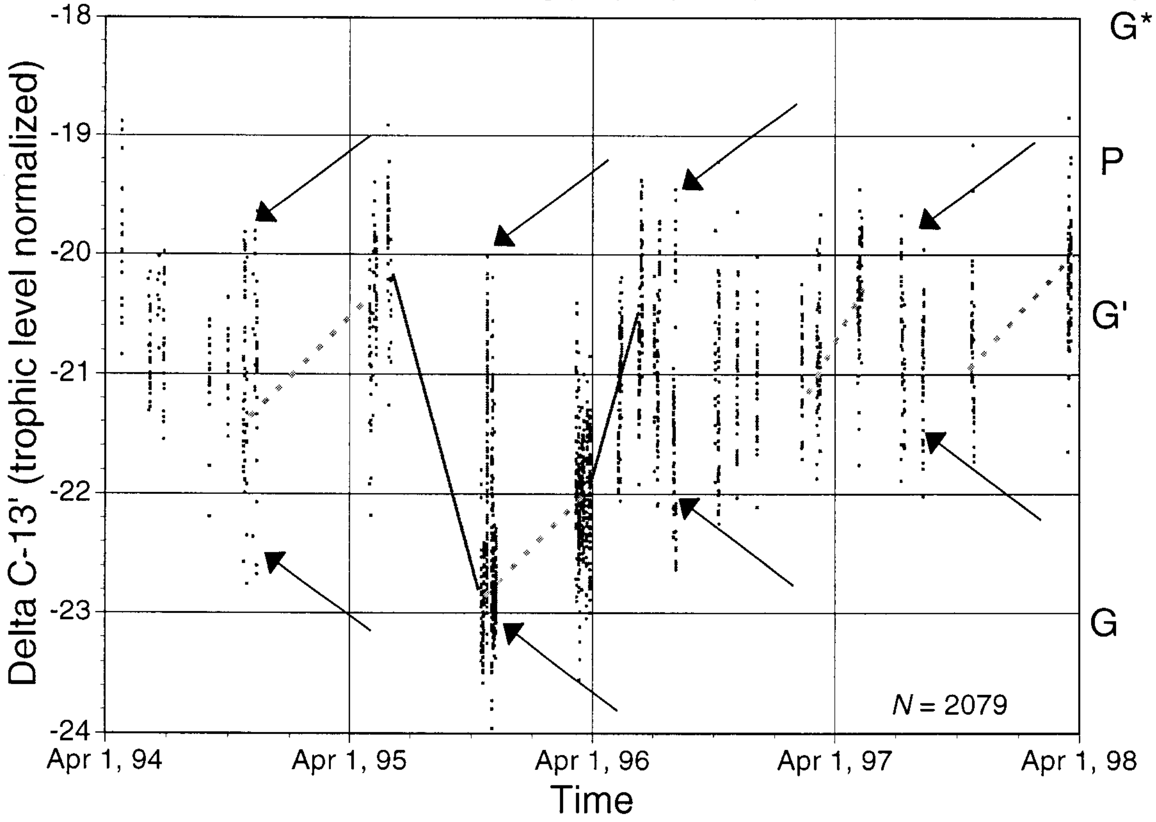
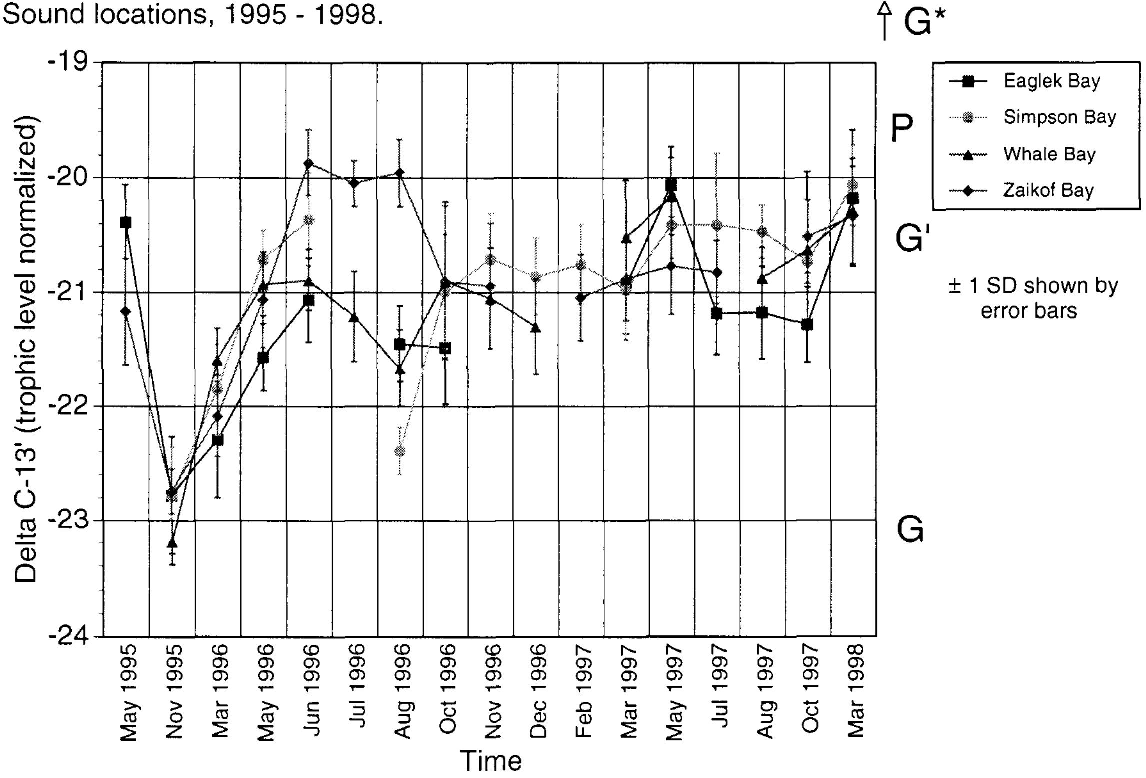


