

AN ABSTRACT OF THE THESIS OF

Henry Alfred Vanderploeg for the Doctor of Philosophy
(Name) (Degree)

in OCEANOGRAPHY presented on 15 November 1972
(Major) (Date)

Title: THE DYNAMICS OF ^{65}Zn IN BENTHIC FISHES AND THEIR PREY
OFF OREGON

Abstract approved: Redacted for Privacy
William G. Pearcy

The intra- and interspecific differences of ^{65}Zn specific activity in benthic fishes on the continental shelf off Oregon during 1970-1971 are examined. The dynamics of ^{65}Zn specific activity in the fishes are shown to be governed by the basic equation:

$$\frac{dS}{dt} = \alpha(F(t) - S) - S\lambda,$$

where S = ^{65}Zn specific activity of the fish (or predator),
 α = rate of input of Zn per body burden of Zn in the fish,
 $F(t)$ = ^{65}Zn specific activity of the prey, and
 λ = physical decay constant of ^{65}Zn .

This equation applies generally to any radionuclide accumulated through the food chain. Differences in S among fishes are thus related to differences in α and $F(t)$. Using existing energy relations in fishes, it was hypothesized that α varies with the weight of the fish, W , and with growth: $\alpha = K(AW^{-0.2} + \frac{1}{W} \frac{\Delta W}{\Delta t})$, where K is a constant for all species, and A varies with temperature.

For a single location on the continental shelf off central Oregon, extensive time series of S and $F(t)$ were obtained for different size classes of two species of benthic fishes. A numerical solution of the basic equation coupled to a least-squares gradient algorithm enabled calculation of α 's from the time series of S and $F(t)$. Usable time series were obtained for a small flounder, Lyopsetta exilis. For L. exilis size classes with "average" weights of 22 and 35 g, the α 's obtained were $2.7 \times 10^{-3}/\text{day}$ and $2.6 \times 10^{-3}/\text{day}$, respectively. The α 's of L. exilis were compared to the α derived from trout data that another worker obtained in the laboratory. The difference in α 's between L. exilis and the laboratory fish are roughly the same as predicted by the hypothetical α -W relationship, thus giving it tentative support.

Although differences in S are expected according to the α -W relationship, these differences are small compared to those caused by the different ^{65}Zn specific activities in different prey. Specific activities of low trophic level pelagic prey were higher than those of high trophic level pelagic prey or of infauna. These trends in the prey were reflected in their predators, the fishes.

The mechanisms behind geographical patterns in ^{65}Zn specific activity in benthic fishes and their prey are discussed; in particular, these patterns are related to the ^{65}Zn specific activities of sediment and water. Near the mouth of the Columbia River which carries ^{65}Zn from the Hanford reactors to the ocean, infauna was seen to be as important

as low trophic level pelagic prey in conveying ^{65}Zn to the fishes. As distance increased from the river mouth, the importance of the infauna diminished relative to low trophic level pelagic prey. Evidence is presented that suggests that ^{65}Zn was in a form more available to the food chain than stable Zn in seawater.

The dynamics of ^{65}Zn SA in the fishes are useful for understanding some aspects of the fishes' ecology. A theoretical framework is set up for determination of energy flow in free-living populations of fishes and other animals from their specific activity dynamics. Geographical patterns in ^{65}Zn specific activity in the benthic fishes and their prey are shown useful for deducing the migratory habits of the fishes. Migration or its absence is suggested for some fishes for which no literature is available.

© 1973

HENRY ALFRED VANDEPLOGE

ALL RIGHTS RESERVED

The Dynamics of ^{65}Zn in Benthic Fishes
and Their Prey off Oregon

by

Henry Alfred Vanderploeg

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

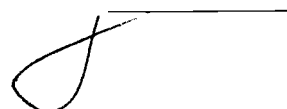
Doctor of Philosophy

June 1973

APPROVED:

Redacted for Privacy

Professor of Oceanography
in charge of major



Redacted for Privacy

Dean of School of Oceanography



Redacted for Privacy

Dean of Graduate School

Date thesis is presented Nov 15, 1972

Typed by Carla Rathbun for Henry Alfred Vanderploeg

ACKNOWLEDGMENTS

I am indebted to Dr. William G. Percy for giving me material support, scientific guidance, and personal encouragement during this study. To Drs. Norman Cutshall, W. Scott Overton, and Laurence F. Small--members of my committee--I extend my thanks for their helpful advice on various aspects of my work.

I wish to thank also Dr. John L. Saugen of the Electrical Engineering Department for his reading and conference courses, which provided me with invaluable insight into the numerical methods necessary for the data analysis used in this dissertation. I have profited too from discussions with Dr. William C. Renfro, who criticized my early attempts at modelling.

I am grateful to Mr. I. Lauren Larsen for the gamma-ray spectrometry analysis and to Mr. Jerome Wagner for the atomic absorption spectrophotometry.

Mr. Robert L. Demory of the Oregon Fish Commission kindly provided me with valuable information on many benthic fishes.

I especially want to thank fellow student Michael Schonzeit for his help with field work under difficult conditions at sea. Mrs. Carla Rathbun patiently and carefully typed this dissertation and its preliminary drafts. Finally, I sincerely appreciate the editorial assistance of my wife, Barbara.

Financial support was provided by the U.S. Atomic Energy Commission (Contract No. AT(45-1)-2227, Task Agreement 12).

TABLE OF CONTENTS

I	GENERAL INTRODUCTION	1
II	THEORY	3
	Basic Model	3
	An Interpretation of α	6
	The Problem of Multiple Compartments	15
III	METHODS	17
IV	DYNAMICS OF ^{65}Zn SPECIFIC ACTIVITY IN BENTHIC FISHES AND THEIR PREY AT NH-23	19
	Introduction	19
	Results	21
	Seasonal Patterns of ^{65}Zn Specific Activity in Major Prey of Benthic Fishes at NH-23	21
	Diets, $F(t)$, and Specific Activities of Benthic Fishes at NH-23	25
	Zinc Uptake Rates of <u>M. pacificus</u> and <u>L. exilis</u>	43
	Discussion	57
	Diet and SA of Fishes	57
	Comparison of α 's	61
	$F(t)$ vs. Proximate Factors	67
	Energy Flow and Radionuclide Dynamics	68
V	GEOGRAPHICAL PATTERNS OF ^{65}Zn SPECIFIC ACTIVITY IN BENTHIC FISHES AND THEIR PREY	70
	Introduction	70
	Results and Discussion	70
	Geographical Patterns of ^{65}Zn Specific Activity in the Prey	70
	Infauna and Sediment	78
	Vertical Transport of ^{65}Zn	82
	Processes Affecting Distribution of ^{65}Zn Specific Activity	85
	Geographical Patterns of ^{65}Zn Specific Activity in Benthic Fishes	87

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
1	Ege and Krogh's goldfish data fit by least squares to the function $Y = ae^{bx} + cx^2$.	8
2	Stable Zn concentration vs. weight in <u>Lyopsetta exilis</u> .	10
3	Stable Zn concentration vs. weight in <u>Microstomus pacificus</u>	11
4	Reactor history and specific activity of euphausiids and infauna at NH-23 before and during the study period.	22
5	Specific activities of the major prey at NH-23.	24
6	The specific activity of <u>Microstomus pacificus</u> and its prey at NH-23.	26
7	The relationship between specific activity and weight of <u>Microstomus pacificus</u> at NH-23 for different collections in 1970.	27
8	Specific activities of the length classes of <u>Lyopsetta exilis</u> and their prey.	36
9	Average weight of <u>Lyopsetta exilis</u> vs. average standard length.	38
10	Regression lines of ^{65}Zn specific activity vs. wet weight of <u>Lyopsetta exilis</u> for 14 collection dates in 1970 and 1971 at NH-23.	41
11	Growth curves for female <u>Microstomus pacificus</u> and female <u>Lyopsetta exilis</u> .	45
12	The best least squares fit to the specific activity data of <u>Microstomus pacificus</u> .	49
13	Residual plots for the <u>Microstomus pacificus</u> analysis.	51

LIST OF FIGURES (CONTINUED)

<u>Figure</u>		<u>Page</u>
14	Best least-squares fit to the specific activities of the 120-140 mm length class of <u>Lyopsetta exilis</u> .	53
15	Best least-squares fit to the specific activities of the 140-160 mm length class of <u>Lyopsetta exilis</u> .	54
16	Sampling locations.	71
17	Salinity profiles.	72
18	Zinc-65 specific activities of infauna superimposed upon isopleths of ⁶⁵ Zn specific activities.	79

LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	The % _i , the SA _i , and the Specific Activity of the Diet of <u>L. exilis</u> by Length Class and Season.	28 31
2	Zinc-65 Specific Activity in Male and Female <u>Lyopsetta exilis</u> .	39
3	Other Benthic Fishes at NH-23: Body Weight, ⁶⁵ Zn Specific Activity, and Feeding Habits.	42
4	Zinc-65 Specific Activity of Food in Different Sections of the Gut of <u>Microstomus pacificus</u> .	48
5	Spatial Patterns of ⁶⁵ Zn Specific Activity in Benthic Fishes and Their Prey on the Continental Shelf, July 1970.	74 75
6	Seasonal ⁶⁵ Zn Concentrations in Mixed Plankton over Washington and Oregon's Continental Shelf, 1961-1963.	77
7	Zinc-65 Specific Activity of Surface Seawater at the VMN Station, 7 July 1970.	88
8	Feeding Habits of Benthic Fishes.	90
9	Feeding Groups of Benthic Fishes.	91

THE DYNAMICS OF ^{65}Zn IN BENTHIC FISHES AND THEIR PREY OFF OREGON

GENERAL INTRODUCTION

Until recently the Columbia River was the most important source of artificial radionuclides in the ocean off Oregon (Osterberg et al., 1966; Perkins, Nelson, and Haushild, 1966; Cutshall et al., 1971). Radionuclides were mainly induced by neutron activation of elements in river water in "single pass" plutonium production reactors at Hanford, Washington. Most of the induced radionuclides having short physical half-lives decayed to insignificant levels during their 370-mile trip down the Columbia River to the Pacific Ocean. Owing to its longer, 245-day half-life and its concentration by the biota, ^{65}Zn was the most common of these artificially induced radionuclides in marine organisms; it has been measured in the plankton, nekton, and benthos off Oregon (Osterberg, Carey, and Curl, 1963; Osterberg, Pattullo, and Percy, 1964; Seymour and Lewis, 1964; Carey, Percy, and Osterberg, 1966; Percy and Osterberg, 1967; Carey, 1969; Carey and Cutshall, 1972; Percy and Vanderploeg, 1972).

This dissertation is a dynamical analysis of those factors that affect inter- and intraspecific differences in ^{65}Zn specific activity in benthic fishes on Oregon's continental shelf.¹ Essential to this study is an evaluation of the processes responsible for transferring ^{65}Zn from the sea surface into the marine food webs and of the pro-

¹ Zinc-65 specific activity, having units of nCi/g, is the amount of ^{65}Zn (nCi) per unit weight (g) of total Zn.

cesses involved in transferring the ^{65}Zn through the food webs to the benthic fishes. Both ecological and oceanographic processes must be studied. Since ^{65}Zn has a moderate half-life, the rates of transfer between various parts of the system are important. In particular, specific activities (SA's) of the fishes and their prey will be used to estimate the fishes' zinc uptake rates, necessary for an understanding of the dynamics of their ^{65}Zn SA.

Benthic fishes off Oregon support a major fishery. Knowledge of the SA dynamics of these fishes allows prediction of the radiological consequences of large-scale ^{65}Zn introduction at the sea surface, since the SA of the fish would be used to estimate the radiological hazard accruing from man's consumption of them (N.A.S.-N.R.C., 1962; Foster, Ophel, and Preston, 1971). In addition, this study illuminates aspects not only of the biogeochemical cycling of Zn but also of other elements that are highly concentrated by the biota. Many of these elements, like Zn, are potentially toxic.

Insight into the ecology of benthic fishes and their prey may be another result of studying their ^{65}Zn SA dynamics. Most importantly, this dissertation sets up the theoretical framework that allows determination of energy flow in free-living populations of fishes and other animals from their SA dynamics.

THEORY

Basic Model

The organizing concept of my entire study is the model derived in this chapter, a differential equation relating the SA of a fish to the SA of its prey. Foster's (1959) SA equation motivated the development of mine. Writing a differential equation to describe the change of SA in an organism, he emphasized its applicability for determining the biological turnover coefficient:

$$\frac{dS}{dt} = \beta C - (\lambda + \beta)S, \quad (1)$$

where S = specific activity of the organism,
 C = specific activity of the organism's source of radioactivity,
 λ = physical decay constant, and
 β = biological turnover or excretion coefficient.

The equation for change in the amount of ^{65}Zn in a fish acting as a single compartment and obtaining all ^{65}Zn from its food can be expressed:

$$\frac{dX}{dt} = rF(t) - r'\frac{X}{Z} - X\lambda, \quad (2)$$

where X = amount of ^{65}Zn in the body of the fish (nCi),
 r = rate of input of total zinc actually assimilated into the fish ($\mu\text{g/day}$),
 $F(t)$ = specific activity of prey (nCi/g), a function of time,
 r' = rate of excretion of total zinc from fish ($\mu\text{g/day}$),
 Z = total zinc in fish, and
 λ = physical decay constant (0.0028292/day).

Justification for food-chain uptake comes from the experiments of Hoss (1964) and of Baptist and Lewis (1969). The material that goes in must be conserved, so

$$r = r' + \frac{dZ}{dt} . \quad (3)$$

(Note that ^{65}Zn decays to stable Cu, but the amount of total zinc lost in this way is negligible.) Substituting for r' from equation (3) into equation (2),

$$\frac{dX}{dt} = rF(t) - \frac{X}{Z}(r - \frac{dZ}{dt}) - X\lambda . \quad (4)$$

Defining the uptake coefficient α by

$$r = \alpha Z \quad (5)$$

and from placing this relation for r in equation (4),

$$\frac{dX}{dt} = \alpha Z F(t) - \frac{X}{Z} \alpha Z + \frac{X}{Z} \frac{dZ}{dt} - X\lambda . \quad (6)$$

We want a specific-activity relationship, i.e., an expression for

$\frac{d(\frac{X}{Z})}{dt}$. By the quotient rule,

$$\frac{d(\frac{X}{Z})}{dt} = \frac{1}{Z} \frac{dX}{dt} - \frac{X}{Z^2} \frac{dZ}{dt} . \quad (7)$$

By dividing equation (6) by Z and using this result for $\frac{1}{Z} \frac{dX}{dt}$ in (7),

$$\frac{d(\frac{X}{Z})}{dt} = \alpha F(t) - \alpha \frac{X}{Z} - \frac{X}{Z} \lambda . \quad (8)$$

Replacing $\left(\frac{X}{Z}\right)$ by S for specific activity of the fish, the basic model is

$$\frac{dS}{dt} = \alpha(F(t) - S) - S\lambda \quad . \quad (9)$$

If the derivation had proceeded in terms of β instead of α , a more complex relation than equation (9), involving terms containing $\frac{dZ}{dt}$, would have been obtained. By using the uptake coefficient α , i.e., the rate of Zn input per body burden of Zn, a simpler relation is obtained. If $\frac{dZ}{dt} = 0$, i.e., no "growth", then $\alpha = \beta$; and equation (9) is equivalent to Foster's equation. Since $\beta = r'/Z$, equation (3) implies that $\alpha = \beta + \frac{1}{Z} \frac{dZ}{dt}$. For rapidly growing organisms, the term $\frac{1}{Z} \frac{dZ}{dt}$ could be larger than β itself (as will be seen in a later chapter).

From the basic model, a number of insights into the dynamics of SA in nature immediately follow. First, as shown by Foster (1959), SA will decrease with increasing trophic level from the level of entry of the radionuclide. This can most easily be seen from the equilibrium solution of the basic model, equation (9):

$$S = \frac{\alpha F}{\alpha + \lambda} \quad , \quad (10)$$

where F is a constant $F(t)$. S must be less than F ; in turn, the predator feeding on the fish characterized by S will have a still lower SA. Second, given an initial condition on S , $S(0)$, and given a particular λ , the time history of S is uniquely determined by $F(t)$

and α . Factors that affect α and hence S through α will be called proximate factors to distinguish them from other oceanographic and ecological factors that affect $F(t)$. Admittedly, this distinction is somewhat artificial in that proximate factors can affect the α 's of organisms in the fishes' food chain, which ultimately affect $F(t)$; nevertheless, this distinction will be useful. A major aspect of the dissertation assesses the importance of proximate factors relative to other oceanographic and ecological factors.

An Interpretation of α

A distinct advantage to the SA model formulated in equation (9) is that α can be related to Winberg's (1956) feeding intensity relations. When these relations are extended to α , they lead to hypothetical predictions about α that can be tested utilizing the basic model. Furthermore, these hypothetical relationships give insight into potential restrictions for using the basic model to determine α from field data.

The balanced equation of Winberg relates ration, growth, and metabolism in fishes:

$$\rho R = T + \frac{\Delta W}{\Delta t} , \quad (11)$$

where R = food intake per unit of time,
 T = total metabolism,
 W = body weight, and
 ρ = constant for correction of ingested to utilizable energy of food.

Also, consider Winberg's relationship between respiration and weight:

$$T = AW^{\gamma}, \quad (12)$$

where A = a function of temperature, and
 $\gamma = 0.8$ for fishes in general.

Krogh's curve (Ege and Krogh, 1914), the name given to a line drawn through data from a single goldfish, is used to predict the effect of temperature on A in equation (12) (Winberg, 1956). The function shown in Figure 1 is fit here to their data by (unweighted) least squares.² To predict A for a fish at temperature T_2 (in C), given A at temperature T_1 , multiply A at T_1 by the fraction

$\frac{O_2 \text{ consumption at } T_2}{O_2 \text{ consumption at } T_1}$, where the O_2 consumption data come from Figure

1; this fraction will be denoted C_{T_2, T_1} . Recently, Paloheimo and Dickie (1966) have verified this use of Krogh's curve for fishes on ad libitum rations. Let us now relate α to R . Assume

$$r = abR, \quad (13)$$

where a is a constant for the assimilation efficiency of zinc, and b is the concentration of Zn in the prey. Then,

$$\alpha = \frac{r}{Z} = \frac{ab(AW^{0.8} + \frac{\Delta W}{\Delta t})}{\rho Z}. \quad (14)$$

² The non-linear least squares program ^{*}CURVFIT available from the O.S.U. Computer Center was used for all non-linear curve fitting analyses.

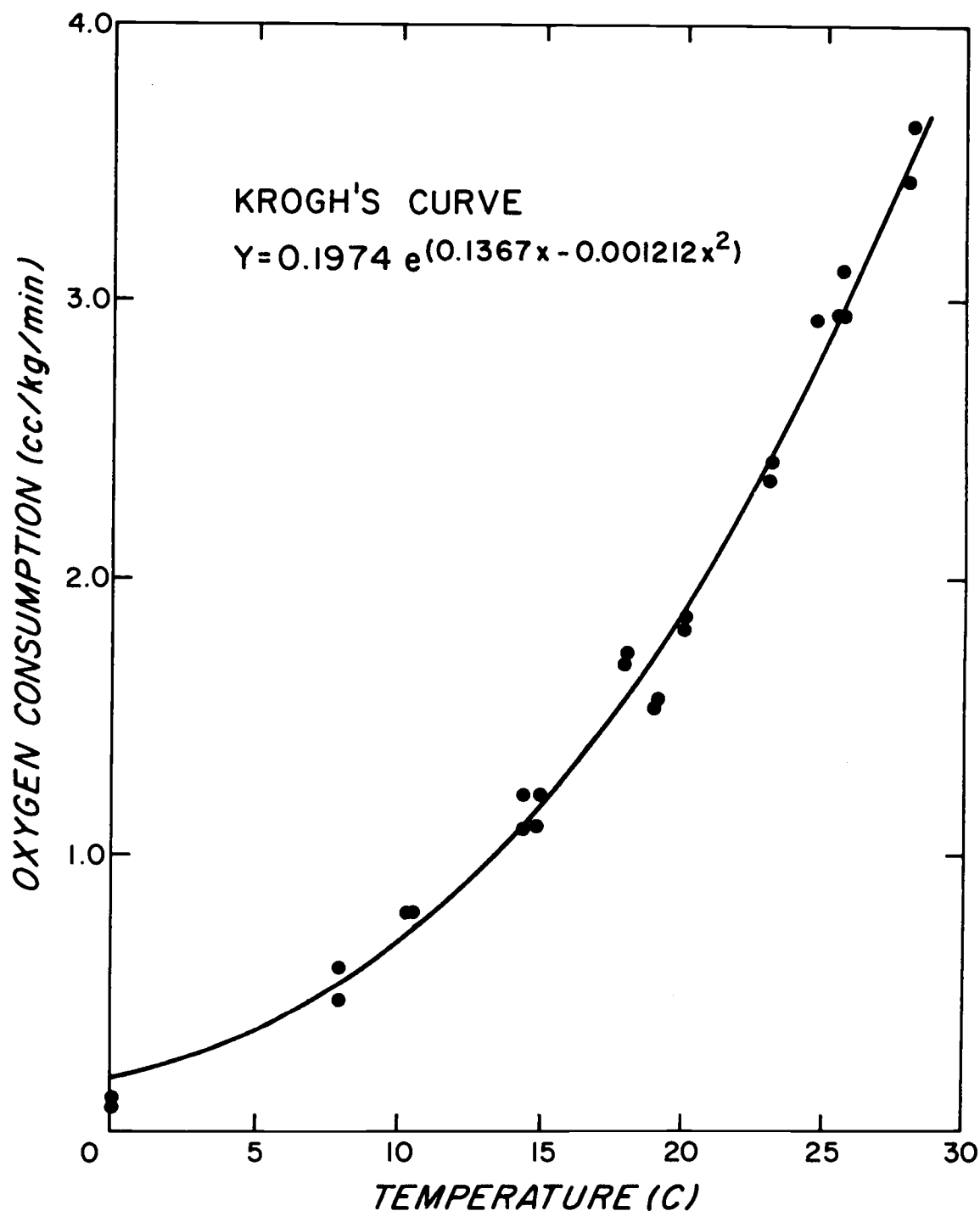


Figure 1. Ege and Krogh's (1914) goldfish data fit by (unweighted) least squares to the function $Y = ae^{bx + cx^2}$; $a = 0.1974 \pm 0.03558$, $b = 0.1367 \pm 0.01732$, and $c = -0.001212 \pm 0.0004071$, where the error terms are standard errors.

