PRINCE WILLIAM SOUND
SCIENCE CENTER
CORDOVA, ALASKA

PRINCE WILLIAM SOUND SCIENCE CENTER ANNUAL REPORT

Exxon Valdez Oil Spill
Restoration Project Annual report

Prince William Sound Food Webs: Structure and Change

Restoration Project 99393
Annual Report

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

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April 2000

Prince William Sound Food Webs: Structure and Change

Restoration Project 99393
Annual Report

Study History: This project, which commenced in on 1 April, 1999, is addressing gaps in our knowledge of Prince William Sound ecological processes. This report provides preliminary results of a planned three-year project.

Abstract: Recent research has shown that the advective regime connecting the northern Gulf of Alaska (GOA) with Prince William Sound (PWS) may affect recruitment and nutritional processes in Fishes (Kline 1999b). Accordingly, food webs are subject to changes in carbon flow occurring between GOA and PWS. This project is: (1) conducting a retrospective analysis of GOA production shifts since EVOS, and (2) addressing Ecopath model validation data gaps. These analyses will enable a better understanding of the ecological role of ‘regime shift” processes conjectured to be impeding the natural restoration of populations in PWS affected by the EVOS.

Key Words: Ecosystem, Food Webs, Prince William Sound, Stable Isotopes

Project Data: (will be addressed in final report)

Citation: Kline, Thomas C., Jr. 2000. Prince William Sound Food Webs: Structure and Change, *Exxon Valdez* Restoration Project Annual Report (Restoration Project 99393), Prince William Sound Science Center, Cordova, Alaska.

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Appendix I. Output of Staview computer program.
Appendix II. Manuscript titled: "The Trophic Position of Pacific Herring in Prince William Sound Alaska Based on their Stable Isotope Abundance." This manuscript was submitted to "Herring 2000, 18th Wakefield Fisheries Symposium" and is presently undergoing peer review for that publication.

Executive Summary

Recent research has shown that the oceanographic conditions connecting the northern Gulf of Alaska with Prince William Sound may affect recruitment and nutritional processes in Fishes (Kline 1999b). Accordingly, food webs are subject to changes in carbon flow occurring between Gulf of Alaska and Prince William Sound. This project seeks to (a) conduct retrospective analysis of Gulf of Alaska production shifts since the oil spill, and (b) address Ecopath model validation data gaps. These analyses will enable us to gain a better understanding of the ecological role of regime shift processes conjectured to be impeding the natural restoration of populations in Prince William Sound affected by the oil spill.

Introduction

Shifts in carbon flow occurring as a result in variations in the physical environment represent fundamental changes in the way the PWS ecosystem supports commercially important species. The availability of macrozooplankton forage for fishes varies in space and time because of changes in physical processes in PWS. The approach using stable isotope ratios of carbon and nitrogen is unique in its ability to integrate time and spatial scales at mesoscale levels. No other technique currently available can generate such results. The natural tracer aspects of the approach emulates artificial tracer experiments without the burden of needing to generate signals or experimental artifacts. Using stable isotopes to rack the effect of Gulf carbon inflow on pelagic production that appears to vary between years will be used to resolve the question of how oceanographic process affect fisheries recruitment. Furthermore, the value of the Ecopath modeling effort funded as restoration tool will be greatly enhanced through a incorporation of a proven stable isotope model validation concept.

Stable isotope ratios of carbon and nitrogen have been shown to serve as effective tracers of energy supply in the Prince William Sound study area (Kline 1997a, 1997b, 1998, 1999b) because of (1) the conservative transfer of carbon isotope ratios between the lower tropic levels (phytoplankton to zooplankton to forage fishes, etc.) of Prince William Sound (PWS) and adjacent Gulf of Alaska (GOA) waters up to the top consumers and (2) the naturally occurring gradient in $^{13}C/^{12}C$ productivity generated in the Gulf compared with the Sound. Organisms acquire these isotope ratios in response to the importance of the food in bulk body tissues. Isotope ratio analysis of tissues thus provide insight into both habitat usage and assist in quantifying amounts derived from various areas. Nitrogen isotope ratios, in turn, provide excellent definition of relative trophic level. The heavy isotope of nitrogen is enriched by about 0.3 % with each trophic level and thus can accurately indicate the relative trophic status of species within an ecosystem (Minagawa and Wada 1984, Fry 1988) which was found to be useful for food web model validation (Kline and Pauly 1998, Kline 1999b).

Results Narrative

Objective 1 - Gathering evidence for production shifts in the GOA-PWS arena

Juvenile herring and pollock, the dominant pelagic fishes that consume zooplankton in PWS, shifted in $^{13}C/^{12}C$ content between 1994 and 1995 from which a shift in PWS versus GOA carbon source dependency was inferred (Kline 1999b). The concordant shift to greater GOA dependency by both fish species in 1995 was also matched by the proportion of *Neocalanus* copepods diapausing in PWS that came from the GOA. These shifts implied that system-wide bottom-up effects permeated the whole ecosystem and so were more likely to be due to oceanographic processes (Kline 1999b).

The carbon stable isotope gradient between PWS and GOA had a consistent relationship in the 1994-1996 period except for May 1996 when the gradient reversed owing to a large magnitude change in the $^{13}C/^{12}C$ content of GOA plankton (Kline 1999a). Whereas the PWS mean $^{13}C/^{12}C$ values ranged within 1 delta unit, and the difference between PWS and GOA averaged 3 delta units, the GOA mean value shifted in Spring 1996 by 5 delta units. This large shift reflected a change in phytoplankon fractionation during uptake of CO_2 which varies as a function of growth rate (Laws et al. 1995, Bidigare et al. 1997). Thus the data suggest that the productivity pattern during the spring bloom of 1996 was markedly different from other times. Large fluctuations in productivity in the GOA further suggest large inconsistencies in food availability for consumers from year to year. If GOA spring bloom productivity fluctuations are typical and can be evidenced by changes in $^{13}C/^{12}C$, we may have a tool for investigating the relationships between planktonic and fish productivity in time-series studies.

Decadal-scale climatically-driven shifts in primary production cycles of the subarctic Pacific Ocean have been conjectured to effect population changes in fishes and their zooplankton forage base (Brodeur and Ware 1992, Francis and Hare 1994). A "ring of zooplankton" occurring near the Gulf of Alaska (GOA) continental shelf break appears to undergo dramatic oscillations in abundance over decadal or longer time scales (Brodeur and Ware 1992). Furthermore, this "ring of zooplankton" is driven onto the continental shelf providing the shelf ecosystem with an important forage base (Cooney 1988, 1993). Furthermore, oceanic zooplankton may be swept by currents into coastal water bodies. For example, the transport of zooplankton from the GOA into Prince William Sound (PWS) may provide significant quantities of forage for food webs and through use of their distinctive stable isotope signature provide a good method for detecting shifts in biophysical coupling in the PWS region (Kline 1999a, 1999b). A recent "regime shift" similar to that seen in the past (Brodeur and Ware 1992, Francis and Hare 1994) is conjectured to be presently occurring in the North Pacific (Anderson et al. 1996). Population recoveries since the *Exxon Valdez* oil spill (EVOS) are uncertain since this regime shift may be impeding population increases.

It has been possible to ascertain that GOA primary productivity patterns vary at inter-annual time scales and that GOA production is important to PWS using NSI techniques (Kline 1999a, 1999b). A retrospective approach is being used by GLOBEC in several projects in the N.E. Pacific as a means of overcoming database temporal limitations (U.S. GLOBEC 1996). Using retrospective NSI analysis, it may be possible to assess whether fluctuations in primary production took place since EVOS. If so, this could explain the poor recovery of some injured species. Furthermore, fluctuations in the mass balance of carbon postulated to be taking place can be incorporated into applications of the Ecopath model being developed by Trustee Council funding which care also be validated using NSI data as objective 2, below, see also Kline and Pauly (1998).

There is a discontinuity between the start of PWS ecosystem studies in 1994 and the timing of EVOS in 1979. Ecosystem shifts occurring in the GOA since 1989 were thus not incorporated in present studies. To overcome this perspective, retrospective NSI analyses may enable a reconstruction systematic ecological changes occurring since 1989. Fixed tissues such as the protein layer on the exterior of mussels provide a recent record of changes in the isotopic composition of their phytoplankton diet.