Figure 3. Juvenile (age 0 - 1) Pacific herring (*Clupea pallasi*) from four Prince William Sound locations, 1995 - 1998.



± 1 SD shown by error bars

Ecosystem Approaches for Fisheries Management
Alaska Sea Grant College Program • AK-SG-99-01, 1999

Monitoring Changes in Oceanographic Forcing Using the Carbon and Nitrogen Isotopic Composition of Prince William Sound Pelagic Biota

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Abstract

Changes in the physical environment known to affect phytoplankton and zooplankton production can be linked to fish production through carbon and nitrogen stable isotope natural abundance measurements. Stable isotopic analyses of herbivorous copepods and juvenile fishes from Prince William Sound (PWS) and the northern Gulf of Alaska (GOA) were conducted as part of the Sound Ecosystem Assessment (SEA) project, a comprehensive multidisciplinary ecosystem study. The advective regime connecting the GOA with PWS was postulated by SEA to affect recruitment and nutritional processes in juvenile fishes. Herbivorous zooplankton, an indicator for pelagic production sources, had distinctive carbon isotope signatures when sampled in the GOA compared to those from PWS. PWS carbon had consistent spring bloom carbon isotopic signatures during 1994-1996 while GOA carbon differed in 1996. Nevertheless, PWS carbon was always distinctive from GOA carbon. This variation suggested that interannual fluctuations occurring at the food chain base are driven by processes in the gulf.

Analyses of nitrogen isotope ratios and C/N ratios of juvenile fishes were used to normalize their carbon isotope ratios, enabling determination of their relative affinity for GOA or PWS carbon. The data suggest a large affinity range, changing on annual time scales, consistent with observed oceanographic phenomena. For example, there was a shift to a greater dependency on GOA carbon in 1995 compared with 1994 and 1996. A parallel shift to increased GOA-originating copepods undergoing diapause (resting phase) in 1995 suggesting an influx of GOA zooplankton,

provided a second line of evidence. Thus herring and other fishes partially dependent on GOA carbon are subject to vagaries of carbon flow that fall under the domain of physical oceanographic processes connecting the GOA with PWS as well as processes occurring on the GOA continental shelf adjacent to PWS.

Introduction

Cycles in the size of fish and shellfish populations have had dramatic effects on Gulf of Alaska coastal fisheries of Alaska (McDowell et al. 1989). Variations in natural stable isotope abundance provide evidence that the advective regime connecting the northern Gulf of Alaska (GOA) with Prince William Sound (PWS) can alter nutritional processes in PWS pelagic food webs (Kline 1999). Gradients of stable isotope ratios of carbon in the PWS study area serve as effective tracers of energy supply due to conservative transfer of carbon isotope ratios between the lower trophic levels (phytoplankton to zooplankton to forage fishes, etc.) up to the top consumers. Fishes acquire these isotope ratios in response to the importance of the food in bulk body tissues (muscle and fat). Isotope ratio analysis of these tissues can provide insight into the effects of fluctuations of GOA carbon sources on PWS fish populations (Kline 1999).