If Z can be expressed as a power function in W , substitution of the power function for Z in equation (14) leads to a simple expression in W for α .

The body burdens of Zn, Z , as a function of W were determined from Zn concentration and weight relationships, also power functions, for Lyopsetta exilis and Microstomus pacificus. This was necessary because Zn concentration in each fish, Z/W , rather than its total quantity of Zn, was measured. The best (unweighted) least-squares fit of Z/W to W is shown for L. exilis and M. pacificus in Figures 2 and 3, respectively. Multiplication of the expressions for Z/W by W gives the desired expressions for Z , W having the exponent 1.02 for L. exilis and 0.96 for M. pacificus. The fit for M. pacificus is not as good as that for L. exilis. The standard error of the exponent is higher in M. pacificus, and it appears that the power function is not as adequate for the M. pacificus data.

Although the exponents of these relationships are appreciably different, separate expression for Z for each species will not be substituted in equation (14), but Z will be taken as directly proportional to W . This compromise will not lead to great error. In addition, remember that Winberg's relations were derived from averages of a great many species; therefore, substitution of the exponent for a particular species would lend only false accuracy to our relations. Substitution of kW for Z in equation (14) results in

$$\alpha = \frac{ab(AW^{-0.2} + \frac{1}{W} \frac{\Delta W}{\Delta t})}{\rho k} . \quad (15)$$

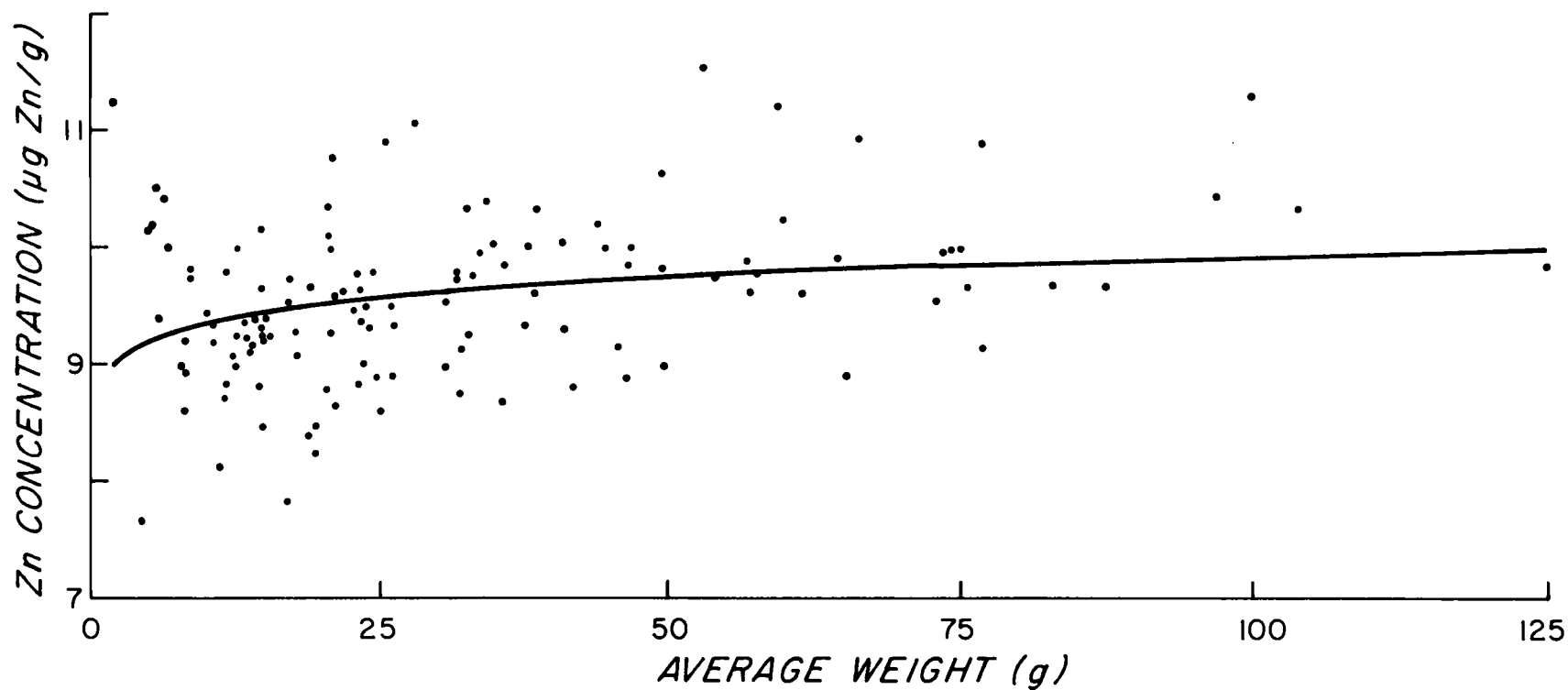


Figure 2. Stable Zn concentration, Z/W , vs. weight, W , in Lyopsetta exilis. $Z/W = 8.83W^{0.0254}$; the standard errors of the coefficient and exponent are, respectively, 0.245 and 0.00829. Each point is a composite sample of 3-34 individuals within a length range of 10 mm.

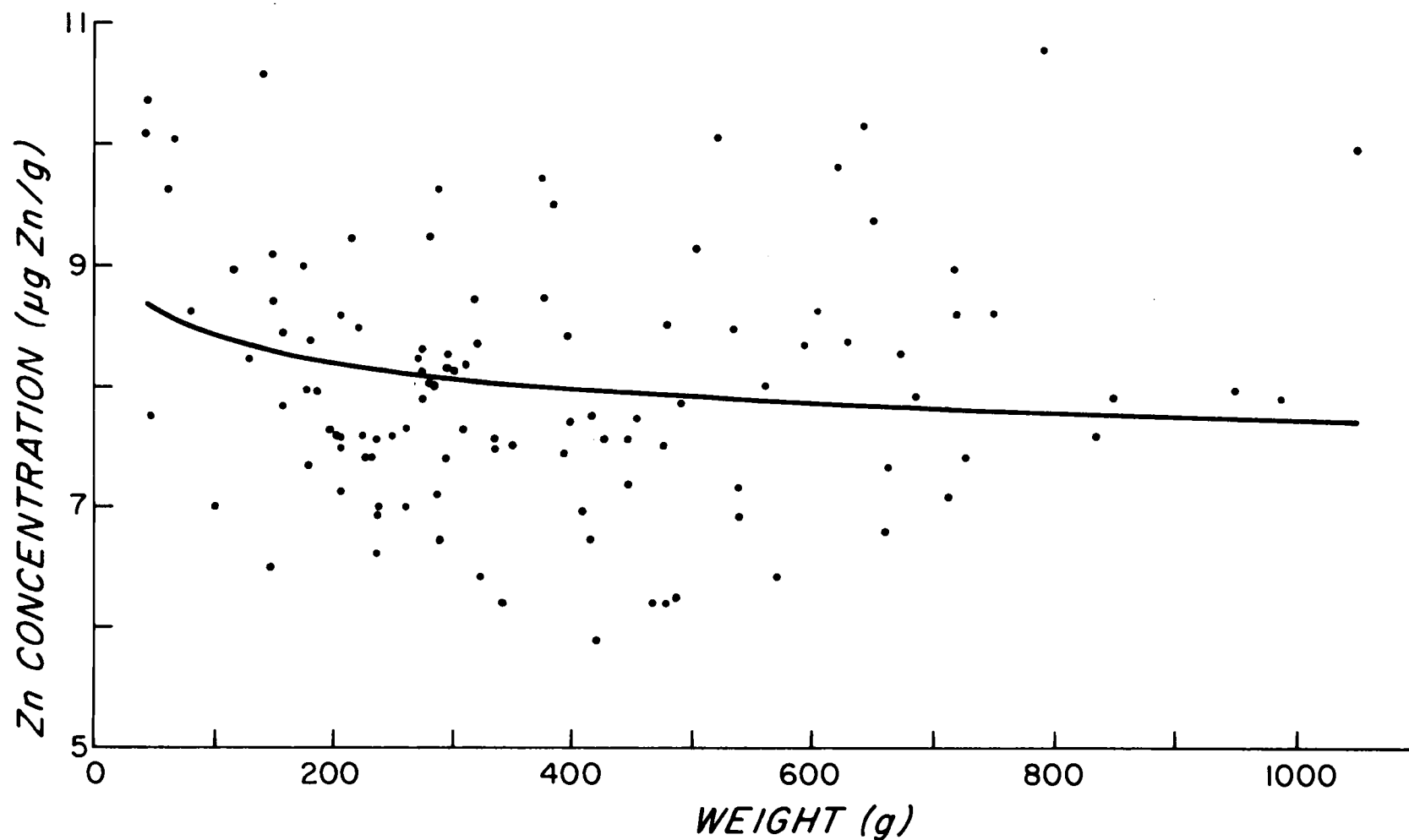


Figure 3. Stable Zn concentration, Z/W , vs. weight, W , in *Microstomus pacificus*. $Z/W = 10.0W^{-0.0381}$; the standard errors of the coefficient and exponent are, respectively, 1.06 and 0.0183. All points greater than 100 g represent single fish.

Collecting the coefficients,

$$\alpha = K(AW^{-0.2} + \frac{1}{W} \frac{\Delta W}{\Delta t}) . \quad (16)$$

Here, for the reader's convenience, is a summary of relationships upon which equation (16) depends:

$$\begin{aligned} \alpha &= r/Z, \\ Z &= kW, \\ r &= abR, \\ R &= \frac{1}{\rho} \left(T + \frac{\Delta W}{\Delta t} \right), \\ T &= AW^{0.8}, \text{ and} \\ K &= ab/\rho k . \end{aligned}$$

If the constant K applies for all species of fishes and if A is known, equation (16) predicts the proportional effect of weight and specific growth rate, $\frac{1}{W} \frac{\Delta W}{\Delta t}$, on α for any species.

Evaluation of A requires further consideration of Winberg's metabolic relationships. Recall that $AW^{0.8}$ is total metabolism and $AW^{-0.2}$ is total metabolism per unit of fish weight. Routine metabolism, Q , per unit weight of any fish can be approximated by Winberg's relationship: $Q/W = 0.3W^{-0.2}$, where Q/W has units of ml of O_2 consumed per g fresh weight per hour at 20C. Multiplication of this expression by $C_{T,20}$ [see text following equation (12)] adjusts the value of 0.3 to the appropriate coefficient at another temperature. Multiplication of Q/W by two gives the total metabolic expenditure per unit weight, T/W , of fishes in nature (Winberg, 1956; Mann, 1967). Since one ml of O_2 consumed equals one mg of dry flesh (Winberg, 1956),

$AW^{-0.2}$ can be expressed in the desired units of day^{-1} . Performing these operations and unit conversions,

$$AW^{-0.2} = (0.0144 C_{T_2,20}/D)W^{-0.2} , \quad (18)$$

and hence,

$$A = 0.0144 C_{T_2,20}/D , \quad (19)$$

where D is the ratio of dry weight to fresh weight in the fish. For the special case where $\frac{1}{W} \frac{\Delta W}{\Delta t} \rightarrow 0$, equation (16) upon collecting coefficients becomes for the slowly growing fish

$$\alpha = \frac{K'}{D} W^{-0.2} , \quad (20)$$

where K' varies in direct proportion to C_{T_2,T_1} .

If k , i.e., Zn concentration, varies among species, this raises question about the reliability of equations (16) and (20) since k would appear to affect K and K' . For example, M. pacificus and L. exilis have different Zn concentrations.³ However, equations (16) and (20) may still apply, whatever the k , provided that $k = cb$, where c is a constant for all species. To verify this, substitute the quantity cb for k in equation (15). This assumption about k is not inconsistent with the accepted mechanism for zinc concentration. Pequegnat, Fowler, and Small (1968), finding that marine organisms accumulate many times the amount of zinc they need for their enzyme

³ Their k 's are about the same on a dry weight basis.

systems, concluded that adsorption exchange is the most probable mechanism of concentration. Before leaving this discussion on k , I want to mention that if the Z-W relationship were markedly nonlinear, K or K' would not be a constant unless this nonlinearity resulted from change of diet or Z/W in the diet. Also if $k = cb$, K is constant regardless of the form of the Z/W or k (where $k = Z/W$, a variable) vs. W relation (Figures 2 and 3). Finally, it is assumed that a is a constant. Before applying the model, one more theoretical aspect, multiple-compartment uptake must be considered.

The Problem of Multiple Compartments

Evidence for multiple-compartment excretion of zinc in fishes comes from Nakatani's (1966) long-term uptake and retention study on trout and Edwards' (1967) retention study with 0 group plaice. During the excretion phase, both workers noted an initial fast decline of ^{65}Zn , followed by a later slower decline. Because an SA equation cannot be written that allows determination of separate α 's and compartment sizes, one cannot avoid working with a single-compartment α , which may be really a composite α of a multicompartment system. To know the consequences of this necessary simplification, α will be related to the separate α 's of a multicompartment system.

Consider α for a two-compartment system. Let the amount of radioactive zinc in the first and second compartments be denoted respectively as X_1 and X_2 . The change in radioactivity for the whole organism is the sum of the changes in X_1 and X_2 , i.e.,

$$\frac{dX}{dt} = \frac{dX_1}{dt} + \frac{dX_2}{dt}. \quad (21)$$

Writing expressions for $\frac{dX_1}{dt}$ and $\frac{dX_2}{dt}$ analogous to $\frac{dX}{dt}$ in equation (4) and substituting them into equation (21) gives:

$$\frac{dX}{dt} = (r_1 + r_2)F(t) - \left[\left(r_1 - \frac{dZ_1}{dt} \right) \left(\frac{X_1}{Z_1} \right) + \left(r_2 - \frac{dZ_2}{dt} \right) \left(\frac{X_2}{Z_2} \right) \right] - (X_1 + X_2)\lambda. \quad (22)$$

Substituting the right-hand side of equation (6) for $\frac{dX}{dt}$, substituting αZ , $\alpha_1 Z_1$, $\alpha_2 Z_2$ for r , r_1 , r_2 , and solving for α leads to

$$\alpha = \frac{\alpha_1 X_1 + \alpha_2 X_2}{X} + \left\{ \left(\frac{dZ}{dt} \right) \left(\frac{1}{Z} \right) - \left[\left(\frac{dZ_1}{dt} \right) \left(\frac{\frac{X_1}{X}}{Z_1} \right) + \left(\frac{dZ_2}{dt} \right) \left(\frac{\frac{X_2}{X}}{Z_2} \right) \right] \right\}. \quad (23)$$

If we can approximate X_1/X and X_2/X by Z_1/Z and Z_2/Z , respectively or if $\frac{1}{Z} \frac{dZ}{dt}$ is small, then the quantity in braces disappears; thus, α becomes the weighted average of α_1 and α_2 , where the weights are the amounts of radioactivity in each compartment.

METHODS

The major study location was NH-23, a 200-m deep station on the outer continental shelf, 23 nm west of Newport, Oregon. There, fishes and shrimps were collected in a seven-meter semi-balloon shrimp trawl. At other locations on the shelf, fishes were caught in a Bureau of Commercial Fisheries (BCF) Mark I Universal trawl, described by Pereyra, Percy, and Carvey (1969). Euphausiids were captured in surface or oblique tows of either a six-ft or ten-ft Isaacs-Kidd midwater trawl (IKMT). Copepods were captured in surface tows of a five-meter-long meter net (VMN) constructed of "0" mesh Nitex[®] netting (0.571 mm aperture). Fishes, shrimps, euphausiids, and copepods were frozen in plastic bags at sea, and care was taken to avoid trace-metal contamination.

In the laboratory ashore, organisms were identified, and standard lengths of fishes were measured. Stomach and gut contents were removed from the fishes. Often, enough contents or "prey" were present for radioanalysis. Stomach contents of all species of fishes except Microstomus pacificus were pooled for radioanalysis according to size class and sampling date. For M. pacificus, gut contents from different sections of their long digestive tracts were either analyzed separately or combined. When the amount of contents for a particular species of benthic fish was too small for radioanalysis, the items comprising its diet frequently were taken in nets or from other species' stomachs to be radioanalyzed instead. In this case, the prey SA was $(\sum SA_i \cdot \%_i) / 100$ where SA_i is the SA of the ith diet item and $\%_i$ is the percentage by weight of the ith diet item in stomach contents.

The samples for radioanalysis, weighing 30 to 4000 g fresh weight, consisted of one to several fish, many shrimps, scores of euphausiids, and stomach contents. Each sample was dried to a constant weight at 65°C, ashed at 420°C for 72 hours, ground with mortar and pestle, and packed into 13 cc counting tubes for gamma-ray counting. Fresh, dry, and ash weights were taken. A portion of the ash was retained for stable Zn measurement by atomic absorption spectrophotometry. This portion was first digested in concentrated HNO_3 , then diluted with 0.36N HCl before analysis. Precision on stable Zn concentration per gram ash was in all cases better than $\pm 2\%$. Radioanalyses were done on a 12.7 x 12.7 cm NaI(Tl) well crystal coupled to a 512 channel analyzer. Samples were counted for one to several 400-minute periods expressing the results per gram ash. Counting precision for most samples was better than $\pm 5\%$, and for nearly all samples was better than $\pm 10\%$. The counts were corrected for physical decay to date of collection. Specific activities were then calculated from the fraction $\frac{n\text{Ci } ^{65}\text{Zn/g ash}}{\text{g total Zn/g ash}}$, which reduces to $n\text{Ci } ^{65}\text{Zn/g total Zn}$.

The numerical analyses to be described in a later section were done on a PDP/15 computer in FORTRAN IV.

DYNAMICS OF ^{65}Zn SPECIFIC ACTIVITY IN BENTHIC FISHES AND THEIR PREY AT NH-23

Introduction

Pearcy and Vanderploeg (1972) reported that differences in ^{65}Zn specific activity among benthic fishes are related to depth of capture, feeding habits, and, possibly, to size, and growth rate. This study, an extension of theirs, attempts to quantify the factors that affect ^{65}Zn SA in benthic fishes at a single location on Oregon's continental shelf. In terms of the theory presented, the importance of proximate factors will be weighed relative to factors affecting $F(t)$ at this location.

Upon entry to the Pacific Ocean, the Columbia River outflow overrides the denser sea water. During the summer, when winds are usually from the north, the Columbia River waters are pushed to the south off Oregon, often as a distinct plume of low salinity water that can be seen as far south as the Oregon-California border. In winter, when southerly winds prevail, the river waters are found north largely along the coast of Washington (Barnes and Gross, 1966; Frederick, 1967). Osterberg et al. (1964) have studied the relationship between Columbia River water and ^{65}Zn concentrations in the euphausiid, Euphausia pacifica off Oregon. Highest concentrations of ^{65}Zn were associated with the presence of the plume off Oregon. During the winter, low ^{65}Zn concentrations were found. Because the input of ^{65}Zn in to the food chain off Oregon is seasonal, understanding the role of

feeding relationships in conveying ^{65}Zn to the benthic fishes requires specific activity data collected over at least the cycle of a year;⁴ furthermore, the basic model requires a reasonable time series of data, which a year period provides.

NH-23 was chosen as the study location for the following reasons. It is close to Newport, Oregon, where the School of Oceanography docks its research vessels, and many common benthic fishes obtainable by otter trawling are there throughout the year. Also, information that was invaluable for the design of this experiment was available for NH-23. Much of the data that Percy and Vanderploeg (1972) reported came from this station. Besides the specific activity values for the fishes themselves, stomach content analyses gave data on the fishes' feeding habits that proved useful to the design of a sampling program to capture the fishes' prey.

Of the most common fishes, their data showed that the small flounder Lyopsetta exilis, which preys on pelagic crustacea, had the highest specific activities and Microstomus pacificus, a large flounder which preys on invertebrate infauna, had the lowest specific activities. Owing to their great differences in specific activity, feeding habits, and size, it was thought that a quantitative analysis of the factors causing the difference in their specific activities would be instructive for understanding the dynamics of ^{65}Zn SA in benthic fishes.

⁴ There are no great fluctuations in stable Zn concentration with season in the fishes or their prey.

Agreement of the difference found between the calculated α 's with the difference predicted by the hypothetical α relationship would verify these relationships. Then, the influence of proximate factors on the SA's of the fishes could be evaluated apart from the oceanographic and ecological factors that affect their SA's through $F(t)$.