Objective 1 - Methods

Mytilus californianus were collected at Middleton Island in September 1997 with help from Cordova fishermen. They provided the P.I. with the knowledge and opportunity to acquire the *Mytilus californianus* samples that are providing an inexpensive approach to retrospective analysis in the present study. Middleton Island's location in the Alaska Current provides an "upstream perspective" on the EVOS area since samples from there will reflect changes in plankton upstream before interaction with PWS-origin carbon is possible.

Stable isotopic analysis is being conducted on the outer protein layer (periostracum) on the shells and body tissues of Sea-mussels (*Mytilus californianus*) of varying ages collected at Middleton Island.

The periostracum is cut into sections (~ 2.0 mg for each analysis) along annular growth rings. Mussels were scored with a scalpel on raised annuli (winter growth checks) and then freeze-dried for 24 hr to initiate periostracum separation. Flakes of periostracum were forcepted from shells and placed into a separate vial for each annulus which were counted from year 1. When periostracum was worn off (early years), the first annulus sample was given its estimated year of life. For example, if periostracum from years 1 and 2 were worn off, the first sample was X-3, where X is the mussel number and 3 is the periostracum growth from the third year of life. A final periostracum sample from a given mussel came from the lip of the shell which will be used for definitive within-year comparisons. Additionally, 1 byssus and 1 soft tissue collection was taken from each mussel to ascertain within organism isotopic fraction effects.

Mussels of different age are being used to extract data from various years (as annuli are wider and more distinct at earlier ages) to reconstruct an isotopic time series retracing conditions from 1997 backwards in time to EVOS and earlier. For example, a 5 to 10 - year old mussel will resolve well recent years whereas a 10 to-20 year old will resolve years when the mussel was younger. Overlapping years (of periostracum samples) of good age resolution will be used to inter-calibrate mussels while younger mussels will be calibrated against our zooplankton database. The goal is to reconstruct a $^{13}C/^{12}C$ time-series covering at least the 1989 - 1997 period. The reconstructed time-series will be compared with observed $^{13}C/^{12}C$ changes in 1994-1997 (Kline 1999a). The following question will be asked: Did changes of the magnitude seen in 1996 occur in other years? If so, how often. If not, then the 1996 will be considered an anomaly rather than a common occurrence. Objective 1 results and discussion will be addressed in the next annual report as data are not yet available. Of particular interest will be comparing the level of inter-annual variability in mussels compared to baleen found by Schell (2000).

Objective 2 - Validation of the PWS Ecopath model

The PWS Ecopath model effected an integration of various regional syn- and autecologial studies through synthesizing the known ecological relationships of certain organisms or groups of organisms inhabiting PWS. A principal goal of Ecopath was to conduct perturbation experiments to examine EVOS and restoration effects (Oakey and Pauly 1998). The utility of perturbation experiments will in part be dependent on how realistic the Ecopath model upon which they are making their predictions truly is. One way to determine if the model is realistic is to compare model predictions with those made using an independent method. Ecopath generates as part of its output the fractional trophic level for each functional group defined by the model. These trophic level predictions can be validated comparing them with trophic level determinations made from $^{15}N/^{14}N$ data (Kline and Pauly 1998). Kline and Pauly (1998) validated a preliminary PWS Ecopath model using this novel approach. However, the preliminary model and validation consisted of only a limited number of functional groups (7 including the calibration point) whereas the full Ecopath model has 46 functional groups. The artifact of functional group over-aggregation, problematic to the preliminary model, is reduced in the full model; therefore a more robust Ecopath validation using $^{15}N/^{14}N$ data is expected in this study.

Objective 2 - Methods

Since the Ecopath model was completed in early 1999, there was some urgency for this project, therefore there was a need to expedite an initial analysis batch in relation to expected delivery of data following project startup on 1 April, 1999. There is always a significant time lag from the date when funding begins to when new data first become be available. First, samples need to be prepared in the laboratory, converting them into a finely-powdered form. Second, samples are sent out for mass spectrometry at the University of Alaska Stable Isotope Facility. It typically takes 6 to 9 months to get data back. Therefore, to expedite analysis during the first 6 months of the project, 1 April to 30 September, samples that were nearly ready were for analysis selected. These (N ~500) samples consisted primarily of fish taxa sampled during the SEA project that were not of primary interest to SEA. Because they were intermingled in the collections with SEA target samples, they were had been cataloged and mainly needed to be pulverized prior to analysis. These samples were sent out during 1999 and their data became available during January, 2000. These data were combined with existing data from SEA and collectively comprise the preliminary results. These data were categorized into the functional groups described in the Ecopath report (Oakey and Pauly 1998) for the preliminary data analysis presented here.

Objective 2 - Results and Discussion

The preliminary data are presented in Table 1. The table compares the trophic levels predicted by the Ecopath model with trophic levels determined empirically using $^{15}N/^{14}N$ abundance. From the latter, it was also possible to present descriptive statistics that enable further evaluation of the results. Additionally, the very extensive data available for Pacific herring (*Clupea pallasi*) from Trustee projects /320I and /311 were used to produce a more in-depth assessment of their trophic level and that of the baseline upon which herring and other higher trophic levels are determined (Kline 2000 - Appendix II). The upshot of this analysis was that the baseline value was updated to 8.4 from the 8.0 value used by Kline and Pauly (1998). This change is equivalent to a 0.1 trophic level difference affecting each estimated organismal trophic level determination systematically. Note that 0.1 is < the standard deviation of the trophic level estimates as well the typical difference between Ecopath and $^{15}N/^{14}N$-content based trophic levels (Table 1.) and thus is a minor correction. The worst-case scenario for baseline error is to consider the alternate and exclusive use of productivity derived from either PWS or the GOA and the maximal observed 1.3 per mil $^{15}N/^{14}N$ gradient between these sources (see Table 1 in Kline 2000 - Appendix II). This worst case scenario would effect a 0.4 trophic level difference. Therefore model-empirical differences of > 0.4 trophic levels are less likely to be explainable by isotopic differences between dichotomous food webs. For example, adult salmon that are in PWS are recent immigrants from the GOA and so have fed upon a totally different food web. Their trophic level could be expected to differ because of "shoehorning" of functional groups originating outside the bounds of the Ecopath model (Kline and Pauly 1998).

The trophic level analysis of > 2000 herring samples suggested slight seasonal shifts to lower trophic levels during summer months (see Fig. 2 in Kline 2000 - Appendix II). While a seasonal shift can be most easily explained by the prevalence of planktonic life forms directly utilizing spring-summer primary production, it underscores the fact that most feeding Alaskan studies and thus data have a summer bias. The lower value empirical trophic level determined for the summer may thus be more comparable to the modeled value explaining their convergence.

The range of herring size in the isotopic database also enabled assessment of ontogenetic trophic level shifts (see Fig. 1 in Kline 2000 - Appendix II). There appears to be an increase in trophic level when length is < ~70 mm. Beyond 70 mm, the trophic level increase (~ 0.2 trophic levels) approximates overall trophic level variability (*s.d.* = 0.2)). The Ecopath model predicted trophic levels of 3.03 and 3.10 for juvenile and adult herring, respectively. The size break between juvenile and adult herring as used by Ecopath was 180 mm (Okey and Pauly 1998). The relatively few herring > 180 mm that were isotopically analyzed had trophic levels within the same range as those much smaller (see Fig. 1 in Kline 2000 - Appendix II). The empirical evidence of little ontogenetic trophic shift at ~

180mm and the mere 0.07 trophic level difference predicted by Ecopath suggest that these functional groups should be either aggregated into one or separated at another size, e.g., 70mm. For the purposes of comparing model predicted with empirically determined trophic levels, isotopic data were aggregated and collectively compared with each Ecopath herring functional group (Table 1).