The large interzonal herbivorous copepods of the genus *Neocalanus*, which comprise the bulk of the zooplankton during vernal zooplankton blooms, have a yearly life history pattern. They undergo a prolonged stage copepodite-V diapause at depth following termination of feeding at the end of the bloom. The diapaused copepods provide the "seed" for the following generation since reproduction takes place at depth in late winter. A portion of PWS has depths great enough to accommodate the *Neocalanus* diapause stage; i.e., depths > 400 m (Kline 1999). The offspring of *Neocalanus* diapausing in PWS form a source of primary consumers of the PWS spring bloom. A secondary source of *Neocalanus* are populations diapausing beyond the continental shelf in the GOA. The Alaska Coastal Current flow in PWS may transport *Neocalanus* into PWS while feeding or during ontogenetic migrations in the water column (Kline 1999).

Diapausing samples were analyzed for $^{13}C/^{12}C$ for comparison with the regional isotope gradient obtained during the bloom to assess input of GOA copepods after feeding is complete. Concomitant shifts in the $^{13}C/^{12}C$ content of diapausing copepods and fishes in PWS during the 1994-1996 study period suggested a common system-wide cause.

Materials and Methods

Copepods were collected at the terminal feeding stage (Copepodite IV and V) throughout PWS and stations in the northern GOA and during diapause (Copepodite V and VI) at stations located in suitable habitat in PWS (Kline

1999). Juvenile Pacific herring and walleye pollock were collected throughout PWS during 1994-1997 from multivessel broad-scale surveys (Kline 1999). Laboratory handling procedures, isotopic analysis preparation, and data analysis were as described by Paul et al. (1998) and Kline (1999).

Normalization for lipid (DeNiro and Epstein 1977) and trophic level effects on $\delta^{13}C$ values of fish enabled "fingerprinting" of their carbon source (Kline 1997, 1999). The McConnaughey and McRoy (1979) lipid normalization based upon the C/N ratio using a $C/N = 4$ as the base level was used. The Kline (1997) method for the normalization for trophic level effects used: (1) the $\delta^{15}N$ value of the herbivore, *N. cristatus*, as the trophic level baseline (Vander Zanden et al. 1997); and (2) an assumed constant N and C trophic fractionation factor ratio of 3.4:1. In general, normalization reduces sources of ^{13}C variability, enabling comparisons among species without the confounding effects of trophic level and lipid content (Kline 1997). Thus, normalized $^{13}C/^{12}C$ content of fishes could be compared directly with *N. cristatus* at a consistent lipid storage level (Kline 1999).

The expressions $\delta^{13}C$, $\delta^{13}C'$, $\delta^{13}C_{TL}$, or $\delta^{13}C'_{TL}$ denote $^{13}C/^{12}C$ abundance in relation to the international standard (Vienna PDB), normalized for lipid content, normalized for trophic level, and normalized for lipid content and trophic level, respectively, using conventional delta notation (the per mil [‰] deviation from the international standard). Whereas $\delta^{13}C'$, $\delta^{13}C_{TL}$, and $\delta^{13}C'_{TL}$ are used in accordance to a particular data analysis context, "^{13}C" is used to reflect generic $^{13}C/^{12}C$ isotopic trends irrespective of normalization. Similarly, $^{15}N/^{14}N$ abundance is expressed relative to air N_2 as $\delta^{15}N$ values.

Results

Neocalanus cristatus sampled throughout the PWS and GOA were consistently different (Kline 1999). The mean values plotted versus time show a consistency for PWS carbon $\delta^{13}C'$ of −19 to −20‰ (Fig. 1). GOA carbon was usually ^{13}C-depleted having $\delta^{13}C'$ values of −22 to −23.5‰. However, in 1996, *Neocalanus cristatus* (as well as other *Neocalanus* species) shifted to an anomalous high $\delta^{13}C'$ of ~ −17.5‰ (Fig. 1).