Results

Seasonal Patterns of ^{65}Zn Specific Activity in Major Prey of Benthic Fishes at NH-23

The major period of study extended from February 1970 to April 1971. Immediately prior to this period, the number of "single pass" reactors was decreased from two to one as seen in Figure 4. Near the end of the study in January 1971, the last reactor was shut down. Plotted also in Figure 4 are ^{65}Zn specific activities in euphausiids, predominantly Euphausia pacifica, and "infauna", prey taken from entire digestive tracts of Microstomus pacificus. During the summer of 1969, the specific activity in E. pacifica was twice that in 1970. Clearly, this is related to the number of reactors on line. Also evident is the higher specific activity for the infauna during September 1969.

Owing to the decrease in ^{65}Zn input at the beginning of the study period and given the long effective half-life⁵ for ^{65}Zn SA in marine

⁵ The time required for an organism to lose half of its SA upon removal of its source of radioactivity is its effective half-life for SA. This half-life results from the influence of both α and λ . From equation (9) it can be shown that the effective half-life is $\frac{0.693}{\alpha + \lambda}$.

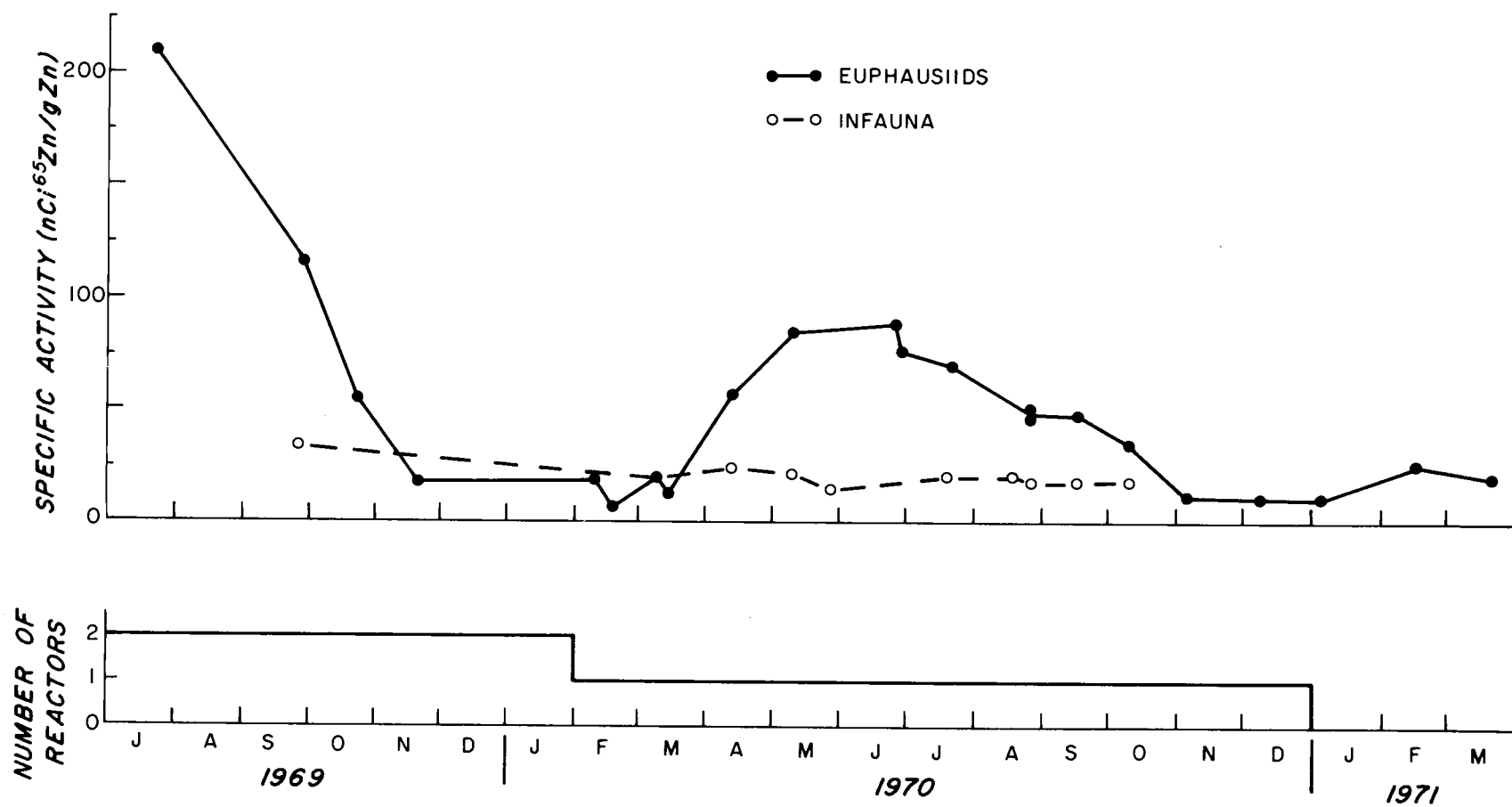


Figure 4. Reactor history and specific activity of euphausiids and infauna at NH-23 before and during the study period.

organisms (as will be shown later), higher elements of the food chain had a higher SA throughout the year than they would ordinarily have had if only one reactor had been operating in the year or two prior to the measurements. Thus, the seasonal pattern of SA seen in the benthic fishes does not follow the pattern expected in a series of years in which the reactor output remained constant. On the other hand, euphausiids (trophic level II^+ ; Lasker, 1966), which can be transported into and out of the area by currents, probably do show a pattern found typically under conditions of equilibrium input of ^{65}Zn . The change in ^{65}Zn input may slightly obscure the role of diet but does not affect the employment of the model.

Analyses of fishes' stomachs (to be discussed below) indicate that euphausiids, shrimps, and infauna were major prey of some or many benthic fishes. Euphausia pacifica, according to Lasker (1966), is omnivorous, feeding on both phytoplankton and small zooplankton, particularly naupliar stages of copepods. Thus, E. pacifica is assigned trophic level II^+ . Pearcy (1970) found that the stomachs of Pandalus jordani captured in midwater trawls contained primarily euphausiids, whereas those captured in otter trawls on the bottom contained benthic organisms and detritus. Of the infauna, polychaetes followed by ophiuroids were the most common taxa; it is likely they are all sediment processors. The marked differences in specific activity of these prey shown in Figure 5 potentially lead to marked differences in ^{65}Zn specific activity among their respective predators.

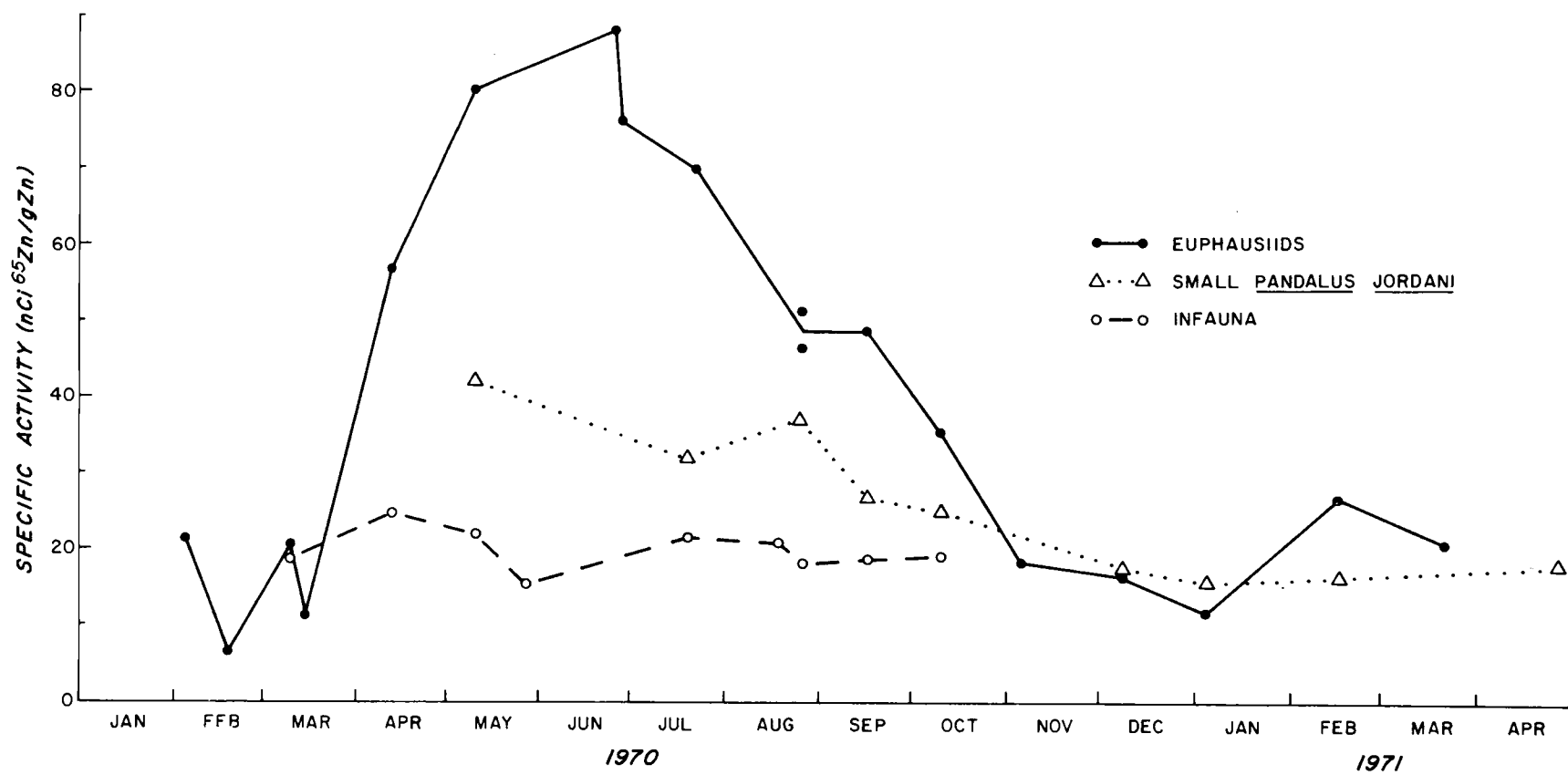


Figure 5. Specific activities of the major prey at NH-23. All P. jordani weigh less than 1.3 g.

Diets, F(t), and Specific Activities of Benthic Fishes at NH-23

M. pacificus and L. exilis. Figure 6 shows the specific activities of M. pacificus and the infauna taken from these fish. Most of the fish were females. No consistent differences in SA were seen for the few males analyzed. In Figure 7 specific activity of M. pacificus is plotted against weight for each month. No apparent trends in specific activity with weight are evident, except possibly for the March fish. Corroborating this, the slope of the linear regression between specific activity and weight was not significant for all fish caught in March ($P > 0.1$), during April-May ($P > 0.5$), or during July-October ($P > 0.5$).

Table 1 displays the diet and the specific activity of the diet by length class in L. exilis on each collection date. Specific activities of the diets were calculated from the formula $\sum SA_i \cdot \%_i / 100$ or actually measured for extracted stomach contents. The calculation of diet specific activity using the formula $\sum SA_i \cdot \%_i / 100$ requires knowledge of all the SA_i . Actually, only major prey were captured in sufficient quantity for radioanalysis: euphausiids, shrimp of different species and sizes, and infauna. The specific activities of these taxa were assigned to other diet items with unknown SA_i on the basis of similarity in diet and size. For example: Decapod larvae, having a size and, presumably, diet similar to the euphausiids', were assigned the SA_i of euphausiids; polychaetes, ophiuroids, and bivalves (all infauna) were assigned the SA of infauna taken from M. pacificus. Thus, every taxon

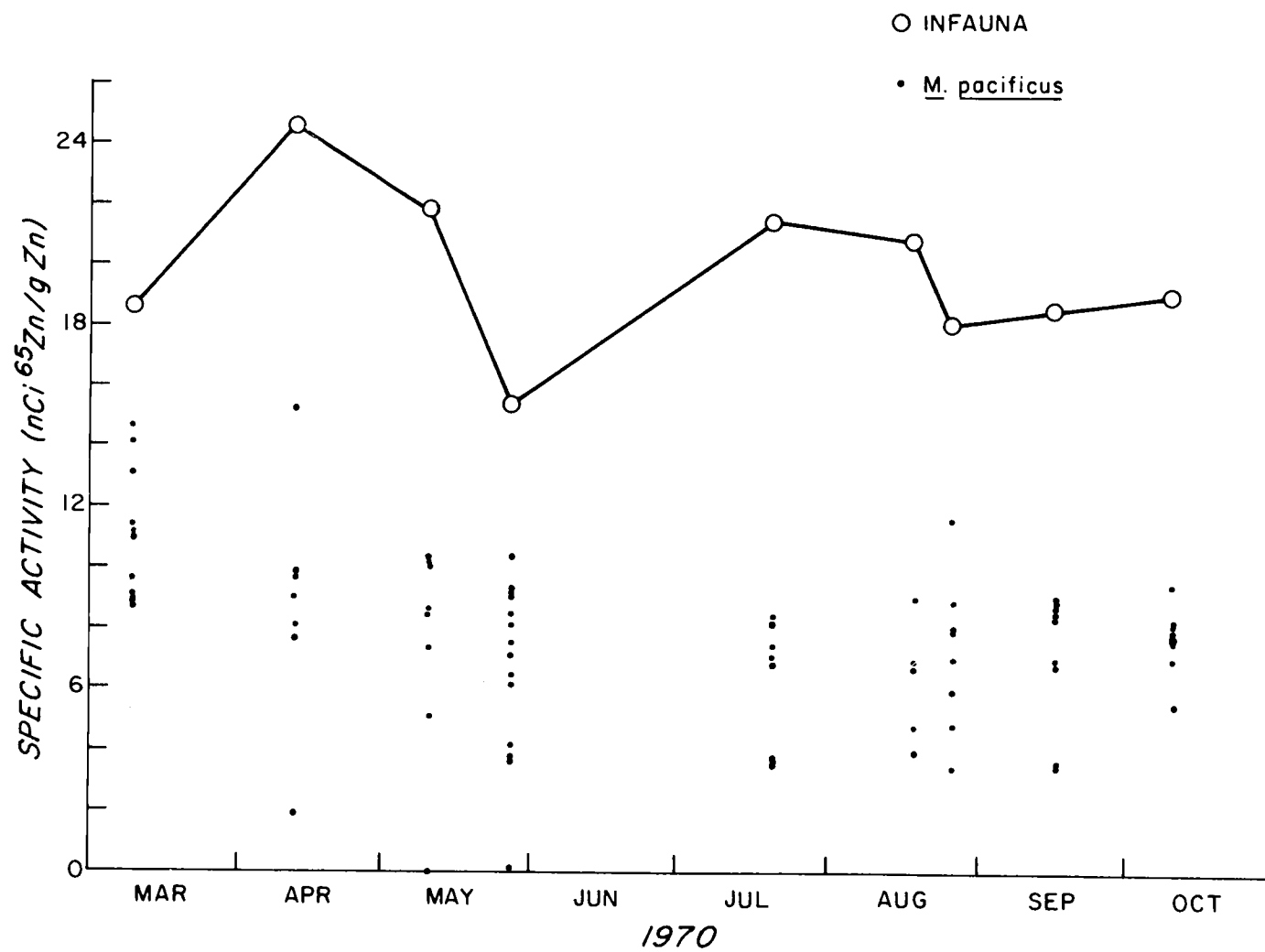


Figure 6. The specific activity of Microstomus pacificus and its prey at NH-23.

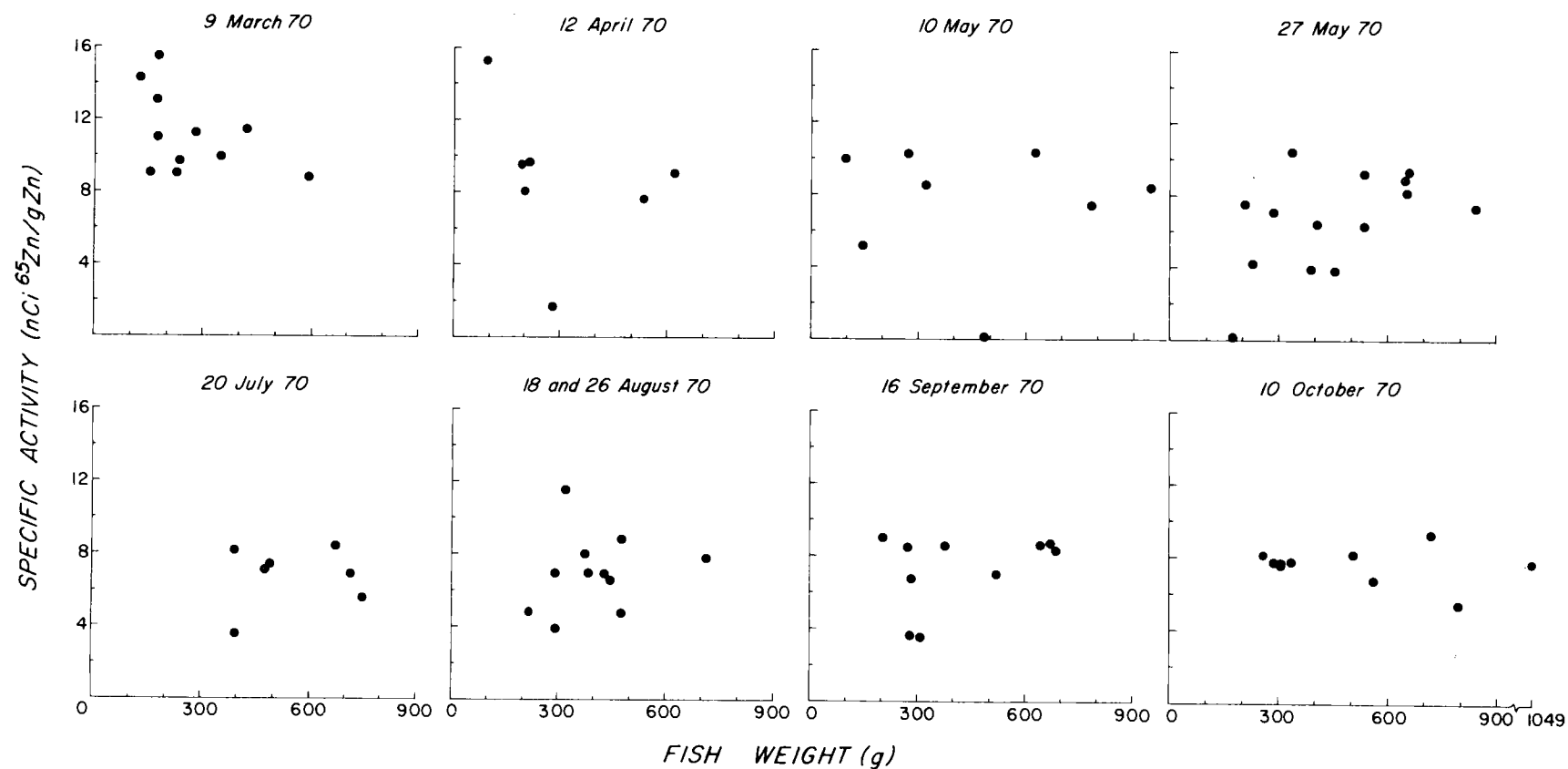


Figure 7. The relationship between specific activity and (wet) weight of *Microstomus pacificus* at NH-23 for different collections in 1970.

Table 1. The $\%_i$, the SA_i , and the Specific Activity of the Diet of L. exilis by Length Class and Season.*

* Script type is used for the SA_i (nCi⁶⁵Zn/g Zn) to distinguish them from the $\%_i$. Blanks in the $\%_i$ imply zeros. Numbered footnotes appear at the end of the table.