Even at this preliminary stage of data analysis there are some interesting departures in model-predicted compared to empirically-determined trophic levels for several of the Ecopath functional groups. Omnivorous zooplankton had the highest deviation in the negative direction, i.e., the $^{15}N/^{14}N$ data suggest a 0.5 higher trophic level than Ecopath. This may, in part, reflect the inclusion of carnivorous meroplankters such as crab larvae as well as the carnivorous copepod *Euchaeta* in this functional group. However, the way the PWS Ecopath model is set up, these taxa are placed into the omnivorous zooplankton functional group. Trophic relationships within the plankton community are problematic to study and so are not as well know nor as well understood as those of fishes, mammals or birds. These modeling-empirical validation studies may therefore help to better elucidate the food web structure within the plankton.

Ecopath trophic levels for functional groups above number 14 were all greater than $^{15}N/^{14}N$-based trophic levels (Table 1). However, the sample sizes are still small and additional samples are expected. For example, two colleagues will be providing T. Kline with salmon and sleeper shark samples. Most of the present shark data are from dogfish which may explain the 1.4 trophic level difference. Sablefish acquired from the commercial fishery presently undergoing analysis may likewise change the value from that shown in table 1 as those were juveniles sampled during SEA. Adult sablefish occur at depth where they are fished for using baited long-lines and may have a $^{15}N/^{14}N$-based trophic level closer to that predicted by Ecopath.

While some functional groups consisted of specific history stages of a single species others were aggregates of many. A potential effect of aggregation is that a functional group will also consist of an aggregate of trophic levels including artifactual cannibalism (D. Pauly, pers. comm.). When aggregate functional groups (Table 1) were removed from the regression of Ecopath and $^{15}N/^{14}N$-based trophic levels, the correlation coefficient, r, increased from 0.80 to 0.91. Aggregation thus decreased functional group fit to an expected linear model (Fig. 1). Kurtosis is a measure of the fit $^{15}N/^{14}N$ data into the normal distribution. Herring were strongly leptokurtic suggesting a well defined trophic level (Kline 2000). While some functional groups had kurtosis values near zero, a few had negative values indicating a tendency for values to be distributed near the tails suggesting multiple trophic levels. Capelin was the only single-taxon functional group to be significantly leptokurtic. Skewness may indicate the direction of a secondary trophic level. That is, if the skewness is positive, the functional group consists of a few individuals feeding at a higher trophic level and vice-versa. For example, herring were negatively skewed because of the lower trophic level of individuals < 7 cm (Kline 2000 - Appendix II).

At the time of this writing, year two of the project is just commencing while budgeting for year three is being made. Therefore the scope of work for project years 2-3, i.e., with the end of the project in sight and these preliminary results in mind, will be to fulfill the model validation goal of providing data to justify preserving as well as some re-organizing of the present model's functional groups. These refinements will make the model more realistic and thus improve the accuracy of its predictive capabilities. Samples not previously considered for isotopic examination for this project are now being considered including larger herring and meroplankters. Samples for these categories exist but only a few have been analyzed (e.g., Fig. 1 in Kline 2000 - Appendix II). Table 1 lists also the possibility of samples that may be available but are not logged and others known to exist but not logged that will be or being processed at the time of this writing. A few functional groups are outside the purview of this project as they would require extensive field sampling that would have added a great cost to the project. Collaboration is presently in progress to obtain mammalian and avian data. Several pelagic "forage" species, northern lanternfish, northern smoothtongue, juvenile snailfish and glass shrimp, cannot be placed into the present Ecopath model. Therefore functional group #47 was added for them, note their close fit to trophic level = 3.0.

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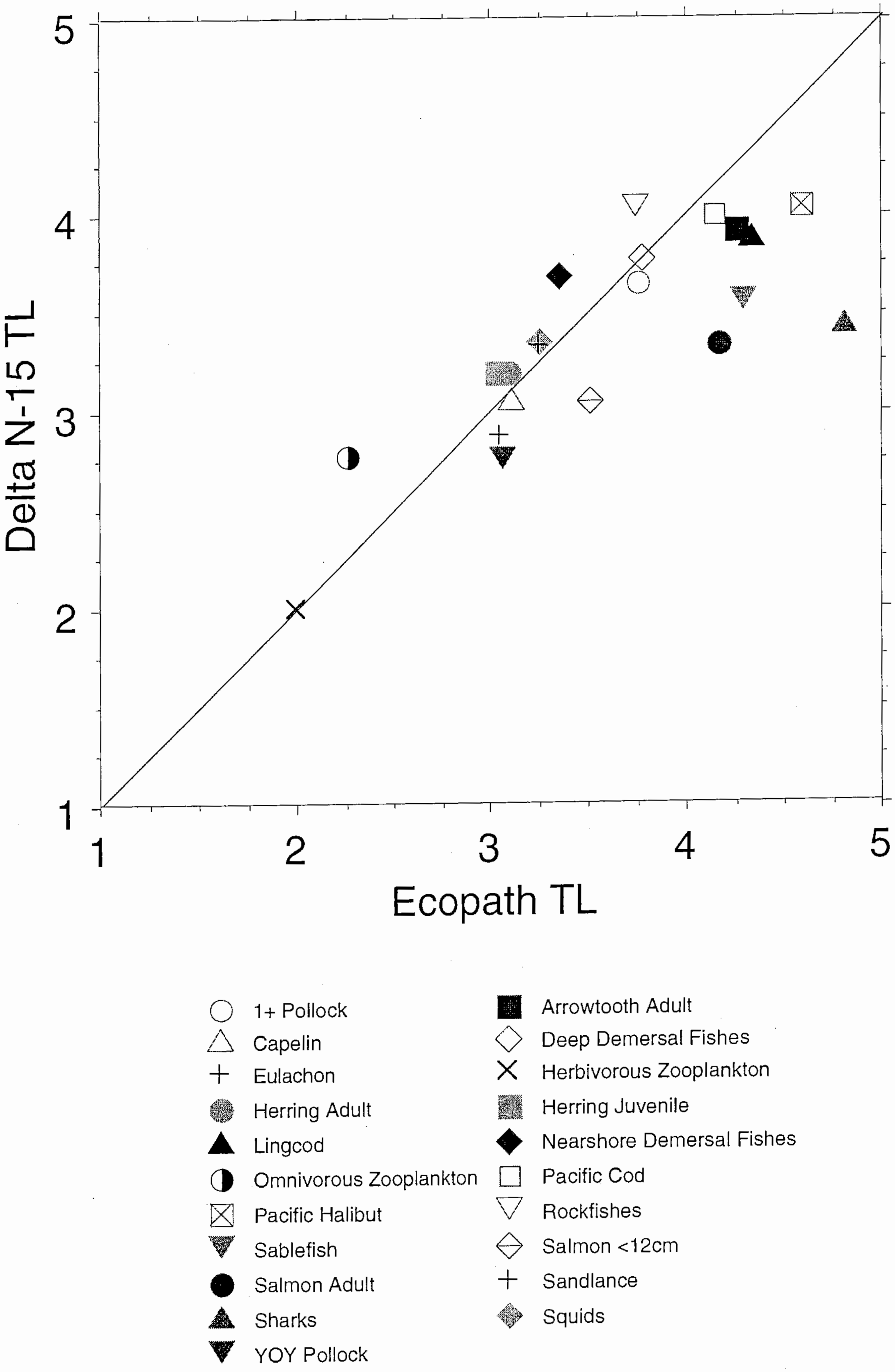
Functional Group #	Transient	Aggregation	Functional Group Name	Ecopath TL (1)	N-15 TL	TL SD	TL Skewness	TL Kurtosis	*N*	*Delta TL*	Comments
1	2		Orca	4.98							
2	1	1	Sharks	4.81	3.43	0.23	0.705	-0.204	25	1.38	Add'l Sleeper and Salmon sharks in process
3	2		Pacific Halibut	4.59	4.05	0.26	-0.003	0.926	39	0.54	Add'l samples from IPHC
4		1	Sm. Cetaceans	4.52							
5		1	Pinnipeds	4.45							Expecting value from Schell & Hirons
6			Lingcod	4.33	3.88	0.36	-0.459	-0.012	37	0.45	Protected species - ltd sampling
7	2		Sablefish	4.29	3.56	0.25	0.659	0.203	20	0.73	juveniles, adults from ADFG longline surveys in process
8			Arrowtooth Adult	4.25	3.92	0.23	-0.163	1.227	72	0.33	
9	1	1	Salmon Adult	4.17	3.34	0.37	-0.113	-0.462	26	0.83	large # samples from comm fishery available
10			Pacific Cod	4.14	4.01	0.47	-0.907	-0.074	46	0.14	
11			Arrowtooth Juvenile	4.01							Possible unlogged samples
12	2	1	Avian Predators	3.89							[2]
13	2	1	Seabirds	3.78							[2]
14		1	Deep Demersal Fishes	3.78	3.78	0.31	-0.335	0.592	140	0.00	flatfishes and skates
15			1+ Age Pollock	3.76	3.66	0.31	0.445	0.648	253	0.10	(prey switching)
16		1	Rockfishes	3.74	4.03	0.44	1.402	3.926	144	-0.29	
17	2	1	Baleen Whales	3.65							
18	3	1	Salmon <12 cm	3.51	3.06	0.31	0.088	-1.052	284	0.46	Higher TL to be eliminated becasue of natal signature
19		1	Nearshore Demersal Fishes	3.35	3.69	0.34	-1.138	2.043	124	-0.34	large # of species
20		1	Squid	3.26	3.36	0.24	0.618	0.573	144	-0.10	
21	1		Eulachon	3.25	3.34	0.32	-0.992	0.072	20	-0.09	Possible unlogged samples
22			Sea Otter	3.23							Necropsy samples?
23		1	Deep Epibenthos	3.16							Unlogged samples in process: pandalids, crabs, sea pens
24	1		Capelin	3.11	3.06	0.21	0.419	-0.800	76	0.05	
25	1		Herring Adult	3.10	3.20	0.18	-1.020	4.720	2084	-0.10	combined all stages - see Kline 2000
26			YOY Pollock	3.07	2.76	0.20	1.378	1.758	93	0.31	
27		1	Shallow Large Epibenthos	3.07							Unlogged samples in process (crabs > 5 cm, octopus)
28		1	Invertebrate Eating Birds	3.07							[2]
29			Sandlance	3.06	2.88	0.09	0.674	0.795	25	0.18	Possible unlogged samples
30			Herring Juvenile	3.03	3.20	0.18	-1.020	4.720	2084	-0.17	combined all stages - see Kline 2000
31		1	Jellies	2.96							Unlogged samples in process
32		1	Deep Small Infauna	2.25							requires sampling (add'l funding)
33		1	Nearshore Omnivorous Zooplankton	2.25							Possible unlogged samples (bay samples 95)
34	1	1	Omnivorous Zooplankton	2.25	2.77	0.44	1.880	9.663	297	-0.52	Kline 1999
35		1	Shallow Small Infauna	2.18							requires sampling (add'l funding)
36		1	Meiofauna	2.11							requires sampling (add'l funding)
37		1	Deep Large Infauna	2.10							requires sampling (add'l funding)
38		1	Shallow Small Epibenthos	2.05							Possible unlogged samples: sm. crabs
39		1	Shallow Large Infauna	2.00							ECOPATH ASSUMED VALUE
40		1	Nearshore Herbivorous Zooplanktor	2.00							ECOPATH ASSUMED VALUE
41	1	1	Herbivorous Zooplankton	2.00	2.00				669		ECOPATH & N-15 ASSUMED VALUE - Reference value
42		1	Nearshore Phytoplankton	1.00							ECOPATH ASSUMED VALUE
43		1	Offshore Phytoplankton	1.00							ECOPATH ASSUMED VALUE
44		1	Macroalgae & Eelgrass	1.00							ECOPATH ASSUMED VALUE
45		1	Inshore Detritus	1.00							ECOPATH ASSUMED VALUE
46		1	Offshore Detritus	1.00							ECOPATH ASSUMED VALUE
47	1	1	Pelagic "Forage Species"		3.02	0.43	-0.987	5.513	74		NOT IN ECOPATH MODEL