The isotopic composition of *Neocalanus cristatus* diapausing in PWS include those with signatures consistent with those feeding in PWS (upward arrows, Fig. 2) and those feeding in the GOA (downward arrows, Fig. 2). While mean $\delta^{15}N$ was consistently ~ +8‰ each year, the relative proportion of high and low $\delta^{13}C'$ varied (Fig. 2.). While the contribution of PWS and GOA copepods was approximately the same in 1994, most of those in 1995 and 1996 originated from the GOA.

Juvenile herring and pollock < 100 mm long shifted in $\delta^{13}C'_{TL}$ content in concert during 1994-1997 (Fig. 3). The lowest $\delta^{13}C'_{TL}$ values measured in juvenile fishes in 1995 coincided with low $\delta^{13}C'_{TL}$ in diapausing *Neocalanus cristatus* (Fig. 2).

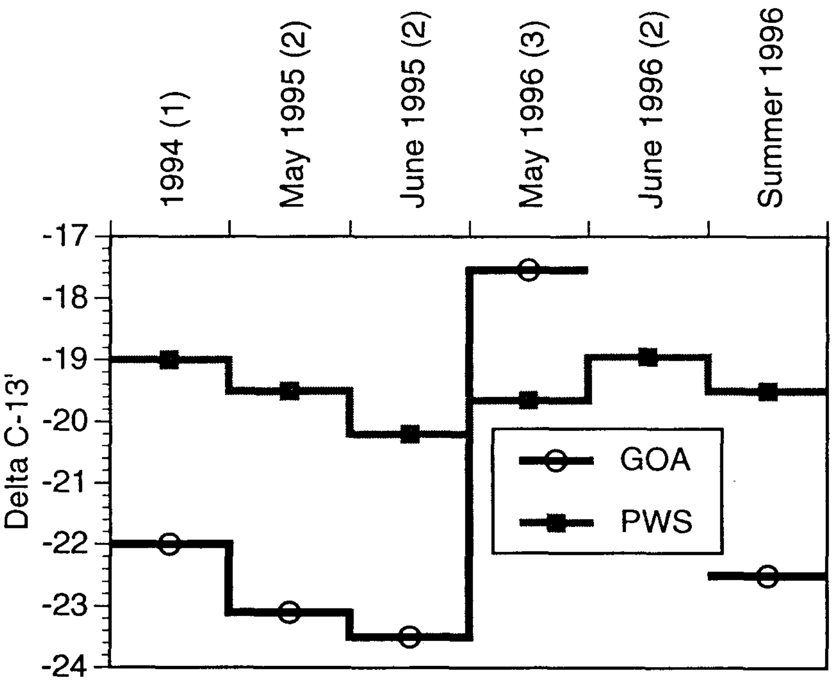

Figure 1. *Time series of $\delta^{13}C'$ measured in feeding Neocalanus cristatus from Prince William Sound (PWS) and the Gulf of Alaska (GOA), 1994-1996. Points indicate mean values, standard deviations were 0.5-1‰. PWS and GOA values were consistently statistically different (t-test $P < 0.05$). (1) Mean values inferred from diapaused population modes. (2) Mean values of terminal feeding stages sampled with 0.5 m diameter plankton net. (3) Mean values of terminal feeding stages sampled with MOCNESS sampler. (4) Mean values inferred from diapaused population modes (Fig. 2: 1996).*