Date SA _i Length Class	Fraction With Contents	Small Shrimp ¹	Medium Shrimp ²	Euphausiids ³	Decapod larvae and post-larvae ⁴	Polychaetes ⁵	Ophiuroids ⁶	Fishes ⁷	Crustacean Fragments ⁸	Other	ΣSA _i % 100	Measured Specific Activity
18 III 70: SA _i 70-200	7/200			6.21								23.4
9 III 70: SA _i 82-184	200/200			20.4								20.4
14 III 70: SA _i All size classes	0/0			12.2							12.2	
12 IV 70: SA _i 85-181	172/172			56.6								56.6
10 V 70: SA _i 80-100 100-120 120-140 140-160 160-200 All Classes Combined	6/16 25/84 22/64 18/34 10/12 81/210	41.7 15.2 18.2 57.4 40.1 36.1	85.0 19.1 28.7 26.8 8.9 17.0		21.8 100 36.5 13.3 29.4 8.7			11.0 33.2 15.8 21.6 20.3	1.5 0.2		85.0 62.2 59.5 53.3 39.7 49.4	39.6
27 V 70: SA _i 103-204	20/37	41.7 ¹⁰ 52.0	86.0 ¹¹ 25.5		15.3 9.4 ¹² 13.2						53.7	
26 VI 70: SA _i No fish collected			87.8									
19-22 VII 70: SA _i 100-120 120-140 140-160 160-194	24/61 25/62 13/28 12/15	31.7 17.8 16.7	69.5 21.5 39.4 42.4 5.0		21.3 19.3 ¹² 21.0 ¹² 5.5 ¹² 41.0	21.3 0.3		9.4 21.4 11.2 ¹⁴ 13.9 ¹⁵	11.3 ¹³ 48.6 62.5 45.6 31.5			

Date SA _i Length Class	Fraction With Contents	Small Shrimp	Medium Shrimp	Euphausiids	Decapod larvae and post-larvae	Polychaetes	Ophiuroids	Fishes	Crustacean Fragments	Other	Σ SA _i % _i 100	Measured Specific Activity
25-26 VIII 70: SA _i		36.8	36.8 ¹⁶	48.0		18.0	18.0					
80-100	3/9	67.8							32.2		40.4	
100-120	22/88	65.2		2.2	7.8 ¹²	3.8		11.9	0.8	8.2 ¹⁷	37.3	
120-140	17/59	78.1		3.2		16.4			2.3		34.3	
140-160	17/27	78.3				10.1	0.9		3.7	6.9 ¹⁸	34.9	
160-206	9/15	29.1	64.7			6.1					35.6	
16 IX 70: SA _i		26.4	26.4 ¹⁶	48.3		18.4						
90-100	3/15								41.6	58.4 ¹⁹	48.3	
100-120	34/107	27.9		7.7	17.3	15.3			22.3	9.7 ¹⁹	37.7	
120-140	15/55	25.6		7.8	6.9 ¹²	20.9		32.3	6.5		29.4	
140-160	11/21	55.1	18.1	4.4		19.7				2.7 ²⁰	25.8	
160-200	12/24	18.1	46.8	0.5	2.8 ¹²	18.4		12.0	1.4		26.0	
10 X 70: SA _i		24.5		35.0		18.8	18.8					
100-120	7/45	70.0				28.4			1.6		23.1	
120-140	13/39	62.8			2.1 ¹²	2.8	7.0	19.6	5.5		24.7	
140-160	7/18	88.9				5.9	2.6		2.5		24.3	
160-200	7/9	53.7			9.8 ¹²	28.6			7.9		24.7	
5-6 IX 70: SA _i		17.3	25.8	17.3		18.8 ²¹	18.8 ²¹					
80-100	5/46				74.6 ¹²				25.4		17.3	
100-120	36/178	19.3		34.4	10.9 ¹²				35.3		17.3	
120-140	25/167	17.4		3.5	8.0 ¹²	37.7	16.9		16.4		18.0	
140-160	20/97	49.4		17.1		7.4		15.3	10.8		17.4	
160-200	17/53	30.6		1.0	3.4 ¹²	25.5	5.1	28.9		5.5 ²²	17.8	

Date SA _i Length Class	Fraction With Contents	Small Shrimp	Medium Shrimp	Euphausiids	Decapod larvae and post-larvae	Polychaetes	Ophiuroids	Fishes	Crustacean Fragments	Other	$\Sigma SA_i\%_i$ 100	Measured Specific Activity
6 XII 70: SA _i		17.3	22.4 ¹¹	16.1								
71-100	8/73			51.4	10.1	17.1 ¹⁶			21.4		16.3	
100-120	5/48	36.5		35.3	28.2 ¹²						16.5	
120-140	16/62	53.1		9.9	9.8 ¹²		3.3 ¹⁶		5.6	18.3 ¹³	17.0	
140-160	15/46	81.4			1.1	11.9 ¹⁶	1.2 ¹⁶		4.0	0.3 ²³	17.2	
160-180	8/25	48.3	25.4			2.9 ¹⁶	1.6 ¹⁶	19.8	1.9		18.6	
180-215	11/19	52.8	37.8					9.4			19.2	
4 I 71: SA _i		15.3	19.7	11.5								
100-120	16/68	63.1		24.7	10.4 ¹²				2.0		13.9	
120-140	10/32	100									15.3	
140-160	5/28	100									15.3	
160-200	19/26	86.5	5.6					7.9			15.6	
21 III 71: SA _i				20.4								
50-180	62/131			100							20.4	
27 IV 70: SA _i		17.5		20.4 ²⁴								
100-120	31/55	10.9		88.9		0.2 ¹⁶					20.1	
120-140	20/34	28.1		71.9							19.6	
140-160	13/28	84.2		13.6					2.2		18.0	

Footnotes to Table 1

- 1 Predominantly Pandalus jordani between 6 and 12 mm in carapace length or 0.31 and 2 g wet weight; occasionally including Crangon communis and Spirontocaris bispinosa.
- 2 Predominantly P. jordani between 15 and 20 mm carapace length or 3 and 6 g fresh weight; occasionally including Crangon communis and Spirontocaris bispinosa.
- 3 Predominantly Euphausia pacifica; Thysanoessa spinifera was the second most common euphausiid in IKMT's and fish stomachs.
- 4 SA_i assumed equal to the SA_i of euphausiids.
- 5 SA_i assumed equal to the SA of infauna taken from the stomachs of M. pacificus.
- 6 Predominantly post-larval flounder; SA_i assumed equal to SA_i of small shrimp.
- 7 SA_i assumed equal to SA_i of euphausiids.
- 8 Stomach contents included E. pacifica, P. jordani and a single large polychaete (Aphrodite sp.); L. exilis < 140 mm ate primarily euphausiids.
- 9 No L. exilis caught on this date; assumed all ate euphausiids.
- 10 SA_i assumed equal to small shrimp collected on 10 V 70.
- 11 SA_i by linear interpolation between nearest collections.
- 12 Predominantly P. jordani.
- 13 The pelagic shrimp, Sergestes similis; SA_i assumed equal to SA_i of small shrimp.
- 14 Munid crab; SA_i assumed equal to SA_i small shrimp.
- 15 Sediment; SA_i assumed equal to SA of infauna.
- 16 SA_i assumed equal to small shrimp.
- 17 Cephalopod; SA_i assumed equal to small shrimp.

- ¹⁸ 5.8% cephalopod, 1.1% bivalves; SA_i of cephalopod assumed equal to SA_i of small shrimp; SA_i of bivalve assumed equal to SA_i of infauna.
- ¹⁹ Mysid shrimp; SA_i assumed equal to SA_i of euphausiids.
- ²⁰ 2.0% bivalves, 0.7% mysid shrimp; SA_i of bivalves assumed equal to SA infauna and SA_i of mysid assumed equal to SA_i of small shrimp.
- ²¹ No infauna collected on this date; SA_i from 10 X 70 infauna used.
- ²² Hyperiid amphipod; SA_i assumed equal to SA_i of euphausiids.
- ²³ Gammarid amphipod; SA_i assumed equal to SA_i of euphausiids.
- ²⁴ SA_i assumed equal to SA_i of previous month.

in Table 1 has a measured SA_i or an assigned SA_i . The assumptions behind the assignment of the SA_i are given in numbered footnotes. Also contained in the footnotes are more detailed descriptions of the taxa.

In Table 1, most diet specific activities are estimated from $\Sigma SA_i \cdot \%_i / 100$. The accuracy of this estimate and, in turn, the accuracy of most of the specific activity values of the diets shown in Table 1 depend on the accuracy of the separate SA_i . On 10 May 1970, the specific activity measured for the prey pooled from all length classes combined was compared to the SA estimated from $\Sigma SA_i \cdot \%_i / 100$ for all length classes combined. In Table 1, the former is seen to be 20% lower than the latter. Perhaps the assumptions behind assignment of specific activities to the unknown SA_i were faulty. At least part of the difference may possibly be explained by measurement error: the percent standard error of the radioactivity measurement was 8.4%. Considering the unusually small size (3 g dry weight) of the sample of stomach contents as well as the handling necessary to extract this very small sample, Zn contamination is also a possibility. Fortunately, much of the diet of L. exilis consisted of euphausiids or shrimps; therefore, few assumptions were made.

Before examining more data, another potential complication in using $\Sigma SA_i \cdot \%_i / 100$ must be discussed. Possibly fish concentrate Zn in direct proportion to the Zn concentration in their prey. Remember, this mode of Zn concentration was hypothesized to justify equations (16) and (20) for interspecies comparisons. If proportional Zn concen-

tration occurs and if differences in Zn concentration occur among prey, application of $\sum SA_i \cdot \%_i / 100$ could potentially lead to biased estimates of diet specific activity. Pequegnat, Fowler, and Small's (1969) tabulation of Zn concentrations showing significant differences among certain animal taxa implies significant differences in Zn concentration for some of the prey of L. exilis. In particular, their tabulation suggests large differences in Zn concentration between some infauna and crustacea. Unfortunately, my data are not useful for evaluating this difference, because the infauna taken from M. pacificus often was found with sediment and because digestion would of course have altered Zn concentration. Since the Zn concentrations of all prey of L. exilis are not known, $\sum SA_i \cdot \%_i / 100$ will be employed. This should not lead to great error in view of the largely crustacean diet of L. exilis.

The specific activities of the prey in Table 1 are plotted in Figure 8A. Contrasting in Figure 8A with Figure 6, it is seen that during the summer the specific activity of the prey of L. exilis is much higher--at least twice as high--than the specific activity of the prey of M. pacificus. Also in Figure 8A, the specific activities of the prey of smaller length classes are often higher than those of larger length classes during summer months. Plotted in Figure 8B are the SA's of L. exilis themselves, generally by length classes of 20 mm. Actually, fish were analyzed originally by length classes of 10 mm. Each point in 8B represents at least the SA of a single sample containing two individuals and at best the weighted (by total Zn in each sam-

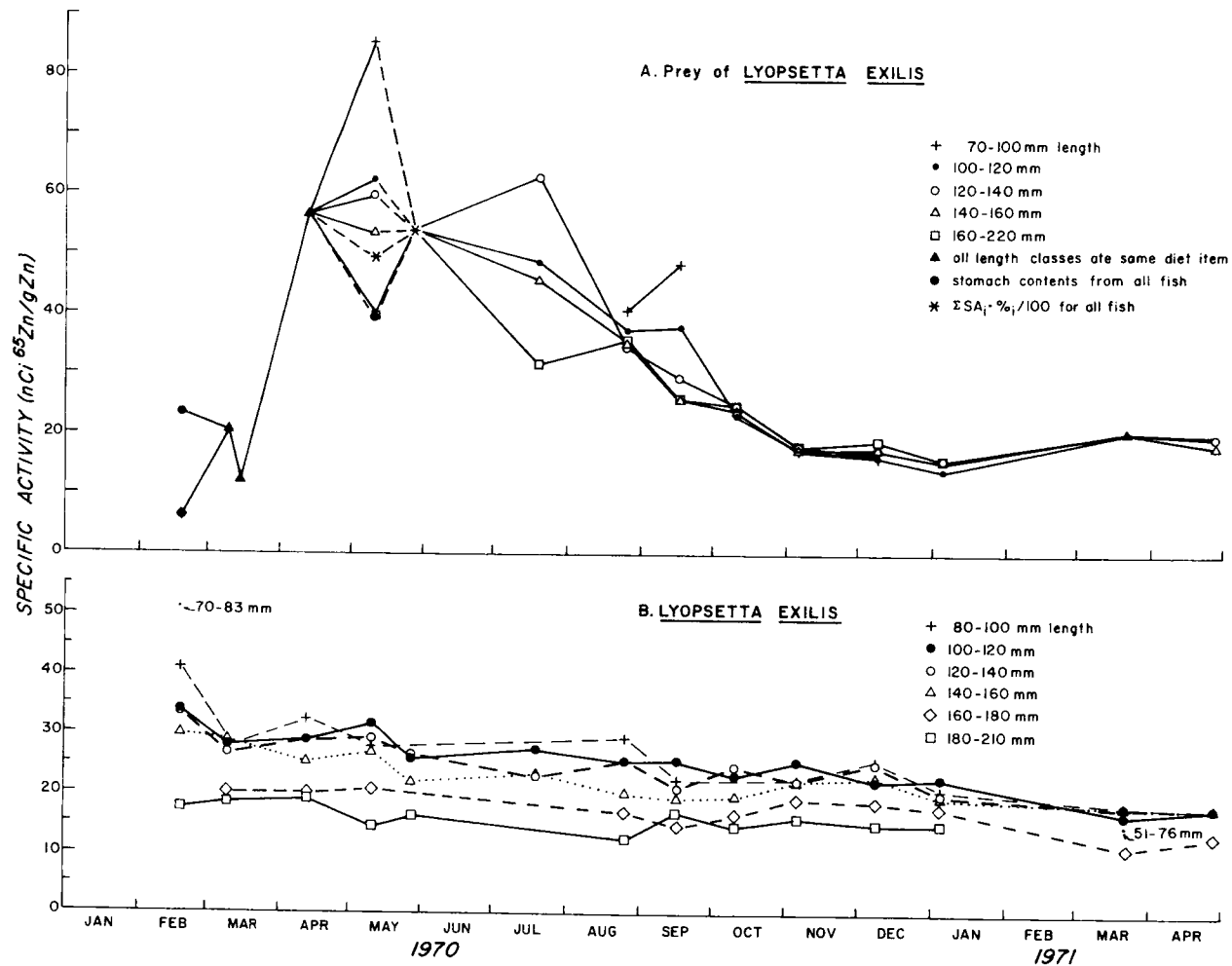


Figure 8A. Specific activities of the prey of L. exilis. A dashed line indicates connection with a specific activity value representing prey pooled from all fish.

8B. Specific activity of the length classes of L. exilis.

ple) average of 6 samples containing a total of 55 fish. To transform length class to weight class, use the weight-length relationship in Figure 9.

Sex of the fish was not distinguished. First, the amount of time necessary to sex the often hundreds of fish analyzed for each collection date was prohibitively long. Second, assuming both sexes live at the same depth and do not migrate, only a significant difference in α , which is not expected, would produce a difference in SA with sex. Table 2 shows the SA of a number of samples of each sex and size for March and April collections. Table 2 suggests that the specific activity of males may be slightly lower than that of females of the same size. Individual variation and the sample number of two perhaps explain the extremely low ^{65}Zn SA of 14.1 nCi/g for the male fish averaging 43 g. Thus, Table 2 generally corroborates the decision not to discern sex. Interestingly, females were more common in the collections. This may indicate a segregation of sex with depth.

Contrasting Figures 6 and 8B, the SA's of L. exilis are higher than those of M. pacificus, which reflects the higher SA of the prey of L. exilis. In 8B, the smallest length classes generally have the highest specific activities. As the prey SA decreases with onset of fall and winter circulation and possibly because of the preceding reactor shutdown, the SA in L. exilis also generally decreases. The decrease in SA occurs more rapidly in smaller length classes, bringing the specific activities of all length classes closer together. These

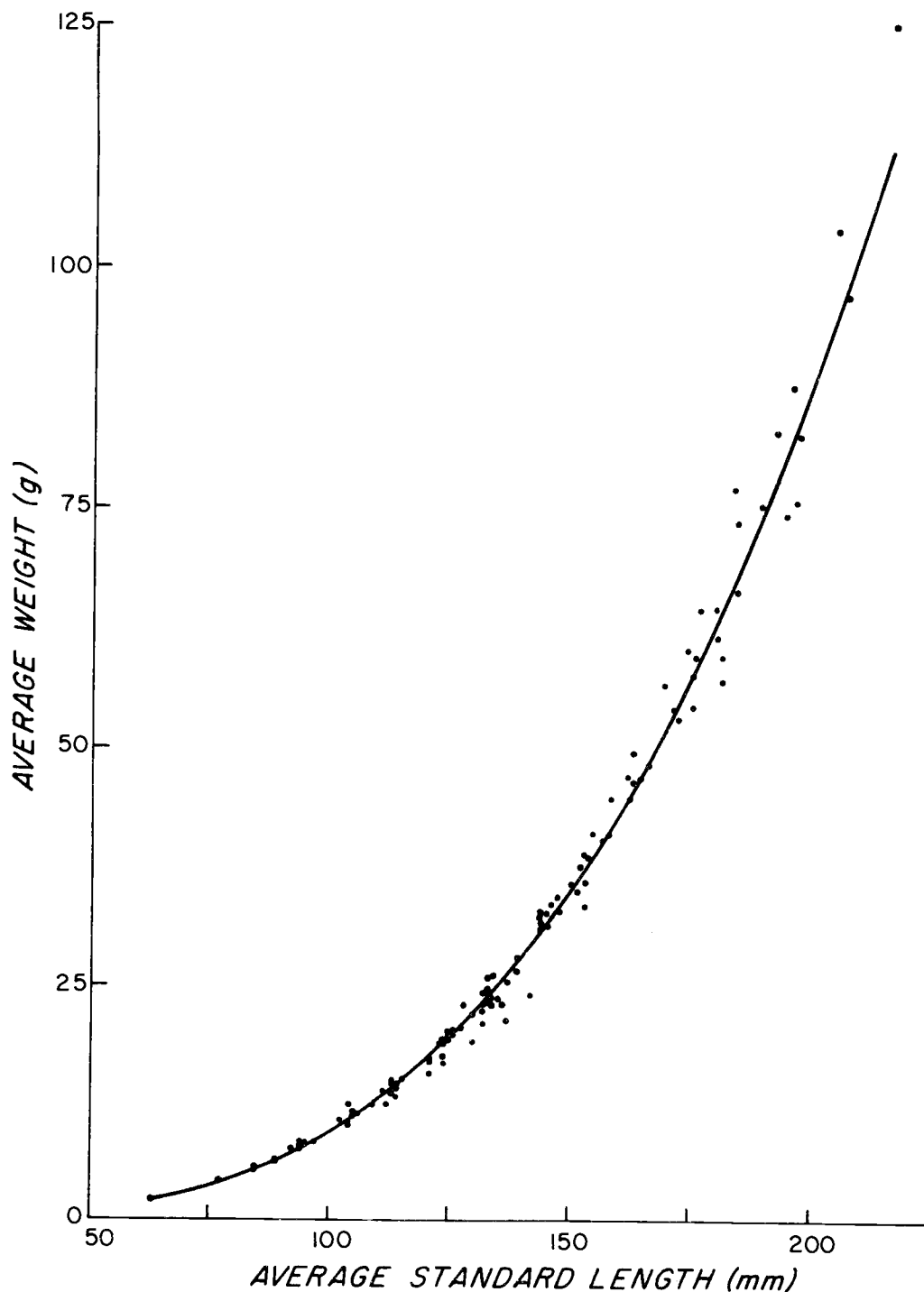


Figure 9. Average weight (g) of *Lyopsetta exilis* vs. average standard length (mm). Points are composite samples of three or more individuals within a 10 mm length range. The line is the best weighted ($1/Y^2$) least-squares fit to $Y = aX^b$, where $a = 3.097 \times 10^{-6} \pm 3.987 \times 10^{-7}$ and $b = 3.241 \times 10^0 \pm 2.621 \times 10^{-2}$.

Table 2. Zinc-65 Specific Activity in Male and Female Lyopsetta exilis.

9 March 70 Males			9 March 70 Females		
N in Sample	Ave. Wt. of Fish (g)	nCi ⁶⁵ Zn/g Zn	N in Sample	Ave. Wt. of Fish (g)	nCi ⁶⁵ Zn/g Zn
8	21	28.4	5	23	27.7
5	21	23.3	5	24	27.2
4	27	25.5	4	41	30.8
4	31	28.3	3	54	20.8
2	43	14.1	3	57	25.0
			1	64	15.1
			1	65	21.9
12 April 70 Males			12 April 70 Females		
9	22	24.8	9	25	29.9
7	23	27.7	9	28	28.0
			8	34	29.1

relationships are prominent when seen in Figure 10 where SA vs. weight is plotted for each collection (Pearcy and Vanderploeg, 1972). The SA's for this figure are for composite samples of fish within 10 mm length ranges. The slopes of all but two of these regressions are significant ($P < 0.05$). The slopes of the regressions in Figure 10 were regressed against time with each slope weighted by the inverse of its standard error. The slope of this regression was significant ($P < 0.05$), thus validating the significance of the decrease in slopes with time in Figure 10.

Other Benthic Fishes. Other benthic fishes were examined to determine the full spectrum of specific activities possible. Table 3 compares the specific activities of the fishes caught at different times during the collection period to weight and diet. Representatives not only of the families of Osteichthyes, but also of the Cyclostomes (Myxinidae) and Chondrichthyes (Rajidae), are tabulated. The species with the highest SA was Thaleichthys pacificus, a predator of euphausiids and possibly other small pelagic crustacea. The fish with the lowest SA is the hagfish Eptatretus stouti, presumably a predator of large fishes. In Table 3, fishes feeding on low trophic level pelagic crustacea usually had the highest specific activities, while higher trophic level fishes or predators of infauna had the lowest specific activities. Except for Glyptocephalus zachirus and, possibly, Xenopyxis latifrons, no marked decrease in SA with increasing weight is seen.