1=outside bounds of model, 2=range >100km from PWS, 3=hatchery input

(1) data from Pauly et al.

(2) Avian data from Bishop, Suryam in progress


5
4
3
2
1
Delta N-15 TL
1
2
3
4
5
Ecopath TL
1+ Pollock
Capelin
Eulachon
Herring Adult
Lingcod
Omnivorous Zooplankton
Pacific Halibut
Sablefish
Salmon Adult
Sharks
YOY Pollock
Arrowtooth Adult
Deep Demersal Fishes
Herbivorous Zooplankton
Herring Juvenile
Nearshore Demersal Fishes
Pacific Cod
Rockfishes
Salmon <12cm
Sandlance
Squids

Appendix I.
Output of Staview computer program.

Regression Summary
Delta N-15 TL vs. Ecopath TL
Inclusion criteria: Non-aggregates from FWEB2000.data (imported)

Count	12
Num. Missing	3
R	.914
R Squared	.836
Adjusted R Squared	.819
RMS Residual	.191

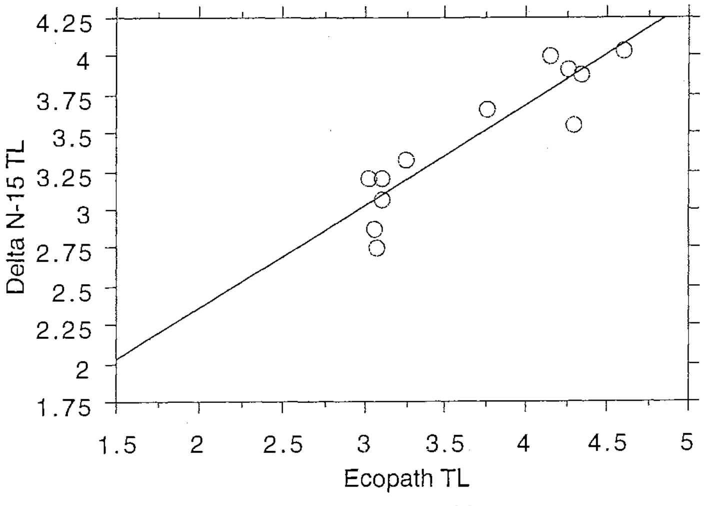
ANOVA Table
Delta N-15 TL vs. Ecopath TL
Inclusion criteria: Non-aggregates from FWEB2000.data (imported)

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	1	1.849	1.849	50.856	<.0001
Residual	10	.364	.036		
Total	11	2.212			

Regression Coefficients
Delta N-15 TL vs. Ecopath TL
Inclusion criteria: Non-aggregates from FWEB2000.data (imported)

	Coefficient	Std. Error	Std. Coeff.	t-Value	P-Value
Intercept	1.024	.346	1.024	2.961	.0143
Ecopath TL	.664	.093	.914	7.131	<.0001

Regression Plot
Inclusion criteria: Non-aggregates from FWEB2000.data (imported)



Y = 1.024 + .664 * X; R^2 = .836

Regression Summary
Delta N-15 TL vs. Ecopath TL
Inclusion criteria: Non Zero N from FWEB2000.data (imported)

Count	21
Num. Missing	0
R	.800
R Squared	.640
Adjusted R Squared	.621
RMS Residual	.318

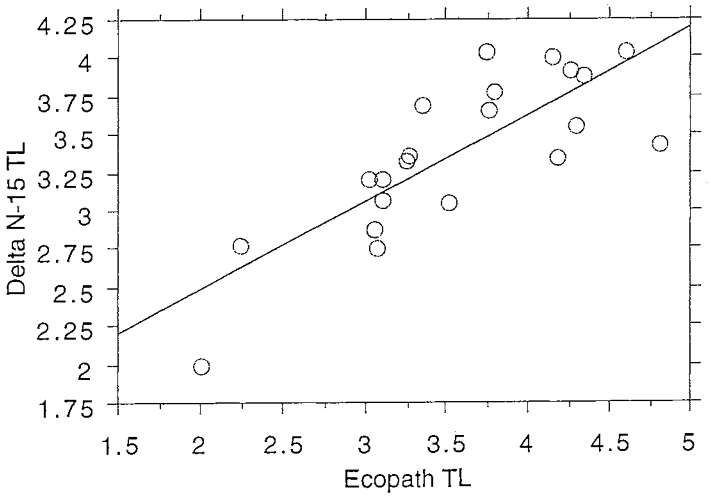
ANOVA Table
Delta N-15 TL vs. Ecopath TL
Inclusion criteria: Non Zero N from FWEB2000.data (imported)