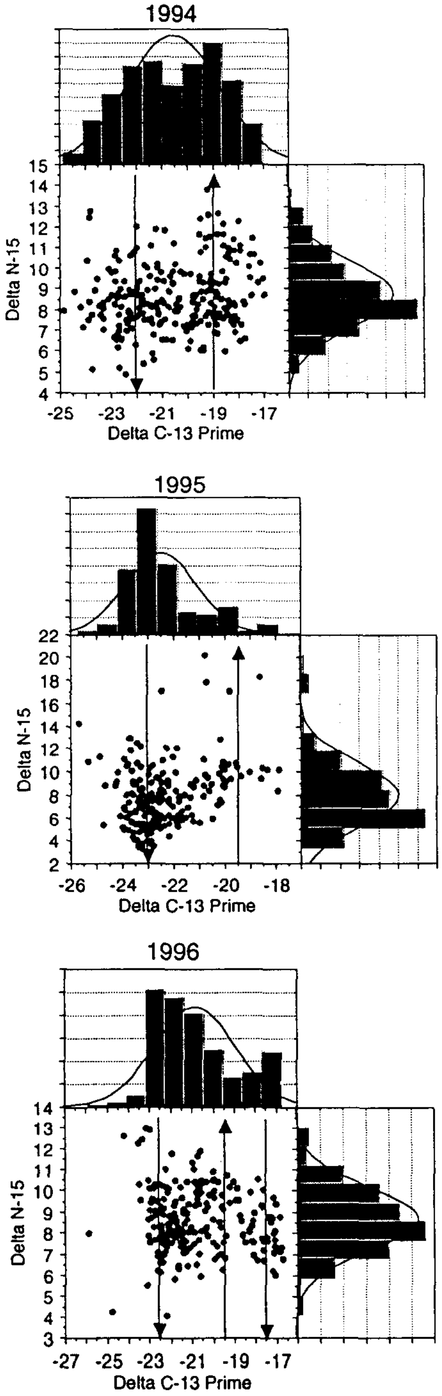

Figure 2. The $\delta^{13}C'$ composition of Neocalanus cristatus diapausing in Prince William Sound (PWS) from three cohorts. The upward-pointing arrows indicate $\delta^{13}C'$values of Neocalanus cristatus originating in PWS which were inferred from mode values (1994) or measured in spring sampling (1995 and 1996; Fig. 1). The downward-pointing arrows indicate $\delta^{13}C'$ values of Neocalanus cristatus originating in the Gulf of Alaska which were inferred from mode values (1994 and −22.5 value in 1996) or measured in spring sampling (1995 and −17.5 value; Fig. 1). The isotopic shifts indicate a greater extent of zooplankton transport into PWS in 1995 than 1994 and 1996.

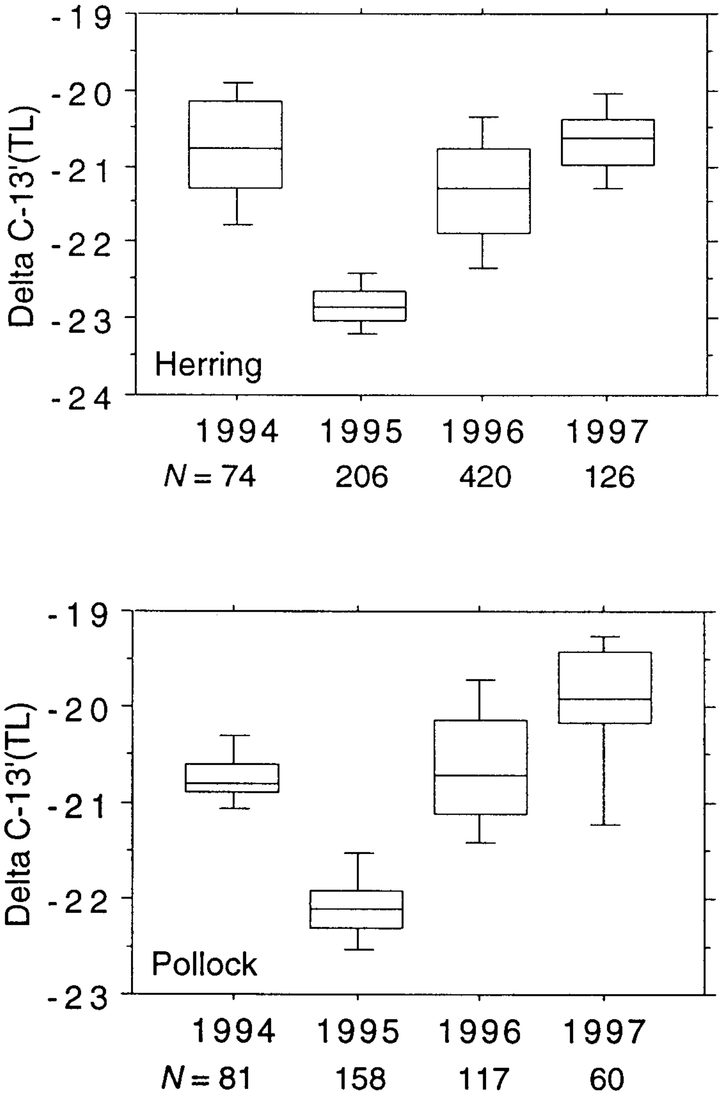

Figure 3. *Shift in $\delta^{13}C'_{TL}$ for Prince William Sound Pacific herring and walleye pollock < 100 mm long in 1994-1997; sample sizes as indicated. The distributions of values are shown as box and whisker plots that denote the 10th, 25th, 50th, 75th, and 90th percentiles. There was a large shift to greater Gulf of Alaska carbon dependency in 1995 for both species as indicated by the low $\delta^{13}C'_{TL}$ values.*