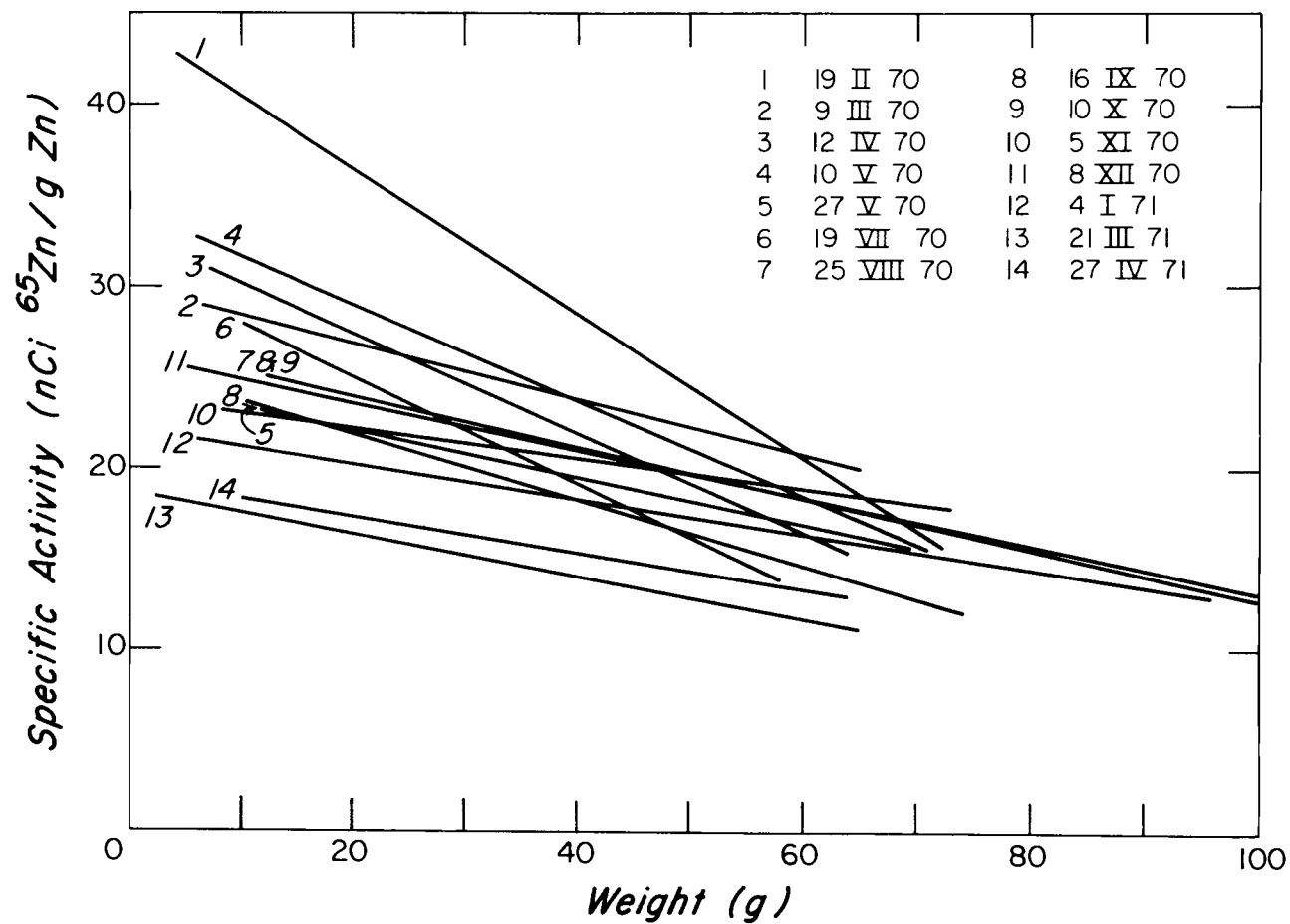


Figure 10. Regression lines of ^{65}Zn specific activity vs. wet weights of Lyopsetta exilis for 14 collection dates in 1970 and 1971 at NH-23.

Table 3. Other Benthic Fishes at NH-23: Body Weight, ^{65}Zn Specific Activity, and Feeding Habits.¹

	Season										Food Habits		
	Feb-Mar. 1970 Ave. Wt. nCi ⁶⁵ Zn/g Zn	Apr-May 1970 Ave. Wt. nCi ⁶⁵ Zn/g Zn	July-Aug. 1970 Ave. Wt. nCi ⁶⁵ Zn/g Zn	Sept., 1970 Ave. Wt. nCi ⁶⁵ Zn/g Zn	Nov., 1970 Ave. Wt. nCi ⁶⁵ Zn/g Zn	Jan., 1971 Ave. Wt. nCi ⁶⁵ Zn/g Zn							
Agonidae:													
<u>Asterotheca</u>													
<u>pentacantha</u>		11	19.6	12	18.7						Small Crustacea		
				25	24.9								
<u>Xenopyxis</u>													
<u>latifrons</u>	3.8	35.4		17	10.8	13	18.6	15	16.1	15	15.8	Small Crustacea	
	6.1	40.3											
	8.9	31.6											
	14	19.9											
Myxinidae:													
<u>Eptatretus</u>													
<u>stouti</u>		101	3.89	106	5.76	85	4.04	130	4.78		Large Fishes ³		
Osmeridae:													
<u>Thaleichthys</u>													
<u>pacificus</u>	12	37.7				34	37.2	57	23.3		Euphausiids ⁴		
Pleuronectidae:													
<u>Atheresthes</u>													
<u>stomias</u>	308 ²	17.0	280 ²	30.1	391 ²	28.6		253	28.1	139	25.3	<u>Pandalus jordanii</u> ,	
	471 ²	16.9	578 ²	27.9	561 ²	28.3		402 ²	26.4	363 ²	25.2	euphausiids, fishes ⁵	
	517 ²	24.8						762 ²	10.8				
	733 ²	20.7											
<u>Glyptocephalus</u>													
<u>zachirus</u>	60	15.7	32	17.0	163	8.90	179	9.83	160 ²	7.98	198	6.91	Polychaetes; small
	163	8.43	80	13.9									crustacea, especially
			162	9.73									amphipods
Rajidae:													
<u>Raja rhina</u>	387 ²	17.8						694 ²	13.0				Crustacea, fish? ⁶
<u>Raja stellulata</u>	699 ²	8.02											Crustacea, fish,
													cephalopods? ⁷
Scorpaenidae:													Fishes, <u>P. jordanii</u>
<u>Sebastolobus</u>													(medium or large),
<u>alascanus</u>				214	14.3	201	18.6						cephalopods ⁸
				553 ²	12.3								

¹ Except where noted, specific activities are either averages of two or more fish, composite samples or composites of composite samples.

² One fish.

³ According to Clemens and Wilby (1961).

⁴ Based on fish from three collection dates; Barraclough (1964) reports that euphausiids are eaten and Clemens and Wilby (1961) report that small crustacea are eaten.

⁵ Based on stomach contents from 14 fish; Gotshall (1969) reports a similar diet for fish from California.

⁶ Based on stomach contents from four fish.

⁷ Based on stomach contents from two fish.

⁸ Based on stomach contents from 14 fish.

Zinc Uptake Rates of *M. pacificus* and *L. exilis*

Modelling Assumptions and Methods. A time history of S and $F(t)$ are all that is required to estimate α using the basic model. Implicitly, the fish sampled for analysis must be members of the same population sampled at earlier times, all having the same α at a given time. Also implicit is that the SA available to the fish from their food must be equal to the SA measured for the food as a whole.

If an analytical solution could be written for equation (9), non-linear least squares would be used to determine the best $S(0)$ and α , assuming α is constant. However, the form of $F(t)$ from field data will often prevent analytical solution. For this reason, a numerical solution must be coupled to a least-squares minimization algorithm.

A Runge-Kutta numerical solution with a step size of one day was employed. The $F(t)$ between sampling dates were entered by linear interpolation. This solution was coupled to a gradient algorithm given by Bevington (1969), slightly modified to accept the multiple observations of S on each sampling date. The Runge-Kutta solution gave results accurate to better than the three significant figures of the data. Tests of the entire algorithm indicated that the α 's obtained are accurate to more than two significant figures. This accuracy was judged adequate for the rough field data available.

In addition to the implicit biological assumptions, other requirements must be satisfied for the method to yield accurate estimates of

α . First, the sampling frequency must be great enough so that reasonable time histories of S and, especially, of the linearly interpolated $F(t)$ are obtained. Second, the model must be adequate. Here we are assuming that α is constant. Third, the residuals of the least squares fit must be independent, have a mean of zero, and have constant variance.

Microstomus pacificus. Consideration of the biological assumptions underlying the application of the basic model is especially important for the analysis of the M. pacificus data. In Figure 7, it was seen that M. pacificus spanned a large weight range, namely, from 96 to 1049 g. Using the weight-length relationship given by Hagerman (1952), this corresponds to a 231 to 446 mm length range.⁶ Reference to the length-age curve for female M. pacificus (from Hagerman, 1952) in Figure 11 indicates the ages of the fish ran from 2 to 12 years. Older fish would have been exposed to higher SA when more reactors were on line (Percy and Vanderploeg, 1972). Nevertheless, during the gradual shut-down in reactors over the years, physical decay would obviate potential differences in SA with age. A problem is suggested by equation (20), which implies a decrease in α with increasing weight; a fish ten times as large as another will have an α that is 63% as large as that of the smaller one. The lower α for larger fish implies a lower SA (assuming

⁶ Hagerman measured total lengths, whereas I measured standard lengths. Since no conversion factor for lengths was determined, weights were transformed by his relationship to lengths.

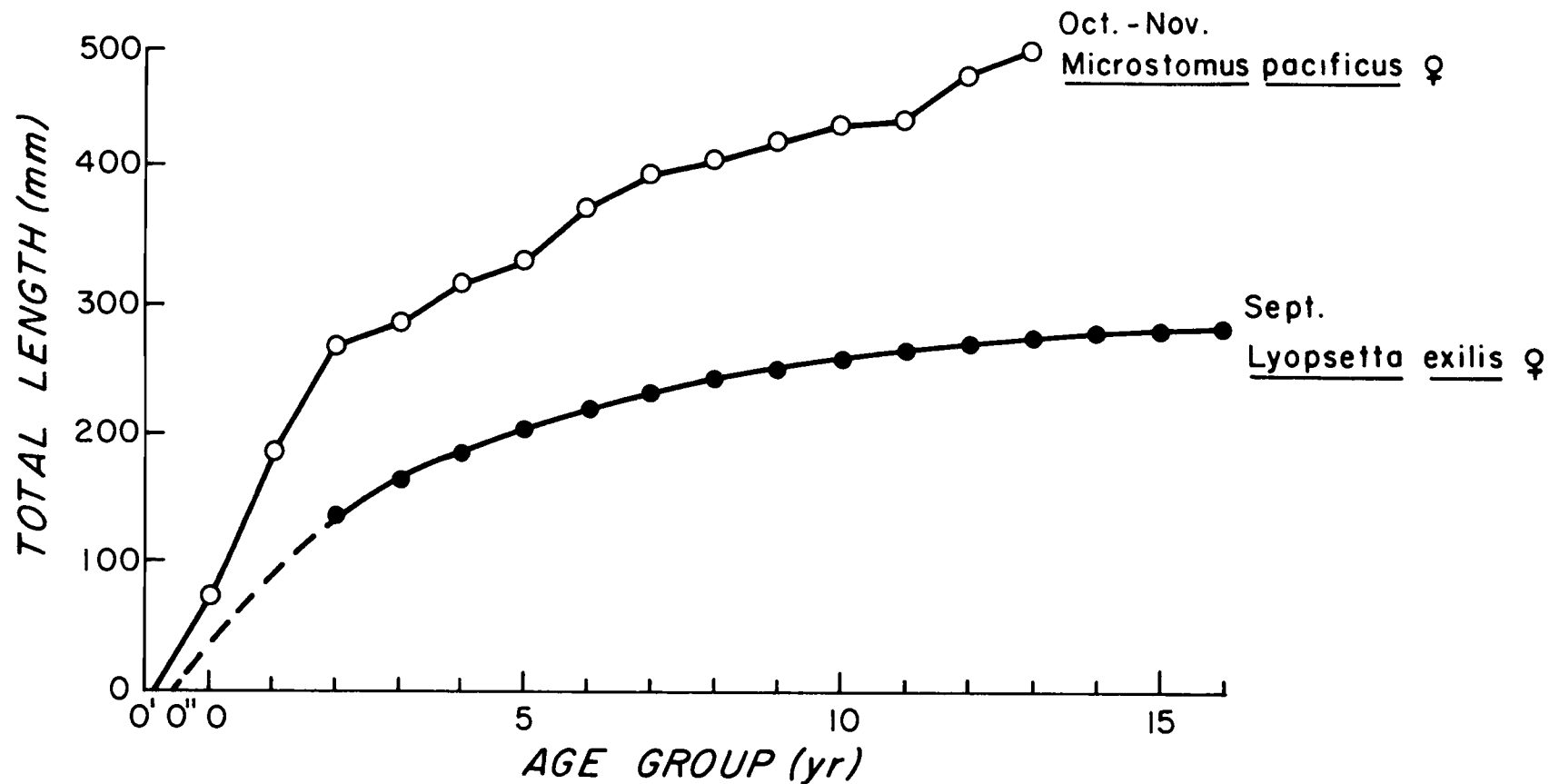


Figure 11. Growth curves for female Microstomus pacificus (Hagerman, 1952) and female Lyopsetta exilis (Demory, 1972). 0' and 0'' are birth dates of fishes. (Note that months of capture explain the lack of coincidence between the birth dates and the zero age class.)

$F(t) > S$). In reality, this trend would be more marked because growth in the smaller fish would increase α . Curiously, a distinct SA-W trend was not seen for M. pacificus.

If after the initiation of the experiment, fish immigrate to NH-23 from a distant place, they could bias the results if the SA of the prey in their earlier location had been different. Carey (1969) noted a marked decrease in SA of echinoderms with increasing depth (as much as 25% per 100 m) and a gradual decrease in SA with increasing distance south of the Columbia River. Percy and Vanderploeg (1972) reported a similar decrease in ^{65}Zn SA with increasing depth in M. pacificus and other fishes. Further discussion of spatial trends in SA on the continental shelf will be made in a later chapter. M. pacificus are thought to be local populations which migrate shoreward during spring and offshore during October and November (Hagerman, 1952). Tagging studies indicate that although a few individuals may move as far as 48-580 km, most M. pacificus tend to remain in a single locality (Westrheim and Morgan, 1963). During the winter the mature M. pacificus usually spawn at depths greater than 300 m (Hagerman, 1952; Harry, 1959), but juveniles and some immatures (< 300 mm = 264 g) remain at depths as shallow as or shallower than 200 m (Hagerman, 1952; Demory, 1972). For this experiment, it is assumed that all the fish originated from the same depth, migrated to the 200 m station at or before initiation of the experiment in March, and that other fish did not immigrate into the study area during the experimental period, March through October.

The possibility that fish might absorb a different SA from their food than that measured for the food as whole was thought to be a potential problem. For example, less easily digestible part of the prey, such as clam shell, could have a different SA from the softer parts having a higher turnover rate. To test for this problem and to determine whether pooling of the gut contents from the entire length of the alimentary tract biased the calculations, I divided the gut into a number of sections and determined specific activity for each section to see if SA of the contents increased or decreased with distance away from the stomach. Table 4 shows that no consistent trend appeared. Interestingly, the hinder part of the digestive tract contained, in addition to well-digested remains of prey, much sediment apparently originating from ingestion of polychaete tubes with the polychaetes.

In view of the higher specific activities exhibited by fish weighing less than 200 g, possibly a result of their size and growth rate or migrating behavior, only fish weighing greater than 200 g were used to estimate α . Also, the three lowest SA's of M. pacificus in Figure 6, which occur in April and May, were discarded. These fish were presumed to have originated from great depths or a great distance to the south. The best least-squares fit shown in Figure 12 yielded $\alpha = 9.9 \times 10^{-4}$ /day. The September 1969 data are included to show that the fish are probably not in equilibrium with their food during the study period. This explains the decrease in their SA during the study period.

Table 4. Zinc-65 Specific Activity of Food in Different Sections of the Gut of Microstomus pacificus.

<u>Date</u>	<u>No. of Fish Analyzed</u>	<u>Section of Gut</u>	<u>nCi⁶⁵Zn/g Zn</u>
12 April 1970	11	Foregut ¹	23.5
12 April	11	Hind gut ²	25.4
10 May	9	Foregut	17.0
10 May	9	Hind gut	23.4
27 May	8	Stomach and first 1/3 ³	16.0
27 May	8	Second 1/3	18.1
27 May	8	Last 1/3	11.8
20 July	8	Stomach	22.2
20 July	8	First 1/3	21.3
20 July	8	Second 1/3	20.6
20 July	8	Last 1/3	21.0
18 August	5	Stomach and first 1/3	19.8
18 August	5	Second and last 1/3	21.5
26 August	8	Stomach and first 1/3	19.9
26 August	8	Second and last 1/3	16.8
16 September	11	Stomach and first 1/3	17.9
16 September	11	Second and last 1/3	19.0
10 October	10	Stomach and first 1/3	17.9
10 October	10	Second and last 1/3	19.6

¹ Stomach contents plus first one-fourth of intestine.

² Last three-fourths of intestine.

³ First 1/3 is first one-third of intestine.

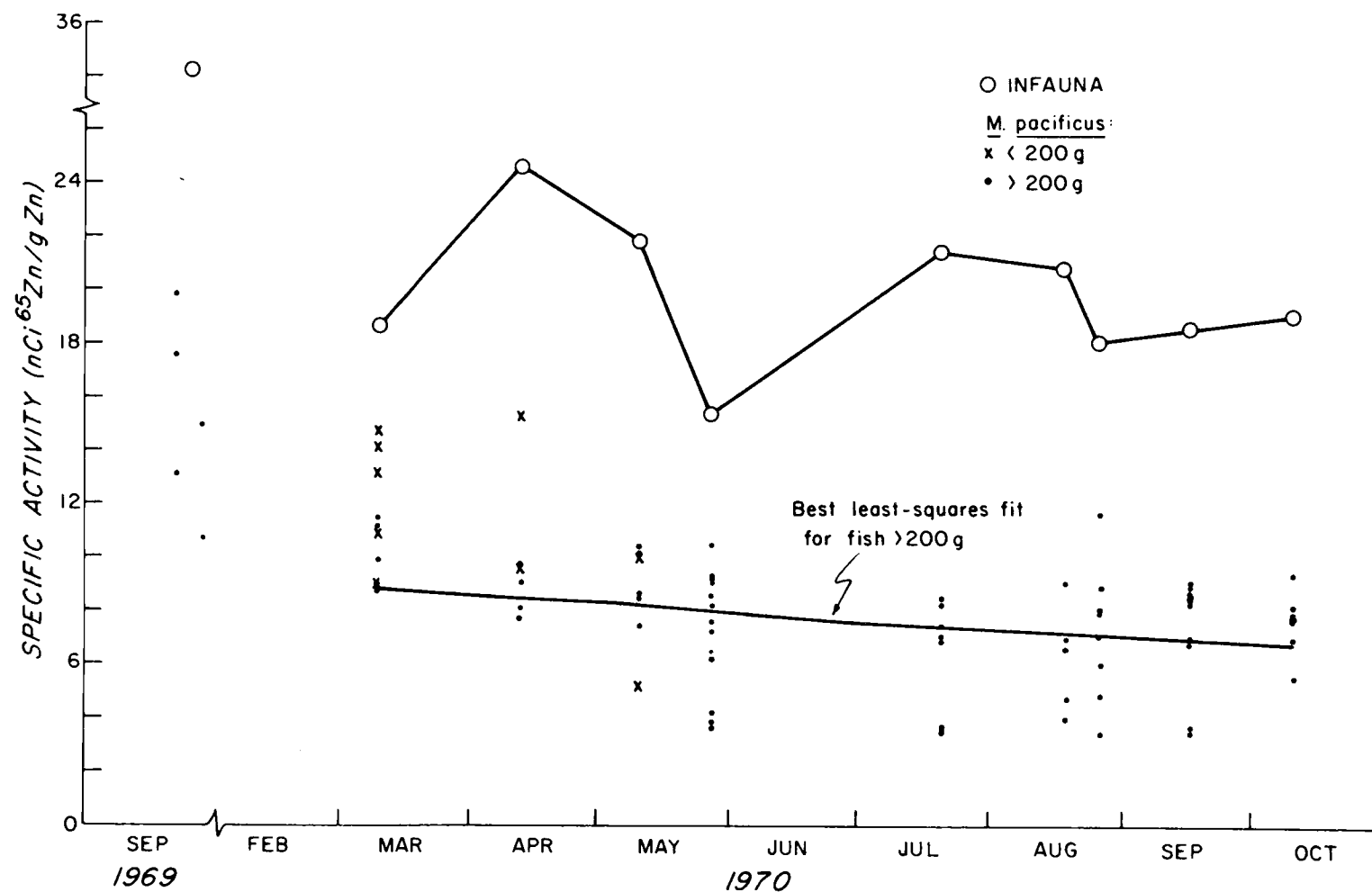


Figure 12. The best (unweighted) least squares fit to the specific activity data of Microstomus pacificus; $\alpha = 9.9 \times 10^{-4}/\text{day}$ for fish > 200 g.

Statistical analysis corroborated the removal of the fish smaller than 200 g (Overton, 1971). Regressions were also computed for all fish included and for the fish less than 200 g. Then, the sum of squares about the regressions (SSE's) were grouped into two sets: the first, the sum of the SSE for the fish > 200 g and the SSE for the fish < 200 g, and the second, the difference between the SSE of all fish and the first set. An F-test showed that the mean square of the difference set was significantly greater than the mean square of the first set SSE at the 1% level ($F = 7.13$; 2,75 df).

Figure 13 shows plots of the residuals of the regression: $S_{ij} - \hat{S}_i$, where S_{ij} and $\hat{S}_i$ are respectively the SA of the j th fish on the i th sampling date and the predicted SA on the i th sampling date. The frequency plot in Figure 13 indicates that a group of low residuals contribute to the skewness of the distribution. The time sequence plot indicates that these low residuals show up in the middle of the time sequence. Finally, the residuals do not increase with $\hat{S}_i$, which implies that a weighting scheme involving the inverse of $\hat{S}_i$ will not be helpful for getting better estimates of α .