	DF	Sum of Squares	Mean Square	F-Value	P-Value
Regression	1	3.423	3.423	33.800	<.0001
Residual	19	1.924	.101		
Total	20	5.348			

Regression Coefficients
Delta N-15 TL vs. Ecopath TL
Inclusion criteria: Non Zero N from FWEB2000.data (imported)

	Coefficient	Std. Error	Std. Coeff.	t-Value	P-Value
Intercept	1.356	.355	1.356	3.820	.0012
Ecopath TL	.568	.098	.800	5.814	<.0001

Regression Plot
Inclusion criteria: Non Zero N from FWEB2000.data (imported)



Y = 1.356 + .568 * X; R^2 = .64

Appendix II.
Manuscript titled: "The Trophic Position of Pacific Herring in Prince William Sound Alaska Based on their Stable Isotope Abundance."

This manuscript was submitted to "Herring 2000, 18th Wakefield Fisheries Symposium" and is presently undergoing peer review for that publication.

The Trophic Position of Pacific Herring in Prince William Sound Alaska Based on their Stable Isotope Abundance

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Manuscript for peer-review
Submitted to: Herring 2000, 18th Wakefield Fisheries Symposium

note on formatting: MS is presently formatted for review purposes only, ** etc. per formatting per request will be added later

The Trophic Position of Pacific Herring in Prince William Sound Alaska Based on their Stable Isotope Abundance

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Abstract

Pacific herring (*Clupea pallasi*), as a conveyor of energy between the plankton and piscivorous organisms, play an important ecological role in Prince William Sound and other coastal waters of the northeast Pacific Ocean. Because of a regional isotopic gradient and the fidelity of consumer isotopic composition with that of their diet, natural carbon and nitrogen stable isotope abundance was used as a tool for an ecological study of Prince William Sound herring. Nitrogen stable isotope abundance, which was used in this study to estimate trophic level, provided evidence for consistency in herring trophic level while there was some seasonal variability during the 1994 to 1998 study period. These results suggest a consistency in herring food chain length. Assuming that energy available for the highest trophic levels is determined primarily by the number of trophic steps, trophic level consistency suggests that energy per unit of biomass is propagated in proportion to its variability at the food web base. Previously, herring carbon isotopic composition suggested the latter to vary on annual time scales. Forage levels for herring consumers may thus fluctuate in accordance with herring food chain length and variability in planktonic productivity patterns if these factors are important to herring productivity. Measurable trophic level shifts would be significant given the narrow-ranging well-defined herring trophic level found in this study.

Introduction

The failure of several Prince William Sound (PWS), Alaska vertebrate species to recover from population crashes following the 1989 *T/V Exxon Valdez* oil spill, has raised concerns that shifts in food web structure may have occurred. Of particular concern is recruitment of *Clupea pallasi* (Pacific herring), presently at a historical low in abundance in PWS, a fjordlike inland sea that receives oceanic water from the Gulf of Alaska via the Alaska coastal current (Niebauer et al 1994). Furthermore, Pacific herring play a keystone role in the subarctic Pacific pelagic ecosystems by being an intermediary trophic position between plankton and consumers of herring such as other fishes, birds, and mammals including man. Recently, Kline (1999b) has shown using natural stable carbon isotope abundance ($^{13}C/^{12}C$) that herring in PWS may be dependent upon carbon generated in the Gulf of Alaska (GOA) and that the degree of this dependency fluctuates from year to year.

Stable isotope ratios effectively provide empirical evidence of trophic relationships in marine food webs because of their predictable relationship when comparing their abundance in consumers and diet. Nitrogen stable isotope ratios provide excellent definition of relative trophic level (Fry 1988). The heavy isotope of nitrogen, ^{15}N, is enriched by about 0.34 % (or 3.4 per mil in conventional delta units, see materials and methods) with each trophic level (Minagawa and Wada 1984) and has been shown to accurately indicate the relative trophic status of species within an ecosystem (Cabana and Rasmussen 1994). Trophic level as used here refers to the average number of feeding steps between predators and their prey. For example, if the diet of predator A was 100% prey B, there would be 1.0 trophic levels between them. However, if A also consumed C, and C was also part of the diet of B, the 1.0 trophic level difference between A and B would most likely $\neq 1.0$. The effective trophic level difference between A and B would then depend upon the relative contribution of B and C in the composition of A's diet as well as the relative trophic level differences between B and C.

Carbon Stable isotope ratios ($^{13}C/^{12}C$) can effectively be used to trace multiple sources of carbon into food webs once it can be established that an ecosystem has carbon sources with distinctive isotopic signatures (Fry and Sherr 1984). This latter point was been established since GOA and PWS carbon sources for PWS have distinctive carbon isotope signatures (Kline 1999b).

Accordingly, stable carbon isotopes measured in herring and other biota suggested that in some years the GOA may supply the majority of carbon for the PWS pelagic ecosystem (Kline 1999b).

An Ecopath model and $^{15}N/^{14}N$ natural abundance data predicted corroborating trophic levels for pelagic biota including herring from PWS (Kline and Pauly 1998) but did not provide details relating patterns of variability of relative trophic level between herring and secondary pelagic producers and between herring and potential teleost consumers. Kline's (1999a) $^{15}N/^{14}N$ inventory for herring from 1994 and 1995 suggested only slight inter-annual and inter-site variability while Kline and Pauly (1998) determined trophic levels of 3.3 and 3.33 (where herbivores are trophic level = 2) based on Ecopath and isotopic analyses of $N = 459$ herring, respectively. Since these publications, a more extensive isotopic database has been generated for herring ($N > 2000$) and other pelagic biota of PWS for the period 1994-1998 from which patterns of GOA carbon were found from $^{13}C/^{12}C$ data (Kline 2000). The purpose of this study was to use the extensive $^{15}N/^{14}N$ data to assess the trophic position of PWS herring during this period seeking potential ontogenetic, spatial, and temporal patterns.

Assessing the trophic position of PWS herring was accomplished through three tasks: (1) by assessing effects of $^{15}N/^{14}N$ variability of PWS herbivorous copepods used as the trophic baseline (Kline 1999b), (2) by assessing herring ontogenetic $^{15}N/^{14}N$ shifts and hence trophic level shifts based on fish size, and (3) by assessing PWS herring temporal and spatial $^{15}N/^{14}N$ variability from a four-bay time-series.

Materials and Methods

Data generation

The sampling and laboratory methods used to generate the isotopic database used for this study have already been described in detail (Kline 1999b) and so are only given briefly here. Copepods were picked in the field from plankton samples that were made with either ring nets or a MOCNESS system and in the case of large the species *Neocalanus cristatus,* analyzed as individuals. Other *Neocalanus* spp. were analyzed by pooling two individuals together. Fishes were collected with seines, traps and trawls. Herring data for those up to length ~ 15 were largely a part of a collaborative effort with A.J. Paul who measured whole-body energetic content of the same individual fish (Kline 1999b). Herring and other fishes were analyzed in replicate and data averaged to provide one isotopic datum per fish for each element (N and C). Only stable isotopes of N are considered here. N stable isotope ratios, $^{15}N/^{14}N$ are expressed in delta (δ) units as the per mil deviation from the $^{15}N/^{14}N$ content of air N_2.

Data selection

The mean $\delta^{15}N$ values of terminal feeding stages of *Neocalanus cristatus* and *Neocalanus* spp. were pooled from PWS and GOA spring (1995) or May (1996-7) oceanographic sampling stations (Kline 1999b). *Neocalanus* spp. included *N. cristatus*, *N. plumchrus* and *N. flemingeri* (1996-7) from the GOA or PWS. A portion of these data were extracted from published data (Kline 1999a, 1999b) while others are reported here for the first time. Obtained similarly were the pooled $\delta^{15}N$ values of diapause stage *Neocalanus cristatus* and *Neocalanus* spp. from the appropriate deep habitat in PWS (Kline 1999b).