Discussion

Regional Isotopic Gradient and Interannual Variability

There was a consistent isotopic gradient between PWS and GOA in the 1994-1996 period except for May 1996 when the gradient reversed owing to a large magnitude change in the GOA signature (Fig. 2). Whereas PWS mean $\delta^{13}C'$ values ranged within 1‰, and the difference between PWS and GOA averaged 3‰, the GOA mean value shifted in spring 1996 by 5‰. This large shift probably reflected a change in phytoplankon fractionation during uptake of CO_2 which varies as a function of growth rate (Laws et al. 1995). Thus the productivity pattern during the spring bloom of 1996 was markedly different from other times. These isotopic values corroborate model predictions made for spring 1996 that suggest poor GOA primary and zooplankton productivity (Eslinger and Cooney 1997). If fluctuations in GOA productivity are typical, they could affect year-to-year inconsistencies in food availability for consumers. Thus the question arises: Are fluctuations in GOA spring bloom $\delta^{13}C'$, and inferred growth rate changes (Laws et al. 1995), typical?

Juvenile Fish Carbon Source Dependencies

A change in carbon source dependency for fishes can be inferred from their $\delta^{13}C'_{TL}$ shifts (Fig. 3). Juvenile herring and pollock are the dominant pelagic fishes in PWS and both consume zooplankton. Juvenile herring and pollock from PWS shifted in $\delta^{13}C'_{TL}$ content during this study from which a change in carbon source dependency can be inferred (Fig. 1). Although both species shifted in concert to lower $\delta^{13}C'_{TL}$ suggesting a greater GOA dependency in 1995 than 1994, pollock were generally 0-1‰ more positive in $\delta^{13}C'_{TL}$ suggesting a lower dependency on GOA carbon. Juvenile pollock and herring occupy different levels in the water column, have different schooling behavior, and recruit from the larval stage at different times, effecting access to a different forage base as confirmed by differences in the data. This difference may not be reflected in the species composition of diet, but instead, the where and when of the production cycle as integrated into the isotopic signature (Kline 1999), which reflects the assimilated carbon pool of the fish. The greater reliance on GOA-derived carbon in herring may reflect their dependence on carbon generated later in the season during the time when advection of GOA production was nearly the sole carbon source in 1995 (Kline 1999).

Significance of Parallel Isotopic Shifts

The concordant shift to greater GOA dependency by both fish species throughout PWS in 1995 implied that system-scale oceanographic process-driven bottom-up effects permeated PWS. Furthermore, *Neocalanus cristatus* diapausing in fall 1995 principally came from the GOA. A common process that explains these observations is the physical transport of water containing zooplankton (both copepods entering diapause and zooplankton fish forage) into PWS from the GOA sometime after the spring bloom via the Alaska Coastal Current or deepwater renewal (Kline 1999). The greater degree of GOA carbon dependency by fishes and the greater proportion of GOA copepods in diapause in 1995 than other years suggests that the influx of GOA water was stronger that year. Variations in zooplankton transport into PWS among years are thus evidenced. Such system-wide changes suggest that there are year-to-year inconsistencies in the food web base and fish production potential for PWS and thus should be a concern for management of exploited populations.

Ecosystem Considerations for Management

Fishes living in PWS but dependent on GOA carbon are subject to changes in carbon flow that result from physical oceanographic processes (e.g., currents and gradients of temperature and salinity) that connect the GOA with PWS. It is conjectured that affinities range from total dependency on PWS carbon to significant input of carbon from the GOA. Fishes wholly dependent on PWS are more likely to be directly affected by internal PWS processes. Increased competition for PWS carbon by all species, however, may occur if GOA carbon is 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 $^{13}C/^{12}C$ signature. Increased competition for PWS carbon by all species, however, may occur if GOA carbon is less available to those that normally use it. Time-series measurements of natural stable isotope abundance in fishes combined with data on fish populations and cogent oceanographic measurements will enable a new understanding of how basic environmental processes affect fish recruitment and interaction.

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