An approximate idea of lack of fit was obtained by comparing the mean square of $SSE - S_{pe}$ with the mean square of S_{pe} , where S_{pe} is the sum of squares of pure error (Draper and Smith, 1966). Utilizing this test, $F(9,16) = 1.12$. By comparison, $F(9,61,0.95) = 2.04$, which suggests that the model does not fit badly.

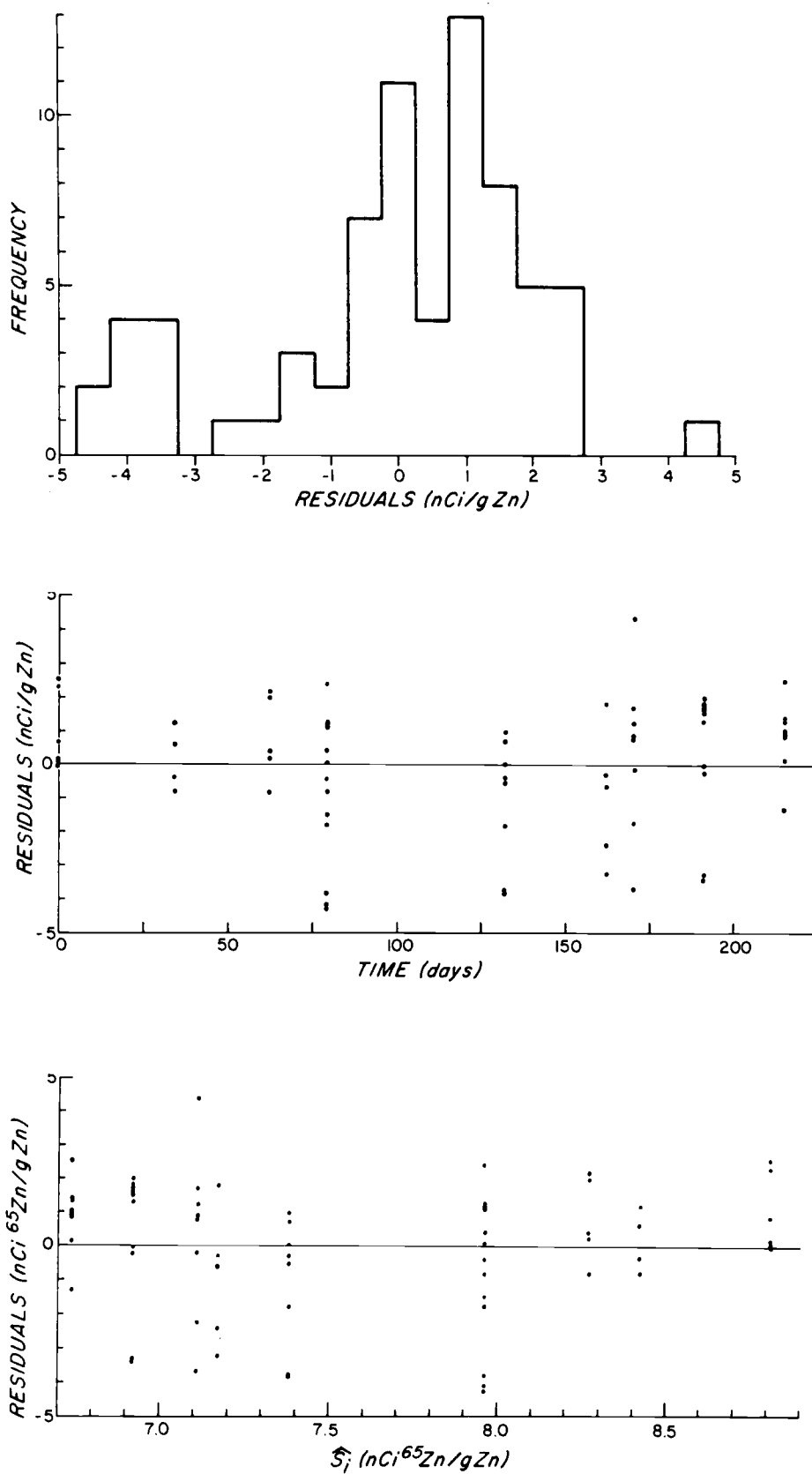


Figure 13. Residual plots for the *Microstomus pacificus* analysis.

Lyopsetta exilis. The large number of fish with stomach contents in the 120-140 mm and 140-160 mm length classes provided the best time series of S and $F(t)$; therefore, they were chosen for estimation of α .

The assumption that fish sampled on a given date are members of the population sampled earlier appears valid for these length classes of L. exilis. Converting standard lengths of L. exilis to total lengths by multiplication of the former by 1.22 and using the length-age curve for L. exilis (Demory, 1972) in Figure 11, an age range of roughly 2.8-3.8 and 3.8-5.0 years is obtained for the 120-140 mm and 140-160 mm length classes, respectively. Using Figure 9, these length ranges correspond to 17-28 g and 28-43 g weight ranges. Note that following each 20 mm length class is not exactly the same as following the trajectory of population growth at this time. Nevertheless, this problem is not felt to be significant because the fish in these length classes during the 15-month study period are not growing rapidly (Figure 11) or changing food habits (Table 1). The restricted depth range of L. exilis also contributes to the validity of the analyses. Although the Oregon Fish Commission has found the fish from 40 to 350 m, its maximum abundance is at 100 to 200 m (Demory, 1972).

Figures 14 and 15 show the SA's of the fish and $F(t)$ used to estimate α for the 120-140 mm and 140-160 mm length classes. Each figure shows the number of fish analyzed for each SA value. The applicability of fish numbers as weights for a weighted least squares analysis was in-

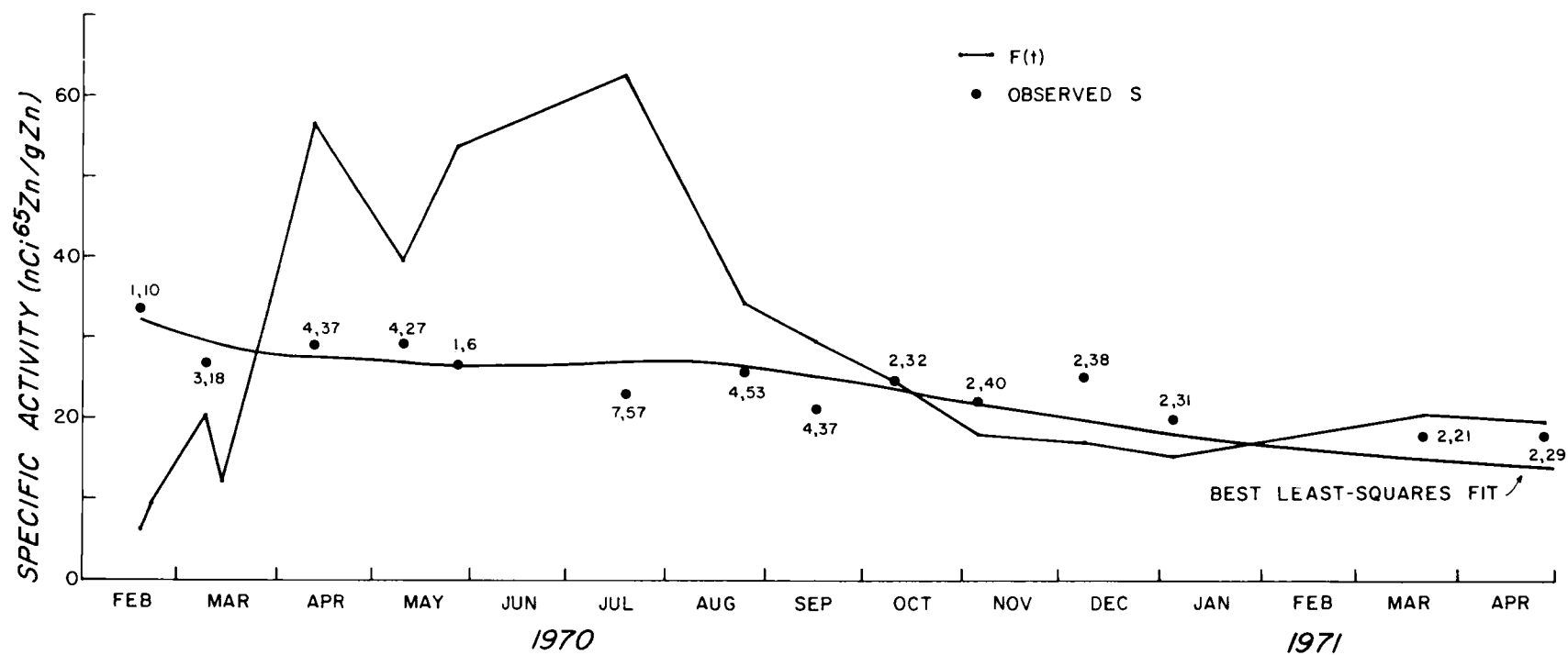


Figure 14. Best least-squares fit to the specific activities of the 120-140 mm length class of *Lyopsetta exilis*; $\alpha = 2.7 \times 10^{-3}/\text{day}$. The first and second numbers by the observed S's are numbers of samples analyzed and total numbers of fish analyzed, respectively.

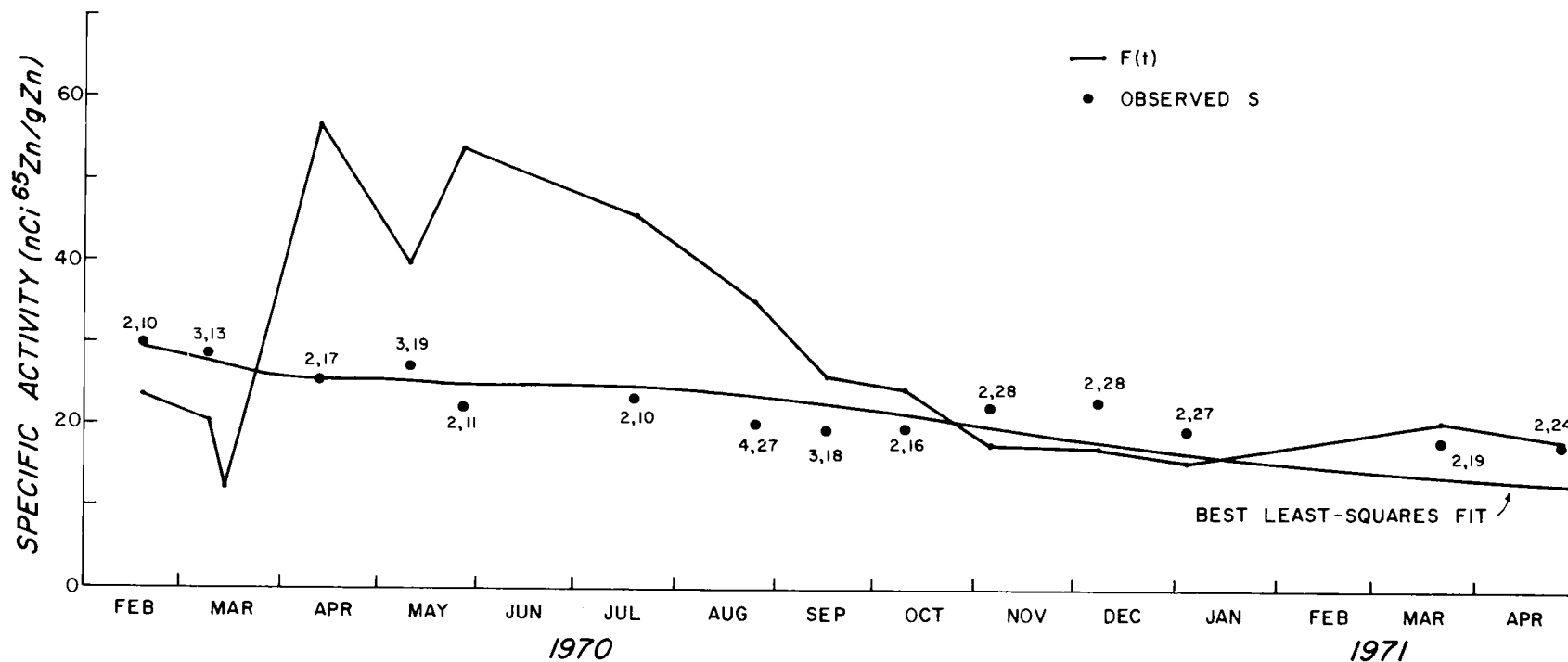


Figure 15. Best least-squares fit to the specific activities of the 140-160 mm length class of *Lyopsetta exilis*; $\alpha = 2.6 \times 10^{-3}/\text{day}$. The first and second numbers by the observed S's are numbers of samples analyzed and total numbers of fish analyzed, respectively.

vestigated. The least-squares method depends on minimizing the weighted sum of squares of the difference between the data, S_i , and the fitting function, $\hat{S}_i$. That is minimize

$$s^2 = \sum (S_i - \hat{S}_i)^2 / \sigma_i^2 ,$$

where σ_i is the standard deviation of S_i . Assuming the σ_i equal σ , a constant for all fish, then σ_c^2 , the variance of a composite sample or composite of the composites is σ^2/n_i , where n_i is the number of fish in the sample(s). Replacing σ_i by $\sigma/\sqrt{n_i}$ leads to

$$s^2 = \frac{1}{\sigma^2} \sum [n_i (S_i - \hat{S}_i)^2] , \quad \text{and}$$

since σ^2 is not known, the quantity minimized is

$$\sum [n_i (S_i - \hat{S}_i)^2] .$$

The applicability of this weighting depends on the magnitude of σ^2 and the n_i . The average percent standard deviation of the M. pacificus (> 200 g) analyzed was 23%. Assuming the same for L. exilis, weighting would not be useful beyond 16 fish, since the percent standard deviation would be reduced to less than 6%, which is about the limit of instrumental precision. Given the usually large number of fish per point in Figures 14 and 15, weighting would not be useful.

Before the α 's could be reported, the dilemma of the 10 May 70 data had to be resolved. A choice had to be made between the 10 May 70

$F(t)$ determined by measurement of stomach contents extracted from all fish and the estimates of each group based on $\Sigma SA_i \cdot \%_i / 100$ (see Table 1). For each length class, separate least-squares analyses were run using $F(t)$ with the 10 May 70 estimates based on measurement and $F(t)$ on $\Sigma SA_i \cdot \%_i / 100$. For both length groups the former $F(t)$ produced a slightly lower variance about the regression; therefore, the α 's were based on $F(t)$'s with the 10 May 70 value based on measurement. For the 120-140 mm group, $\alpha = 2.7 \times 10^{-3}/\text{day}$ (Figure 14); for the 140-160 mm group, $\alpha = 2.6 \times 10^{-3}/\text{day}$ (Figure 15).

Residual plots for the L. exilis data need not be made, as the trends in residuals can easily be seen in Figures 14 and 15. Both figures show more positive deviations than negative deviations, especially the 120-140 mm group. Negative residuals are seen in summer, whereas positive residuals are seen during fall and winter. The positive residuals in fall and, particularly, the fall increase in the S_i are surprising given the decreasing $F(t)$ during this period. Perhaps an assumption underlying the model is violated.

Discussion

Diet and SA of Fishes

Our perspective on the SA dynamics of the prey at NH-23 will be the same as the fishes', who have, hypothetically, an Eulerian view of their pelagic prey. The prey are transported by the prevailing currents into which they migrate. Since ^{65}Zn distribution is not uniform, the prey's ^{65}Zn intake is affected by its Lagrangian history. Thus, along with its trophic position, its migratory behavior and the prevailing current system are major factors in its ^{65}Zn dynamics.

The currents over Oregon's shelf are less than 25 cm/sec (Osterberg et al., 1964). The surface currents are the result of local wind stress superimposed upon the residual geostrophic current of 16 cm/sec to the south (Collins and Pattullo, 1970). At depths below 40 m, the near bottom currents on the shelf are northward during all seasons (Gross, Morse, and Barnes, 1969). Below the permanent pycnocline between 80-150 m, a 10 cm/sec poleward current was measured during the summer (Smith, Mooers, and Enfield, 1971).

As Osterberg et al. (1964) assert, vertical migration of E. pacifica would help to maintain the population off Oregon during the summer. At night E. pacifica feeding above the permanent pycnocline (Brinton, 1967) and possibly in the ^{65}Zn -rich Columbia River plume above the seasonal pycnocline (averaging about 20 m; Schonzeit, 1973) would be transported southward. During the day, they would be

below the permanent pycnocline (Brinton, 1967) and being transported northward. In this way they can accumulate ^{65}Zn and not be transported out of the area as rapidly as if they remained constantly at one level.

Osterberg et al. (1964) noted that ^{65}Zn did not fall to background levels during the winter. Figure 5 also shows this pattern. The lowest SA is about 6.5 nCi/g which is much higher than the background level of $10^{-2} - 10^1$ pCi/g (Alexander and Rowland, 1966; Wolfe, 1970). From this they hypothesized that (1) ^{65}Zn in E. pacifica has a long biological half-life, which was later confirmed by Fowler, Small, and Dean (1971) and (2) the euphausiids transported southward by net flow were returned during the winter. Unfortunately, the SA data cannot be used to separate decrease in SA caused by advection from that owing to turnover, as the SA of the prey of the euphausiids is not known.

Pandalus jordani, too, is a vertical migrator (Pearcy, 1970). This shrimp, particularly those individuals weighing less than 1.9 g⁷, frequently occurred in midwater trawls from August to April. Even if P. jordani ate primarily euphausiids, its SA plot would not result from consuming euphausiids with the SA shown in Figure 5.

In contrast to these elements of the pelagic food web, the infauna remains in place, concentrating ^{65}Zn from sediment or from the sediment surface. The ^{65}Zn , of course, has its origin in surface waters and is certainly transported to the sediment surface via particles or organisms. Because of the current regime above, the SA of the detrital food

⁷ Pearcy reported the length of shrimp caught; the weight-length data of Butler (1964) were used to convert length to weight.

web (infauna) does not necessarily owe its SA to particles in the surface waters directly above or necessarily reflect the SA of organisms in surface waters above.

At NH-23, both the SA of the major prey and the relationship between the SA of benthic fishes and their diets show that the pelagic food web is generally more important than the detrital food web (infauna) for conveying ^{65}Zn to the benthic fishes. The question arises as to whether the SA's of the representatives of Cyclostomes and of Chondrichthyes can be compared to those of Osteichthyes. Winberg (1956) concludes that the metabolic levels of these diverse taxa are very similar;⁸ therefore, all differences in SA among fishes in Table 2 are probably related to diet, size, and growth rate. That only the hagfish E. stouti had a lower SA than M. pacificus indicates that transfer of ^{65}Zn from the surface waters (not necessarily directly above) to infauna, then to M. pacificus, is the equivalent of passage through several trophic levels of the pelagic food web. As Pearcy and Vanderploeg (1972) have indicated, the importance of the pelagic food web for conveying ^{65}Zn to the benthic fishes rests in large measure on the vertical migration of its components which quickly transfers ^{65}Zn from the surface to the fishes on the bottom.

The inverse relationship between size and specific activity in some benthic fishes may result in part from the diet of the different size classes. In L. exilis, the SA of the prey of the smaller length

⁸ This is, certainly, approximately true; further discussion of this aspect is made below.

classes was higher for some months. The smaller fish, in selecting smaller prey, chose small crustacea, which happened to be of lower trophic level than the larger diet items. The importance of diet is also indicated by the more rapid decreases in SA of the smaller length classes, which follow from the more rapid decreases in their $F(t)$'s during and prior to the study period. From February to October 1970, the more rapid decreases exhibited by the smaller length classes can be explained only by more rapid decreases in their $F(t)$'s. During this period, when each $F(t) > S$, the larger α 's of the smaller classes would actually cause their SA's to decrease less rapidly in response to a given decrease in $F(t)$ than would the SA's of larger fish with smaller α 's in response to the same decrease in $F(t)$. This can be verified from equation (9). So long as $F(t) > S$, the term $\alpha(F(t) - S)$ increases dS/dt , whereas $-S\lambda$ decreases dS/dt . Therefore, the larger α is, the less rapid the decrease in S in response to a decrease in $F(t)$. During November-January, when $F(t) < S$, the larger α 's would also be accelerating the decrease of S in the smaller length classes.

The inverse relationship between SA and size was well developed in two other species. Again diet seems implicated. Small G. zachirus have a greater proportion of their diet composed of small crustacea than larger G. zachirus (Hancock, 1972). In X. latifrons, the smallest fish might be eating the smallest crustacea of lowest trophic level. Since small crustacea are the staple in diets of many young

fishes, it is likely that young fishes will often have high ^{65}Zn specific activities. The lack of a well-defined decrease in SA with increasing W in M. pacificus may result from larger fish somehow selecting prey of higher SA than smaller fish.

Before extrapolating these SA-trophic relations to other locations, we must remember that there may be some dependence of these relations on distance from the source of ^{65}Zn input. This is the subject of the next chapter.