All herring sampled from April 1994 to March 1998 for which length data (standard length) were available were pooled and analyzed for trend using a scatterplot and regressed for best fit using R^2 and P values. Commencing in the fall of 1995, juvenile herring ~ < 15 cm in length were sampled at four sites within PWS at approximately 1.5 month intervals between March 1996 and October 1997 (Kline 2000). This four-bay time-series enabled assessing finer scale temporal variability in several parameters (whole-body and diet energetics, growth, diet composition) for age 0 and 1 PWS herring than had been previously examined (Norcross et al. 1996). The ~ N = 25 from each site-sampling that were isotopically analyzed are reported here with SD estimation. Age 0 and 1 herring were pooled for this analysis since it was not possible to split the data by age and also retain both the temporal and spatial coverage. Thus ontogenetic effects were examined using a separate data selection that also benefited by including data from additional PWS sites (Kline 1999b).

Comparing the trophic level of herring to other organisms from PWS was facilitated by pooling $\delta^{15}N$ data of herbivorous copepods and large teleosts to reflect herbivore (potential herring forage) and piscivores (potential herring predators), ie., expected to have, respectively, lower and higher trophic levels. Diapausing *Neocalanus cristatus* were selected as a proxy for the PWS herbivore trophic level based upon their previous use and the observation that the fraction originating from the GOA matched the fraction of GOA carbon in PWS herring (Kline and Pauly 1998, Kline 1999b). Potential piscivores consisted of larger-sized (~ > 20 cm) taxa. Juvenile stages (< 20 cm) and taxa known to have similar trophic level as herring (Kline 1998) were therefore excluded. The *N* for copepods and teleosts selected were ~ 700, sufficient for generation of histograms for comparison with herring *N* ~ 2000.

Trophic level was determined by comparing $\delta^{15}N$ values to a reference value (Vander Zanden et al. 1997). The $\delta^{15}N$ of higher trophic levels were calculated by adding the trophic enrichment factor, 3.4 (Minagawa and Wada, Kline 1997) to the reference value. The herbivorous copepod *Neocalanus cristatus*, i.e., trophic level = 2, was used as the reference (Kline and Pauly 1998, Kline 1999b).

The following formula was used to calculate trophic level:

$$TL_i = (\delta^{15}N_i - \delta^{15}N_H / 3.4) + 2$$

where TL_i is the trophic level of organism i, $\delta^{15}N_i$ is the mean $\delta^{15}N$ value of organism i, and $\delta^{15}N_H$ is the mean herbivore $\delta^{15}N$ value.

Statistical analysis of the data was facilitated by using the Statview 4.5 (Abacus Concepts, Inc. Berkeley, CA) computer program while the Deltagraph 3.1 (Delta Point, Inc. Monterey, CA) computer program was used to generate the figures.

Results

There were only slight variations in the mean $\delta^{15}N$ values for the species *Neocalanus cristatus* and for the three *Neocalanus* spp. (Table 1). The lowest $\delta^{15}N$ value of 7.3 was found for 1995 feeding stage GOA *N. cristatus* while the highest $\delta^{15}N$ value of 8.9 was found for both feeding stage PWS *N. cristatus* and PWS *Neocalanus* spp. mean values. Diapausing copepods had a smaller range in values reflecting the integration of GOA and PWS copepod sources also suggested through their $\delta^{13}C$ values (Kline 1999b). Note however, that the mean diapausing value for *N. cristatus* in 1995 and 1996, 7.8 and 8.6, respectively more closely matched those from the GOA, 7.3 and 8.5, respectively, rather than those from PWS, 8.6 and 8.3, respectively, corroborating the significant contribution of GOA-generated production for PWS deduced from $\delta^{13}C$ (Kline 1999b). The mean $\delta^{15}N$ for all 1996 diapausing species, 8.5, was ^{15}N-depleted compared to both PWS and GOA but more closely matched PWS at 8.6 than the GOA at 8.8. The collective mean for *N. cristatus* sampled diapausing from the entire study was 8.4 ± 2.0 (*SD*) is discussed in greater detail below in relation to herring and potential piscivorous teleosts.

There was only a slight shift in $\delta^{15}N$ and hence trophic level as a function of size for PWS herring (Fig. 1). Only herring < ~ 10 cm were TL < 3.0 while very few herring at any size were TL > 3.5. The slight $\delta^{15}N$ shift with size was reflected in the regressions which only explained 16% of the variability. There appears to be a trophic level break for herring < ~ 7 cm as these were mostly TL < 3.0 whereas the majority of the larger herring were between TL = 3 and TL = 3.5.

Spatial and temporal variability of PWS herring $\delta^{15}N$ and hence trophic level was only slight (Fig. 2). Herring feed on low trophic levels during summer months when 0-age fish are still small, but at least some of the variability among sites could be explained by unequal representation of year classes (Norcross et al. 1996)

There was slightly more than one trophic level difference between herring and herbivores while there was slightly less than one trophic level difference between herring and their potential predators (Fig. 3). Diapausing *Neocalanus cristatus* copepods (N = 669) which were used as the trophic level = 2.0 (herbivore) baseline had a mean $\delta^{15}N$ = 8.39 with a standard deviation of 2.01. They were slightly skewed to higher values (skewness = 0.79) and were leptokurtic (kurtosis = 3.46). Large teleosts (> ~ 20 cm; N = 727) had a mean $\delta^{15}N$ = 14.66 (interpreted trophic level = 3.85) with a standard deviation of 1.22 (0.36 trophic levels) were similarly leptokurtic (kurtosis = 3.37) and positively skewed (skewness = 0.73). Herring (N = 2084), which had a mean $\delta^{15}N$ = 12.47 (interpreted trophic level = 3.20) with a standard deviation = 0.60 (0.18 trophic levels), were more strongly leptokurtic (kurtosis = 4.72) and skewed to lower $\delta^{15}N$ (skewness = -1.02). The negative skewness was due to the lower trophic level of smaller herring while the high kurtosis and narrow standard deviation suggests a well-defined $\delta^{15}N$-based trophic level for herring. The difference of 1.20 trophic levels between herring and herbivores is consistent with herring also consuming carnivorous zooplankters. The difference of 0.65 trophic levels between herring and large teleosts is consistent with prey-switching by larger fishes. For example, PWS walleye pollock (*Theragra chalcograma*), a major constituent taxon, consume zooplankters (including *Neocalanus* spp.) as well herring and other prey. However, note the positive skewness and sample distribution indicating that teleosts can feed as high as trophic level five.

Discussion

Herring production levels is of particular concern for recruitment of herring, presently at a historical low in abundance in PWS. In particular, forage levels for herring consumers may fluctuate in accordance with herring food chain length and variability in planktonic productivity patterns if these factors are important to herring productivity. While carbon stable isotope ratios provided strong evidence for large inter-annual-scale shifts in source of production supporting PWS, measurable trophic level shifts would be significant given the narrow-ranging well-defined herring trophic level found in this study. The narrow $\delta^{15}N$ range of herring compared to herbivores conferred a well-defined trophc position during the period of this study.

Potential errors in estimating herring trophic level from $\delta^{15}N$ were likely to be less than ~1/3 trophic levels based on the relatively small temporal and spatially-dependent departures of mean herbivore $\delta^{15}N$ from a value of 8.4. The sources of $\delta^{15}N$ variation arise in the phytoplankton, varying among phytoplankton species because of size and species-dependent differences in isotopic fractionation and isotopic effects arising from their selective draw-down of ^{14}N in the dissolved inorganic nitrogen pool (see review by Owens 1987). Kline 1999b estimated that 40% of $\delta^{15}N$ variability of PWS zooplankton could be ascribed to nitrogen cycling isotope shifts while spatial gradients account for 1 per mil differences, equivalent to the trophic fractionation of ~ 1/3 trophic levels. However, the spatial gradient was weaker in later years of the study so $\delta^{15}N$-based errors should be less than 1/3 trophic level overall. There were a few copepods with anomalous $\delta^{15}N$ values for a herbivore. One interpretation for copepods with very high $\delta^{15}N$ and hence high a trophic level is feeding on micro-heterotrophs that feed on fish detritus, either spawned-out salmon carcasses or anthropogenic fish wastes such as from the numerous PWS processing plants. Since these were small in number they had only negligible effect for this study since the central value of a large sample size was used for the calibration point ($\delta^{15}N$ = 8.4). Furthermore, carnivorous copepods and omnivorous euphausiids and amphipods had appropriate $\delta^{15}N$ values, consistently higher than 8.4 (Kline 1999b).