Comparisons of α 's

Placing the fishes' weights, growth rates, and the temperature of their environment in equation (16) enables calculation of the theoretical α/K for M. pacificus and for each of the two length classes of L. exilis. By dividing the α/K of each length class of L. exilis by the α/K obtained for M. pacificus, the theoretical ratio of the α for each size group of L. exilis to the α of M. pacificus is obtained. These theoretical ratios then can be compared to the ratios of α 's determined from least-squares analysis. Off Oregon, at a depth of 200 m, temperature is nearly a constant 8°C , which by Krogh's curve implies $C_{8,20} = 0.29$ for both species. The median weight of M. pacificus (> 200 g) analyzed was 376 g, and Hagerman's (1952) data imply that $\frac{1}{W} \frac{\Delta W}{\Delta t} = 9.5 \times 10^{-4}$ for fish of this weight. Also, the dry to wet weight ratio, D , = 0.17. Using this information in equation (16), $\alpha/K = 8.4 \times 10^{-3}$ for M. pacificus. For L. exilis, the weight of each

size group was taken as the mean of the two weights corresponding to the limits of the length class. The mean weights were 22.5 and 35.5 g with corresponding $\frac{1}{W} \frac{\Delta W}{\Delta t}$ values of 1.3×10^{-3} and 9.6×10^{-4} , respectively, and $D = 0.21$. The α/K values obtained for the smaller and the larger size classes of L. exilis were 1.2×10^{-2} and 1.1×10^{-2} . Dividing the α/K values for the 120-140 mm and for the 140-160 mm L. exilis by the α/K of M. pacificus gives the theoretical ratios of α 's of 1.4 and 1.3, respectively. Since the respective ratios of α 's determined from field data are 2.7 and 2.6, the theory and results are open to question.

A clue to the source of the discrepancy is given by the relationship, $\alpha = \beta + \frac{1}{Z} \frac{dZ}{dt}$. Since $Z = kW$, $\alpha = \beta + \frac{1}{W} \frac{\Delta W}{\Delta t}$. For M. pacificus the calculated α of 9.9×10^{-4} is almost entirely explained by its specific growth rate, $\frac{1}{W} \frac{\Delta W}{\Delta t}$. In contrast to M. pacificus, the specific growth rates of L. exilis groups represent only modest percentages, 50% and 37% for the 120-140 mm and 140-160 mm groups, respectively. The literature available for ^{65}Zn retention in fishes (Renfro and Osterberg, 1969; Nakatani, 1966) would suggest β 's considerably larger than implied by the estimated α and the specific growth rate of M. pacificus. In particular, the β from Nakatani's long-term retention study on trout receiving a chronic dose of ^{65}Zn may be compared because the trout were in good health (witness their growth) and because the fish were roughly the same size as the M. pacificus--270 g at the beginning and 1760 g at the end of the experiment. From his effective half-life of 134 days for the long component of ^{65}Zn retention, $\beta > 2.3 \times 10^{-3}$. His fish were maintained between 11 and 22°C. Assuming this is roughly

equivalent to keeping them at the mean of these extremes, namely 16C, and assuming Krogh's curve applies to β , $\beta > 9.9 \times 10^{-4}$ at 8C. However, the trout were rapidly growing ($\frac{1}{W} \frac{\Delta W}{\Delta t} = 8.2 \times 10^{-3}$). Thus, to apply this β to M. pacificus, β must be independent of $\frac{1}{W} \frac{\Delta W}{\Delta t}$. Assuming independence, the estimated α for M. pacificus is therefore too low.

As a further test, the ratios of the α of the trout to the α of M. pacificus and to the α of each size class of L. exilis may be compared to the respective ratios of α/K 's. Before developing the comparison, it is necessary to consider further Winberg's relationships.

For Winberg's equation for routine metabolism, $Q = vW^\gamma$, I have used the general averages for all fish of 0.3 for v and of 0.8 for γ . Winberg found that γ was often very near 0.8 for most fish taxa. Almost all had γ 's between 0.71 and 0.81. In contrast, v was more variable. It is important here that for salmonids, $v = 0.5$, which is much larger than the 0.3 representing the average for both freshwater and marine fishes.

Several authors have examined Winberg's method and reported that the level of metabolism, v , is dependent on ration. Davis and Warren (1968) found that the metabolic requirements of trout on ad libitum rations was three to four times as high as for trout on maintenance rations. Also, Paloheimo and Dickie (1966) examined the data on Pentelov's trout (1939), Dawes' plaice (1930-31), and Gerking's bluegills (1955); and they found that the level of metabolism at ad libitum rations was 5, 4.5, and 4 times the level at maintenance rations, respectively. Mann (1965) compared the ration consumed by Pentelov's

trout to that predicted by Winberg's method. This comparison will be useful for calculating the α/K of Nakatani's trout. He made two estimates of food consumption. The first, called Winberg 1, assumed that total metabolism equals routine metabolism, as predicted by $Q = \nu W^Y$ with the parameters appropriate to salmonids. The second, called Winberg 2, assumed that total metabolism was twice routine metabolism. Krogh's curve was used to adjust for the effect of temperature. Actual food consumption at maintenance rations was a bit higher than predicted by Winberg 1. Winberg 2 described well the food consumption of fish on a constant ration above maintenance. For trout on ad libitum rations, the food consumed was higher than that predicted by Winberg 2. This last result is based on the food consumed by a single trout at two different weights. Winberg 2 was 94% and 71% of the rations consumed. It should be apparent now that Winberg's relations, because of dependence of metabolism on rations, are approximations. Nonetheless, since better relationships are lacking, the α/K of the trout will be calculated, and the ratios of α/K 's for trout and for the fishes in this study will be compared to the ratios of α 's.

The α/K of Nakatani's trout can be roughly approximated by assuming they weigh the same (376 g) and have the same dry weight to wet weight ratio (0.17) as M. pacificus. Also, since salmonids have a metabolism 5/3 times that of the average metabolism, A must be multiplied by 5/3. Thus, for Nakatani's trout, $\alpha/K = 3.84 \times 10^{-2}$ at 16C assuming total metabolism is twice that of routine metabolism. This α/K is 4.6, 3.2, and 3.6 times the respective α/K 's of M. pacificus

and of the smaller and larger length classes of L. exilis. Since Nakatani's trout exhibited rapid growth, their level of metabolism was probably at least twice the routine level. Their ration was described as 2-3% of body weight. The maximal ratios of α/K 's can be determined if they are divided by 0.71 to account for the greater difference between Winberg 2 and the ration Pentelov's trout consumed when rations were unrestricted. The maximal theoretical ratios are, respectively, 6.5, 4.5, and 5.1.

Based on Eberhardt and Nakatani's (1968) data, $\frac{1}{W} \frac{\Delta W}{\Delta t} = 8.2 \times 10^{-3}$ for the exponentially growing trout. Using this specific growth rate and using $\beta \cong 2.3 \times 10^{-3}$, $\alpha \cong 1.05 \times 10^{-2}$. The ratios of calculated α 's corresponding to the α/K 's above are 10.6, 3.9, and 4.0. Since the trout-L. exilis ratios of α 's fall between the ratios of α/K 's above, the α 's estimated for L. exilis are probably in the correct neighborhood. This analysis again suggests that the α estimated for M. pacificus is too low.

Examination of the data and residuals for M. pacificus tend to corroborate the hypothesis that its calculated α errs on the low side. First, compared to L. exilis, fewer fish extending over a shorter time period were analyzed. Second, onshore-offshore migration may have affected the estimate of α . If shoreward migration does not occur as a more or less simultaneous event during March, but instead occurs over an extended period during spring and summer, fish of lower specific activity will be moving into the population. The particularly low residuals seen in Figure 13 during the summer could represent late migrants. Given the $F(t)$ measured for fish at NH-23, these late mi-

grants, by lowering the SA of the population, will yield a low estimate of α . The higher SA's seen in September and October could possibly represent fish that were on their way back from depths shallower than 200 m.

The L. exilis results, too, must be viewed somewhat cautiously. The low residuals during summer followed by the unexpectedly high residuals in fall and winter, when S should be decreasing with $F(t)$, make it appear as if L. exilis, too, has an offshore-onshore migration. Because the longer time sequences of SA's for L. exilis covering 15 months (Figures 14 and 15) contain more cycles of high and low points, the estimates of α 's are less likely to be seriously biased.

The agreement between the trout-L. exilis α and α/K ratios offers tentative support for the α -model. Although the α of M. pacificus was lower than expected according to the model, the discrepancy can be explained by the bias in the M. pacificus data. Support for the α -model comes also from the fact that only a few assumptions are inherent in its construction. Given that Winberg's relations are generally correct, all that has been assumed is that (1) $\underline{a}$, the assimilation efficiency, is constant and (2) $k = cb$.

Tentatively, the α -model predicts roughly the effect of size and growth on α . Difficulties arise in evaluating the size of $AW^{-0.2}$ relative to $\frac{1}{W} \frac{\Delta W}{\Delta t}$ because the size of A might be open to question. However, when $\frac{1}{W} \frac{\Delta W}{\Delta t}$ is small relative to $AW^{-0.2}$, equation (20) may be used in place of equation (16), which eliminates the problem of the

relation between total and routine metabolism. In the present case, equation (20) would have predicted nearly the same α/K 's for L. exilis and M. pacificus and the same L. exilis-M. pacificus α/K ratios as did equation (16).

Problems may arise in using equation (20) if families of fish having very different v 's are compared. Above, it was seen that salmonids have a very much higher than average v . For marine fishes, not enough measurements of their respiration have been made to say how v may vary with family or even with higher taxonomic rank.

F(t) vs. Proximate Factors

Since $F(t)$ varies greatly among different prey, differences in diet explain much of the differences in ^{65}Zn SA among benthic fishes. Tentatively, the effect of proximate factors on SA of the fish can also be evaluated. The effect of size on α is given by equation (20). In turn, the hypothetical effect of the size of α on S can be easily seen from equation (10) for the equilibrium case. Assuming that the α of 2.6×10^{-3} for the 35.5 g L. exilis is correct, the α of a fish 10 times as large--a fish about the size of M. pacificus--would be 1.64×10^{-3} by applying equation (20). Placing these α 's (and the correct decay constant) in equation (10), S equals $0.48F$ and $0.37F$ for the smaller and larger fish, respectively. The former is 77% of the latter.

Since $\alpha > \frac{1}{W} \frac{\Delta W}{\Delta t}$, specific growth rate could be an important factor affecting α and hence S in very young fish. The effect of temperature was not important here, as all the fish were exposed to the same, constant temperature. Tentatively, although proximate factors at NH-23 may well have a significant effect on S through α , they appear of secondary importance to the ecological and oceanographic factors that have their ultimate effect on S through $F(t)$.

Energy Flow and Radionuclide Dynamics

This chapter has emphasized the use of Winberg's feeding relations to predict the size of α under different conditions. In turn, the converse proposition of using α calculated by the least-squares methods above to predict feeding rate deserves serious consideration. Ecologists have estimated food consumption rates from the α 's of radionuclides by assuming that the rate of input of the radionuclides is proportional to feeding rate (Kevern, 1966; Kolehmainen and Nelson, 1969; Reichle, 1969; O'Neil, 1971). Other workers determine α from β and change of body burden of the radionuclide. Their equations for estimating β , and hence α , which utilize only radioactivity data, apply only for a few special time series of radioactivity in the prey: the radioactivity in the prey must either be zero (the retention experiment), constant, or exponentially decreasing (O'Neil, 1971).

For larger, mobile animals, these restricted equations have forced the ecologist to determine α under the necessarily artificial condi-

tions imposed by the laboratory. Kevern (1966) and Kolehmainen and Nelson (1969) estimated the α 's of ^{137}Cs in fishes to determine the fishes feeding rates. Their estimates of α depended on the determination of β from laboratory retention experiments. Thus, these feeding rates must be viewed cautiously. In contrast, the basic model and gradient algorithm, which allow calculation of α from any time series of SA in the prey and fishes (except when both are zero), can be applied to free-living populations of fishes or other animals in environments having measurable quantities of appropriate radionuclides. Therefore, the basic model can be viewed as a potential breakthrough for studying energy flow in free-living populations. In the present study, feeding intensity, i.e., α/K , of Lyopsetta exilis might have been determined from α if laboratory experimentation had been done to determine K .

GEOGRAPHICAL PATTERNS OF ^{65}Zn SPECIFIC ACTIVITY IN BENTHIC FISHES AND THEIR PREY

introduction

This chapter will describe the geographical patterns of ^{65}Zn SA in benthic fishes and their prey and attempt to isolate the mechanisms responsible for these patterns. Specifically, patterns in different trophic levels, in sediment, and in water will be treated. The approach followed will be to examine the ^{65}Zn SA patterns in the prey first. Then, ^{65}Zn SA patterns in the prey and the fishes will be used to deduce the migratory habits of the fishes, which is requisite to a full understanding of their ^{65}Zn SA dynamics.

Results and Discussion

Geographical Patterns of ^{65}Zn Specific Activity in the Prey

To determine ^{65}Zn SA patterns in various trophic levels, a single series of collections was made on and over Washington and Oregon's continental shelf during June and July 1970. This period was chosen because the plume is well developed off Oregon at this time with a concomitantly high ^{65}Zn input. Figure 16 shows the sample locations, and Figure 17 shows salinity profiles along the salinity station transects. The 32 ‰ salinity contour is a conservative delimiter of plume water (Osterberg et al., 1964; Barnes and Gross, 1966). Using this delimiter, the large scale of the July plume is apparent. As reported by others (Osterberg et al., 1964; Barnes and Gross, 1966), the July

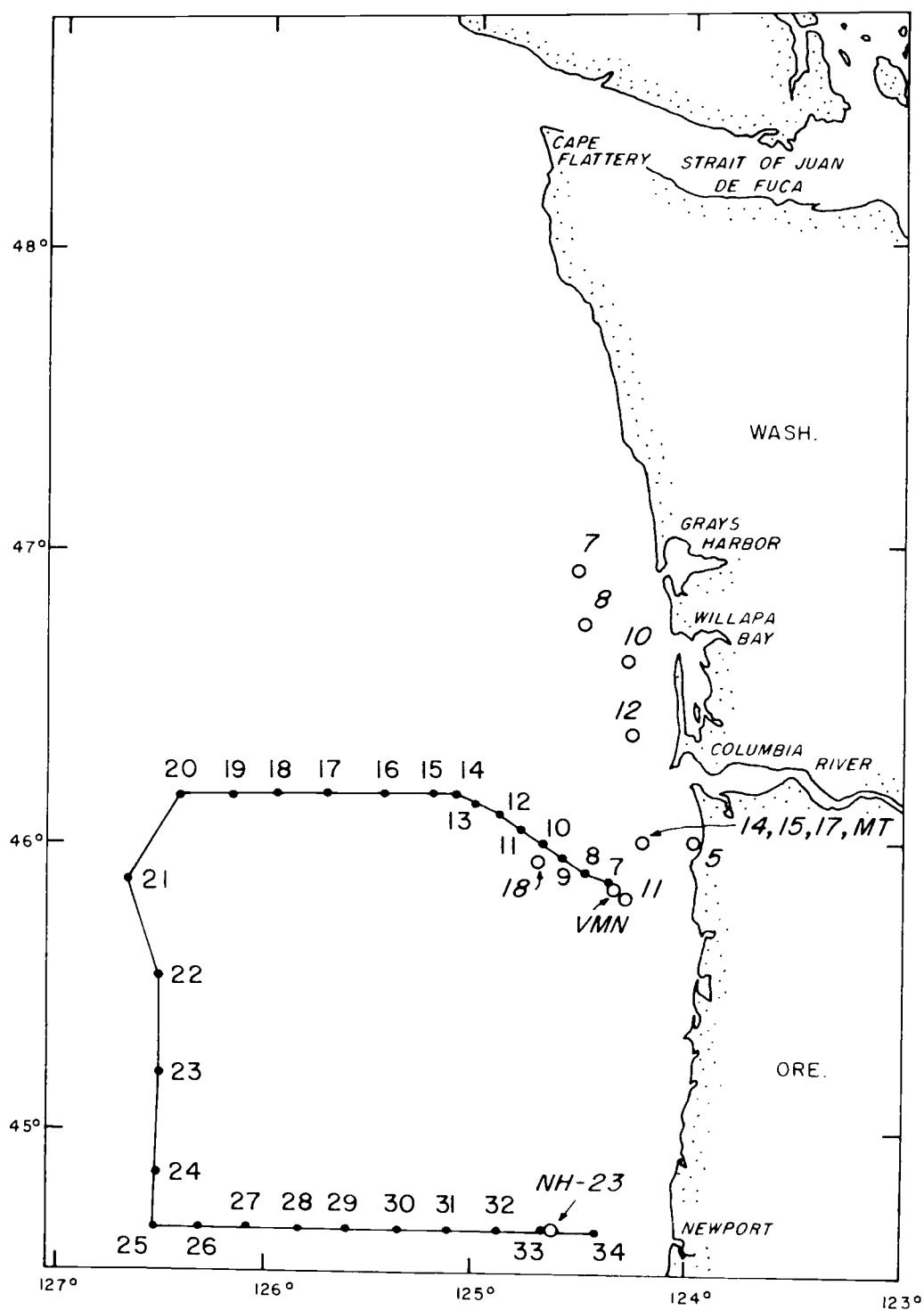


Figure 16. Sampling locations. The stations labeled VMN and MT are VMN and IKMT stations, respectively. Numbered open circles are locations of BCF trawls. Closed circles are stations where salinity casts were made (7-10 July 1970).

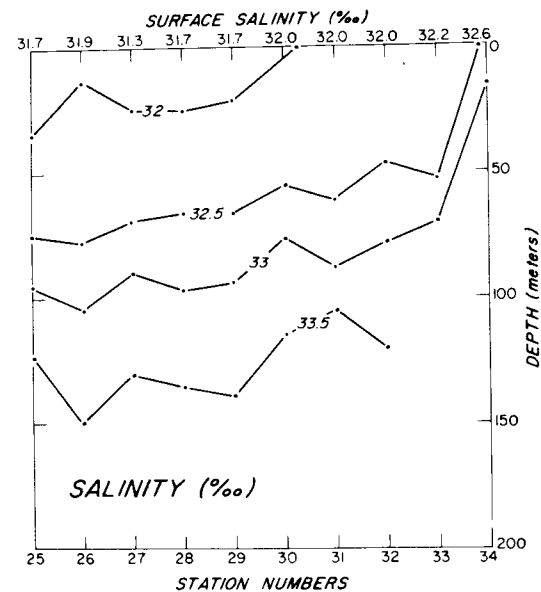
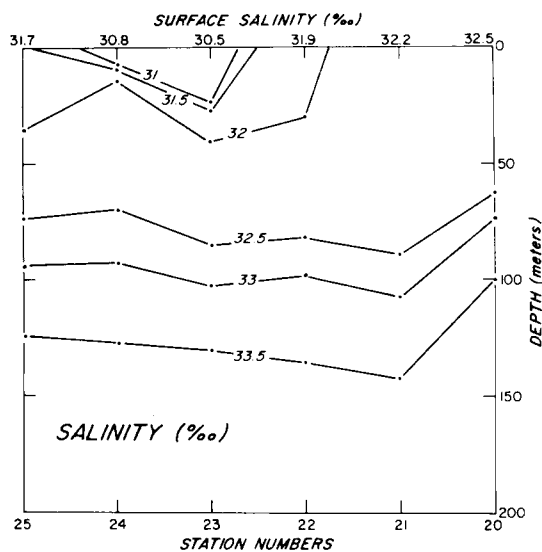
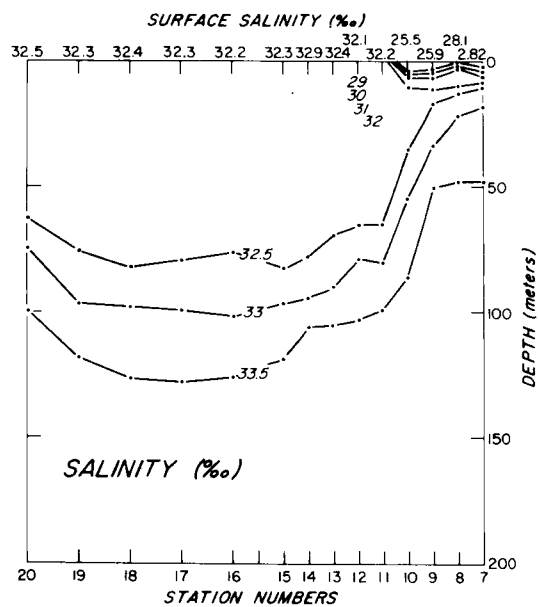


Figure 17. Salinity profiles (7-10 July 1970) along salinity station transects of Figure 16.

plume, a shallow feature limited to the upper 50 m, extends to the southwest from the Columbia River mouth. Zinc-65 specific activities of the prey collected in various sampling gear or from fish stomachs are shown in Table 5. It is assumed that the SA's of the prey are unaffected by their having been in the fishes' stomachs. The geographical pattern of ^{65}Zn SA in the pelagic food web will be examined first.

As expected, the herbivorous copepods, captured at the VMN station, had the highest ^{65}Zn specific activity of all organisms, 186 nCi/g. The next highest trophic level captured was the euphausiids. Enough collections of euphausiids were made to get a good picture of their spatial pattern of ^{65}Zn specific activity. At the two northernmost BCF stations, Stations 7 and 8, the lowest euphausiid ^{65}Zn specific activities of 26.2 and 24.9 nCi/g were observed, respectively. At Station 10, the specific activity increased to 45.4 nCi/g. At the MT station, the highest specific activity of 113 nCi/g was observed. Furthest downcurrent at NH-23, the level decreases to 69.5 nCi/g. Predictably, lowest values were north of the plume, and highest values, to the south in the area within, beneath, or near the plume. These results complement those of Osterberg et al. (1964), who observed higher ^{65}Zn concentrations in euphausiids off Newport than directly off the Columbia River mouth. The highest ^{65}Zn SA's occur in fact between these locations.