The relatively slight shifts of herbivore $\delta^{15}N$ cannot explain the pattern of herring seasonal shifts $\delta^{15}N$ up to near 3 per mil. Therefore, a seasonal shift to lower trophic level feeding interpretation is more valid. The preponderance of smaller newly-recruited herring in summer and their suggested ontogenetic trophic level shift at ~ 7 cm length found in summer can only explain a part of this shift since all age classes apparently shifted to lower trophic levels during summer of 1997.

An Ecopath model for the same time period as these data conferred trophic levels of 3.10 and 3.03 for adult (fish > 18 cm) and juvenile herring, respectively (Oakey and Pauly 1998 - Table 74), slightly lower than the over all trophic level estimate of 3.2 for all stages estimated here. These differences could be explained in part to seasonal shifts since Alaska field data (used for Ecopath input) tend to have a 'summer-bias' which is when trophic levels are lower. The less than 0.1 trophic level difference between adult and juvenile herring found by Ecopath is closely reflected by the $\delta^{15}N$-based trophic levels. However, the range in herring trophic level independent of fish length as well as variability in space-time was greater than the small differences found for the two herring Ecopath functional groups. Given that the number of functional groups that can be incorporated into an Ecopath model is limited to 50 (Oakey and Pauly 1998), it would be prudent to pool herring into one. Given a standard deviation of 0.18 trophic levels for the $\delta^{15}N$-based trophic level of PWS, the Oakey and Pauly (1998), Ecopath-based trophic level was in good agreement, closely reflecting the previous Ecopath-isotope comparison of Kline and Pauly (1998). This assessment thus increases our confidence that we have made a good estimation of the trophic status of PWS herring.

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Figure captions

Figure 1. Scatterplot of $\delta^{15}N$ versus standard length for Prince William Sound, Alaska herring sampled between April 1994 and March 1998 with interpreted trophic levels. The fourth order polynomial shown provided a better fit to the data than a linear regression, explaining 16 per cent of the variability compared to 10, respectively (coefficient and regression $P < 0.0001$).

Figure 2. Temporal and spatial variability in $\delta^{15}N$ and interpreted trophic level for Prince William Sound herring. Error bars depict standard deviations. Lower trophic levels occurred during summer when new recruits were small. Trophic level variability was otherwise slight.

Figure 3. Comparison of $\delta^{15}N$ and interpreted trophic level variability through histograms of a large database.

Table 1. Mean δ^{15}N and *SD* of terminal feeding and diapause stages of the large (length ~ 9 mm) herbivorous copepod *Neocalanus cristatus* (except as noted) from PWS and the GOA collected from indicated sources.

sample	δ^{15}N	*SD*
feeding		
PWS		
1995[a]	8.6	1.1
1996[b]	8.3	0.8
1997[c]	8.9	1.2
1996[c, d]	8.6	0.7
1997[c, d]	8.9	0.9
GOA		
1995[a]	7.3	0.7
1996[b]	8.5	1.1
1997[c]	7.8	1.3
1996[b, c, d]	8.8	1.0
1997[c, d]	7.6	1.0
diapause (PWS)		
1994[a]	8.7	1.6
1995[a]	7.8	2.8
1996[b]	8.6	1.5
1996[b, c, d]	8.5	1.1
1994-6[c]	8.4	2.0

a Kline 1999b
b Kline 1999a
c this study
d all *Neocalanus* spp., otherwise only *N. cristatus*

14.15

14'11

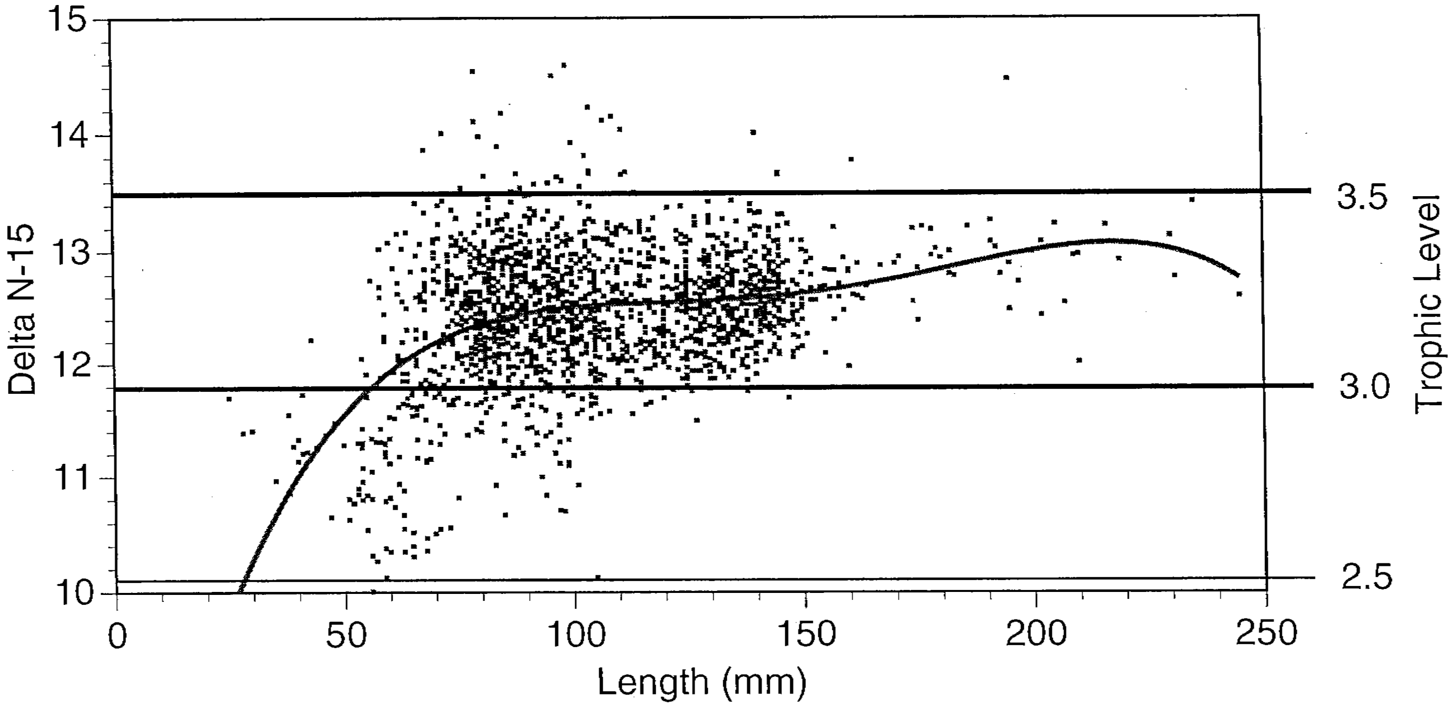


Figure 1

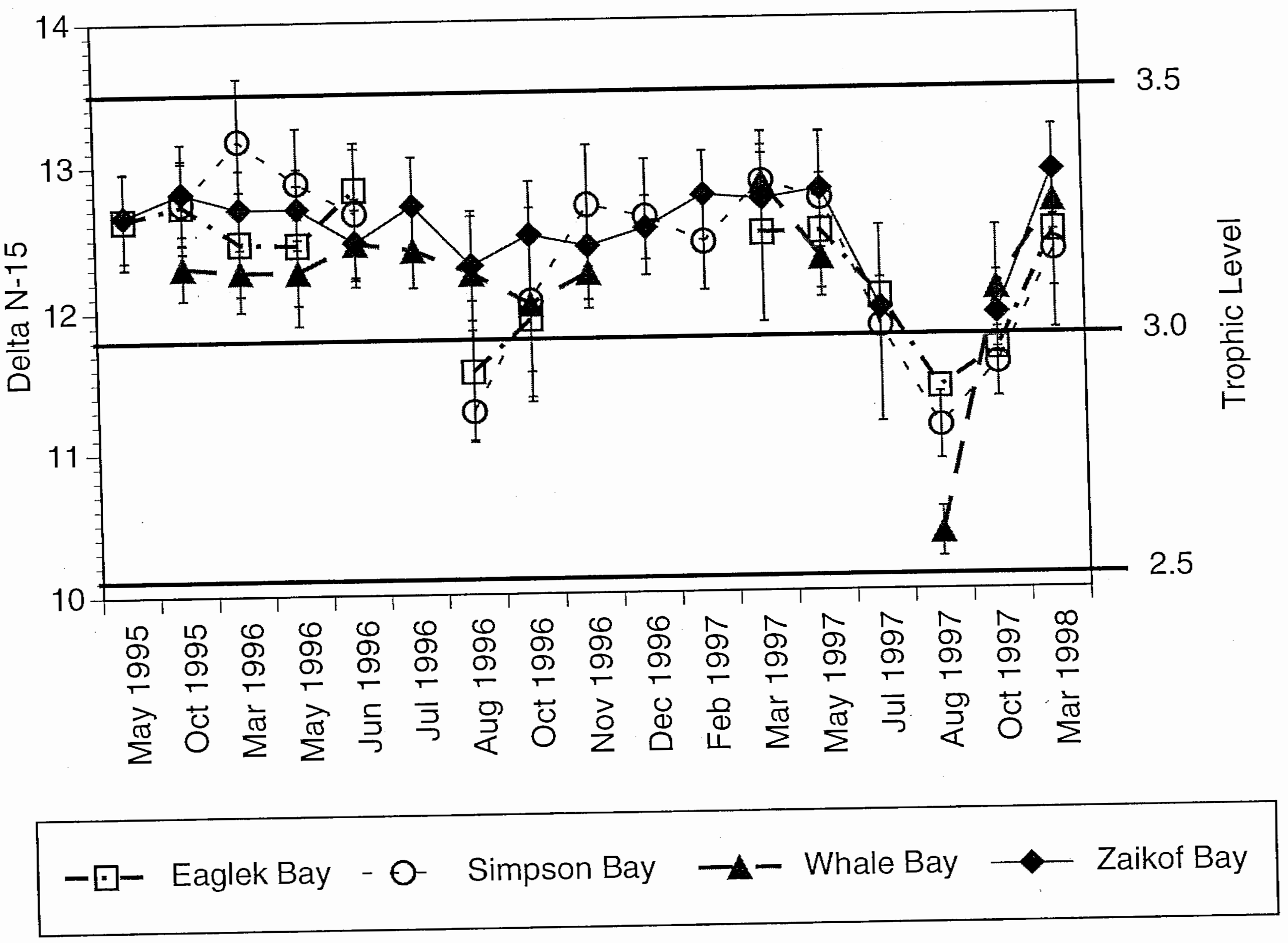
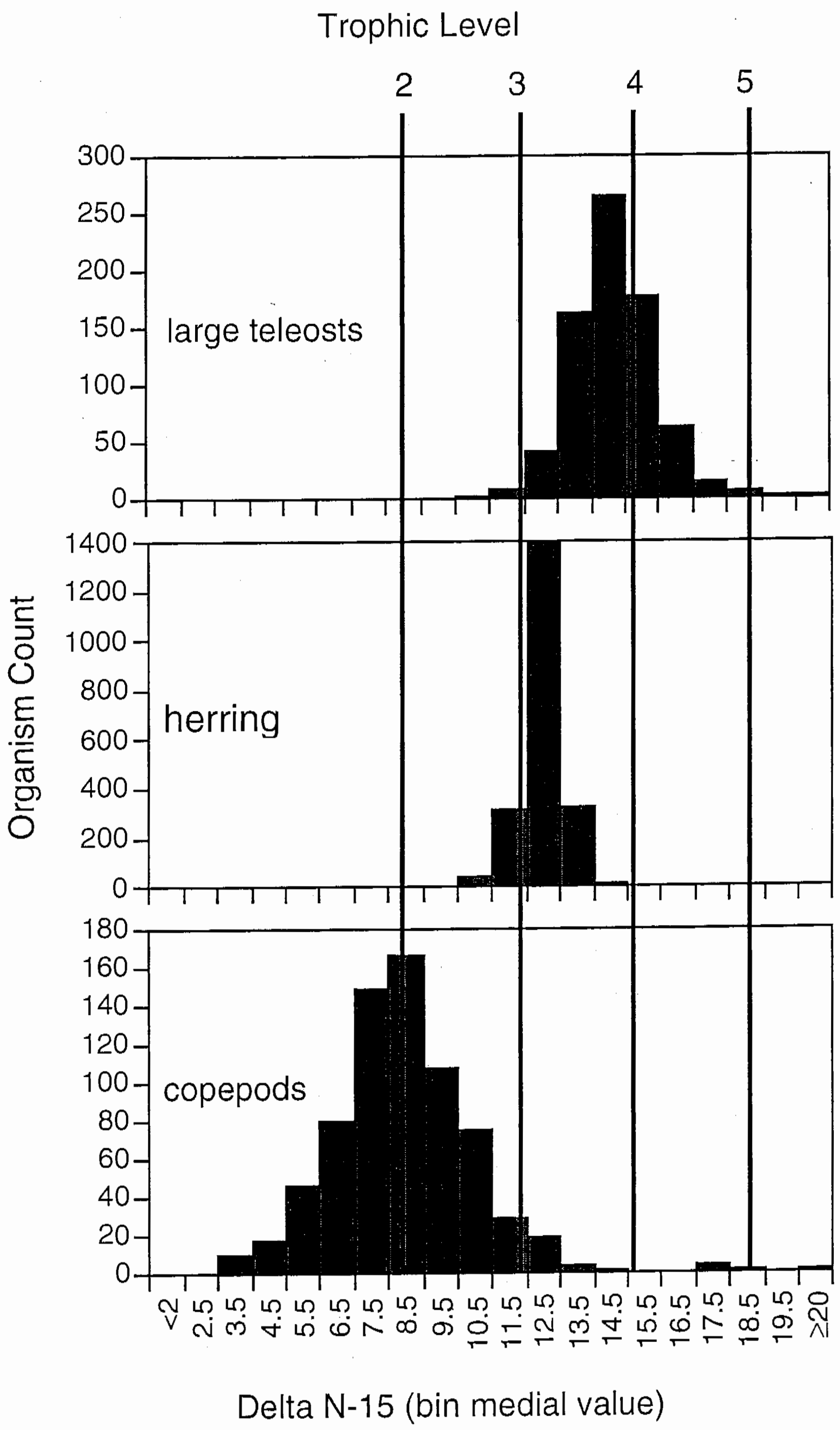

14
13
12
11
10
Delta N-15
3.5
3.0
2.5
Trophic Level
May 1995
Oct 1995
Mar 1996
May 1996
Jun 1996
Jul 1996
Aug 1996
Oct 1996
Nov 1996
Dec 1996
Feb 1997
Mar 1997
May 1997
Jul 1997
Aug 1997
Oct 1997
Mar 1998
Eaglek Bay
Simpson Bay
Whale Bay
Zaikof Bay

Figure 2



Trophic Level
2
3
4
5
Organism Count
300
250
200
150
100
50
0
large teleosts
1400
1200
1000
800
600
400
200
0
herring
180
160
140
120
100
80
60
40
20
0
copepods
<2
2.5
3.5
4.5
5.5
6.5
7.5
8.5
9.5
10.5
11.5
12.5
13.5
14.5
15.5
16.5
17.5
18.5
19.5
≥20
Delta N-15 (bin medial value)

Figure 3