The following group of stomach contents is at most one trophic level higher than euphausiids: Engraulis mordax at Station 12, with a specific activity of 117 nCi/g; juvenile Sebastes sp. at Station 12,

Table 5. Spatial Patterns of ^{65}Zn Specific Activity in Benthic Fishes and Their Prey on the Continental Shelf, July 1970.

Taxa			Stomach Contents of Fishes				
Station, Date, Taxon	Total No. of Individuals	Number of Samples	Ave. Fresh Weight or Range (g)	Specific Activity (nCi ⁶⁵ Zn/g Zn)		Description	Specific Activity (nCi ⁶⁵ Zn/g Zn)
				Sample Mean	Std. Error		
VMN, 8 July 1970 Copepods	--	4	-----	186	5.25		
BCF Haul 5, 3 June 1970 Fishes: <u>Isopsetta isolepis</u>	5	2	174	64.7	5.02		
BCF Haul 7, 25 June 1970 Fishes: <u>Sebastes flavidus</u>	1	1	1687	12.6	----	Euphausiids	26.2 ¹
BCF Haul 8, 27 June 1970 Fishes: <u>Merluccius productus</u>	2	2	881-999	16.4	3.45	Euphausiids ²	24.9
BCF Haul 10, 28 June 1970 Fishes: <u>Glyptocephalus zachirus</u> <u>Merluccius productus</u>	5 2	1 2	83 807-1207	21.1 11.3	---- 0.31	Euphausiids ³	45.4
BCF Haul 11, 1 July 1970 Fishes: <u>Sebastes flavidus</u>	2	--	~1700	----	----	<u>Thaleichthys pacificus</u> , juvenile <u>Sebastes sp.</u>	72.9
BCF Haul 12, 3 July 1970 Fishes: <u>Atheresthes stomias</u> <u>Citharichthys sordidus</u> <u>Eopsetta jordani</u> <u>Glyptocephalus zachirus</u> <u>Lyopsetta exilis</u> <u>L. exilis</u> <u>L. exilis</u> <u>Merluccius productus</u> <u>Microstomus pacificus</u> <u>Oncorhynchus tshawytscha</u> <u>Ophiodon elongatus</u> <u>Parophrys vetulus</u>	1 9 3 7 5 6 4 3 23 15 1 4	1 2 3 3 1 1 1 3 13 -- 1 3	1347 70-92 224-288 124-267 52 82 125 931-962 42-318 910-3620 3724 90-275	9.25 31.0 37.2 54.0 53.7 51.5 40.7 23.2 51.9 ---- 24.2 74.0	---- 0.45 4.74 4.12 ---- ---- ---- 2.01 3.76 ---- ---- 7.19	Engraulis mordax ⁴ (northern anchovy) Ophiuroids, polychaetes, bivalves Juvenile <u>Sebastes sp.</u>	117 88.3 57.9
MT & BCF Hauls 14,15,17; 6-7 July 1970 Medusae	3	1	236	39.7	----		
Euphausiids	--	4	----	113	4.37		
Fishes: <u>Sebastes entomelas</u> <u>Sebastes flavidus</u> <u>Thaleichthys pacificus</u>	2 2 36	2 2 2	1202-1367 1338-1492 24	22.7 23.8 54.5	1.10 5.30 4.31	Euphausiids, juvenile <u>Sebastes sp.</u> , shrimp	72.7

BCF Haul 18, 10 July 1970

Fishes:

<u>Atheresthes stomias</u>	1	1	445	23.3	----
<u>A. stomias</u>	1	1	871	17.9	----
<u>A. stomias</u>	1	1	946	16.0	----
<u>A. stomias</u>	1	1	1288	9.50	----
<u>Glyptocephalus zachirus</u>	10	10	141-224	15.4	3.24
<u>Microstomus pacificus</u>	6	6	188-571	9.51	1.83
<u>Raja stellulata</u>	2	2	436-535	18.5	2.70
<u>Sebastes alascanus</u>	2	1	175	15.7	----
<u>S. alascanus</u>	2	1	290	12.2	----
<u>S. alascanus</u>	1	1	447	13.1	----
<u>S. alascanus</u>	1	1	808	8.16	----
<u>S. alascanus</u>	1	1	995	7.72	----

Polychaetes

32.8

Fishes, cephalopods,
Pandalus jordani⁵

24.1

NH-23, 19-22 July 1970

Euphausiids

	--	1	-----	69.6	----
Shrimp:					
Mixed Shrimp ⁶	69	1	0.37	31.7	----
<u>Pandalus jordani</u>	19	1	5.9	49.5	----
<u>P. jordani</u>	24	1	8.3	44.6	----

Fishes:⁷

<u>Asterotheca pentacantha</u>	17	2	18	21.8	3.07
<u>Atheresthes stomias</u>	2	2	391-561	28.5	0.16
<u>Eptatretus stouti</u>	8	1	106	5.76	----
<u>Glyptocephalus zachirus</u>	3	3	136-203	8.90	1.10
<u>Lypsetta exilis</u>	4	1	49	17.7	----
<u>L. exilis</u>	2	1	81	10.8	----
<u>L. exilis</u>	1	1	122	15.4	----
<u>Microstomus pacificus</u>	21	21	220-711	6.60	0.46
<u>Sebastes alascanus</u>	4	1	214	14.3	----
<u>S. alascanus</u>	1	1	553	12.3	----
<u>Xenopyxis latifrons</u>	4	1	17	10.8	----

Euphausiids, polychaetes, fishes⁸

31.5

Polychaetes, ophiuroids
Large Pandalus jordani,
cephalopod, fish⁹

21.3

34.7

¹ Measurement based on euphausiids taken from eight Merluccius productus stomachs at this station.

² Contents taken from eight stomachs.

³ Contents taken from 10 stomachs.

⁴ Contents taken from 14 stomachs.

⁵ Contents taken from seven stomachs.

⁶ Pandalus jordani, Crangon communis, Spirontocaris bispinosa.

⁷ Fishes are from both the 19-22 July and the 25-26 August collections. Stomach contents are from the 19-22 July collection.

⁸ Stomach contents based on the 160-194 mm length class shown in Table 1.

⁹ 57.4% large Pandalus jordani, 17.5% cephalopod, and 13.4% Lycodopsis pacifica, a small fish that eats infauna (Clemmens and Wilby, 1961); SA of stomach contents is based on $ESA_i \cdot \% / 100$, where the SA_i of the cephalopod and L. pacifica were assumed equal to the SA of infauna.

with a specific activity of 57.9 nCi/g; euphausiids, juvenile Sebastes sp., and shrimp at Stations 14-17, with a specific activity of 72.7 nCi/g; and Thaleichthys pacificus and juvenile Sebastes sp. at Station 11, with a specific activity of 72.9 nCi/g. Engraulis mordax eats primarily plankton less than one mm in length (Baxter, 1967). Juvenile Sebastes sp. probably eats planktonic crustaceans (Paraketsov, 1963). Both the euphausiids and these stomach contents show high ^{65}Zn SA's near the river mouth, whether directly north or south of it. This agrees with the results of Seymour and Lewis (1964), who observed the highest ^{65}Zn concentrations in mixed plankton in this region during the summer (see Table 6). High ^{65}Zn SA's north of the river mouth during July result either from recent ^{65}Zn input into this region or from residual ^{65}Zn remaining from the pelagic prey's winter or spring accumulation of ^{65}Zn over the continental shelf off Washington. This latter explanation is plausible in view of the especially high ^{65}Zn concentrations that Seymour and Lewis observed in mixed plankton over Washington's continental shelf during winter and spring and in view of the probable vertical migration of these pelagic components, which would prevent them from being transported too quickly southward with the drift of the surface currents during summer.

Table 5 also shows the spatial distribution of specific activity in infauna taken from the guts of Microstomus pacificus. At NH-23 the specific activity of 21.3 nCi/g for the infauna is much lower than the 69.5 nCi/g of the euphausiids. Also, the infauna SA is lower than the SA of the Sebastolobus alascanus prey, 34.7 nCi/g, and is also lower than that of the large L. exilis, 31.5 nCi/g. At Station 18, the in-

Table 6. Seasonal ^{65}Zn Concentrations (pCi per gram dry weight) in Mixed Plankton over Washington and Oregon's Continental Shelf, 1961-1963 (Seymour and Lewis, 1964).

	Winter	Spring	Summer	Fall	Total
Washington (46°20' - 48°15')	200	160	29	19	408
Central Shelf (45°55' - 46°20')	130	200	110	36	476
Oregon (44°00' - 45°55')	62	160	69	41	332

fauna SA of 32.8 nCi/g is higher than that of 24.1 nCi/g for S. alascanus stomach contents. At Station 12, the 88.3 nCi/g of the infauna is not quite as high as the 117 nCi/g of the low trophic level Engraulis mordax but is higher than the 57.9 nCi/g of the low trophic level Sebastes sp.. These results indicate that the difference in SA between low trophic level pelagic prey and infauna is small near the ^{65}Zn input but increases with distance away from the input. However, this picture may be somewhat distorted by the shallow 100-m depth of Station 12, compared with the 200-m depth of the other stations where infauna was collected, because, as already mentioned, ^{65}Zn SA generally decreases with depth (Carey, 1969; Carey and Cutshall, 1972).

Infauna and Sediment

Figure 18 shows the specific activities of the infauna obtained from fish guts superimposed upon the sediment specific activity data of Cutshall et al. (1971). Specific activities of the sediment were obtained from ^{65}Zn and stable Zn leached with CuSO_4 from the upper cm of sediment taken in a Smith-McIntyre bottom grab. The SA's of the infauna at the two southern stations are higher than the SA's of the sediment. The ^{65}Zn SA of the infauna at Station 12 is about the same as the sediment. Sediment SA's outside of the 10 nCi/g contour fall very rapidly and are less than 3 nCi/g at Newport (Cutshall et al., 1971).

Carey and Cutshall (1972) compared SA's of mixed epibenthic fauna with the SA's of the sediment. They found the SA's of epibenthic invertebrates were often higher than the SA's of the sediment. The

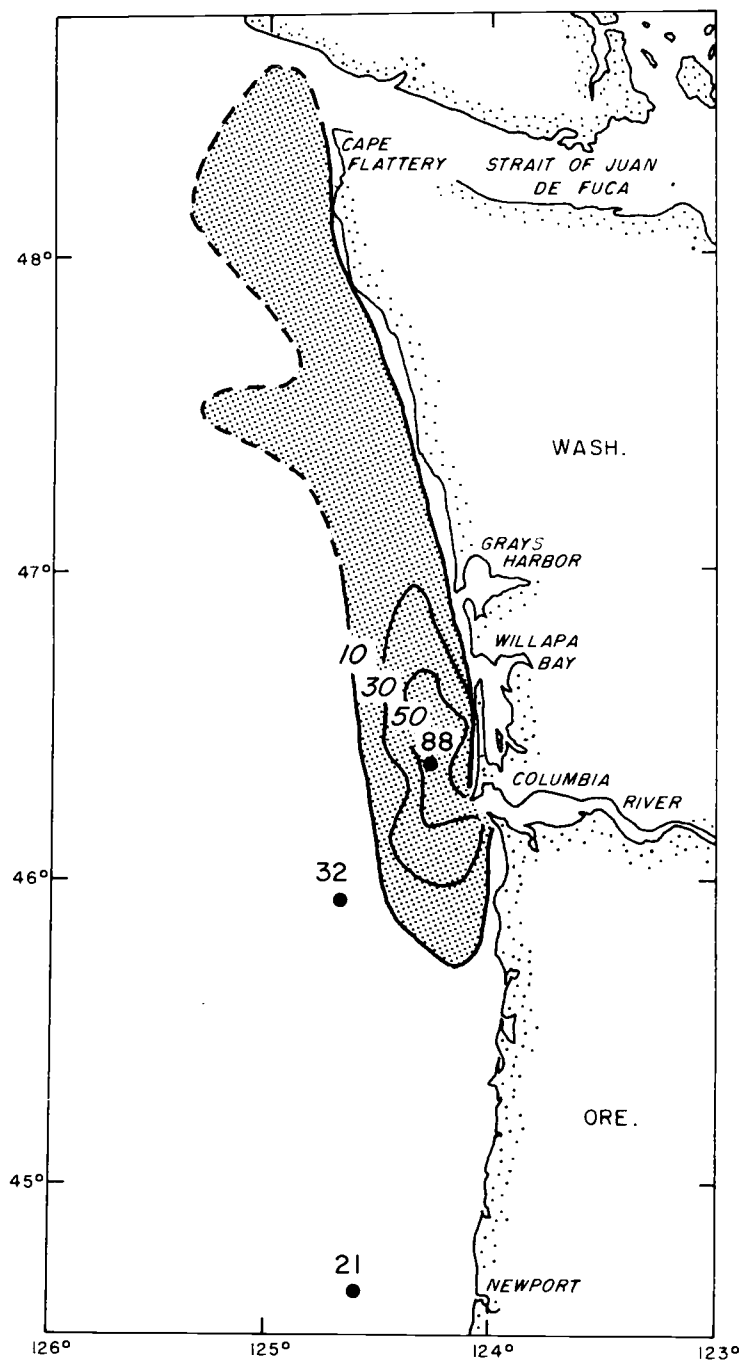


Figure 18. Zinc-65 specific activities of infauna (Table 5) superimposed upon isopleths of ^{65}Zn specific activities (nCi/g) for upper cm of sediment (Cutshall *et al.*, 1971). Sediment was collected in January, March, and December 1970.

higher SA's for infauna may result in part from their feeding on material at the sediment surface, which contains freshly deposited ^{65}Zn . In contrast, the deeper sediment taken from the grab contains a larger proportion of stable zinc, thus diluting the ^{65}Zn with stable Zn to give a lower SA for the sediment than for the infauna. On the basis of the mismatch between faunal and sediment SA's, Carey and Cutshall (1972) asserted that some source of ^{65}Zn other than the sedimentary source reaches the benthic fauna. They hypothesized that the detrital food web may be the primary pathway of ^{65}Zn to the benthic fauna. Interestingly, Carey and Cutshall observed nearly mirror image decreases in SA in the epibenthic fauna with increasing distance north and south of the Columbia River mouth along three transects of different depth.⁹ This pattern for the animals of course contrasts with the sediment patterns in Figure 18, in which SA is high in sediment north of the river mouth and low south of it. In fact, sediment SA's north of the river mouth were sometimes higher than SA's of the epibenthic fauna.¹⁰ The higher SA in the sediment to the north of the river may follow from the longer duration of the northward-flowing surface currents during the fall, winter, and early spring months and from the northward flow of water near the bottom that is probably common throughout the year (Carey and Cutshall, 1972). Another explanation is that

⁹ Sediment was sampled from January-March 1970. Invertebrates described here were sampled from December 1970-October 1971. The last reactor was shut down January 1971 (Figure 4).

¹⁰ These observations were based not only on sediment and invertebrates described in the preceding footnote, but also on other collections when invertebrates and sediment were sampled simultaneously.

the winter plume is restricted to Washington's continental shelf, whereas the summer plume overlies Oregon's continental slope and abyssal plain as well (Cutshall, 1972; see Figure 17). Thus, the winter plume off Washington drops a greater proportion of its high SA particles on the shelf than does the summer plume off Oregon.

The equally high ^{65}Zn SA's in epibenthic fauna south of the Columbia River mouth may be explained as follows. First, organic detritus rather than a sedimentary input of ^{65}Zn must be responsible. Second, the mechanism behind this pattern should be consistent with Table 6, which suggests that the average ^{65}Zn concentration in mixed plankton over Washington's continental shelf is higher than the ^{65}Zn concentration in plankton over Oregon's continental shelf. This, in turn, suggests a higher ^{65}Zn SA for organic detritus over Washington's continental shelf. The mechanism hypothesized is the coincidence of high primary production in summer (Small, Curl, and Glooschenko, 1972) with the presence of the Columbia River plume off Oregon. Increased primary production implies an increased production of organic detritus, which, in turn, may imply a greater flux of ^{65}Zn -bearing detritus to the detritus feeders on Oregon's continental shelf. Upon reaching the bottom, these particles enter a compartment composed of Zn from detritus and from sediment. This compartment is the "prey" of the infauna. Increased primary production may imply a greater α for the compartment and hence a greater ^{65}Zn SA for the compartment and its predators, the infauna. Perhaps the increased α of the sediment-detritus compartment on Oregon's continental shelf compensates for the possibly

lower ^{65}Zn SA of incoming detrital material suggested by the plankton data. The ^{65}Zn transport mechanisms necessary for this production mechanism to operate will be discussed below. The difference between ^{65}Zn SA's of organic detritus reaching the Oregon shelf and that reaching the Washington shelf could be small despite the zooplankton data, which would obviate the need for this mechanism; or the current regime may be such in winter over Washington's continental shelf as to prevent deposition of organic detritus, but not prevent deposition of possibly higher specific gravity inorganic particles.

Vertical Transport of ^{65}Zn

Carey (1972) calculated that the change in mean ^{65}Zn specific activity between detrital-feeding holothuroids on the upper continental shelf and on the abyssal plain was equivalent to 3.6 half-lives or 2.4 years. This implies an apparent vertical transport rate for ^{65}Zn of 100 m per month. Assuming this rate applies to organic detritus, it implies that the extra ^{65}Zn associated with organic matter during the summer will settle out on Oregon's shelf before the surface currents change with the onset of fall and winter circulation. The actual rate of zinc transfer is at least this fast. Particles in transit possibly would be exchanging ^{65}Zn for stable Zn, thus decreasing their specific activities.

A major mode of vertical Zn transport to the infauna could be fecal pellets and to a lesser degree moults and carcasses. Lowman, Rice, and Richards (1971) reviewed the role of zooplankton in vertical

transport of radionuclides. First, their calculations indicated that for biological vertical transport, the sinking of fecal pellets, moults, and dead zooplankton combined makes up approximately 90% of the total biological transport. Vertical migration accounted for the small fraction remaining. Second, they concluded that this organic detritus can profoundly affect vertical transport of Zn in coastal areas and especially in upwelling areas, where standing stocks of zooplankton are high. This would apply to Oregon coastal waters, which are in an upwelling area. Johannes and Satomi (1966) concluded that the egestion of organic matter in the feces of marine herbivores equals 20% of the organic matter consumed, which exceeds the net production growth of the herbivores themselves. They concluded that fecal pellets constitute a large potential source of food for marine organisms. High rates of fecal pellet sinking, namely 43 m per day, were reported for the fecal pellets of E. pacifica feeding on diatoms in the laboratory (Osterberg et al., 1963). Recently, Fowler and Small (1972) determined that fecal pellets from freshly collected euphausiids sink at the very high rate of 126-862 m/day. The difference is attributed to the natural food of the freshly collected euphausiids. Furthermore, Small, Fowler, and Kečkeš (1972) reported that more than 90% of the input of zinc in the food of euphausiid Meganycitiphanes norvegica appears in fecal pellets. Low assimilation efficiency of Zn is largely responsible for this high defecation rate of Zn. For this mechanism to be effective in transporting Zn to the ocean bottom, the Zn must stay with the fecal pellet during its descent (Lowman, Rice, and Richards, 1971).

Given the high rate of production of fecal pellets and the low assimilation efficiency of Zn, fecal pellets may rapidly convey ^{65}Zn to benthic fauna, assuming that ^{65}Zn stays with the fecal pellet. Small and Fowler (In preparation) report that the fraction of Zn lost from the fecal pellets of M. norvegica in time equivalent to descents of 500 m and 2500 m was 40% and 91%, respectively. This result may explain some conflicting results of Osterberg et al. (1963). They found nearly similar concentrations of ^{95}Zr - ^{95}Nb in holothuroids from 200-m and 2800-m depths off Oregon. Calculations based on radioactive decay indicated a 7-12 day transit time to explain the observed difference, which falls within the range of sinking rates of euphausiid fecal pellets determined by Fowler and Small (1972). In contrast, much lower ^{65}Zn concentrations were found in the 2800-m holothuroids than in the 200-m holothuroids, suggesting to Osterberg et al. (1963) that Zn was not readily excreted or that Zn was lost from the fecal pellet during descent. Small and Fowler's fecal pellet retention study corroborates this latter explanation. However, average sinking rates of the fecal pellets of all herbivores combined and hence ^{65}Zn transport rates downwards may not be this rapid because the biomass of copepods, which produce smaller and less compact fecal pellets than euphausiids (Small, 1972), is generally higher than euphausiids off Oregon (Schonzeit, 1973).

Processes Affecting Distributions of ^{65}Zn Specific Activity

Assuming certain of the above mechanisms for ^{65}Zn transport and other from the literature, the spatial patterns of ^{65}Zn SA in the food webs may be tentatively explained. The soluble ^{65}Zn or some part of it as it mixes with sea water is available for probably rapid (Bowen et al., 1971) uptake by phytoplankton and other small particles.¹¹ A fraction of the ^{65}Zn enters as suspended particulate material. A portion of the suspended particulate ^{65}Zn desorbs (Evans and Cutshall, 1972) and is possibly available for sorption to particles of marine origin. Within the head end of the plume, rates of ^{65}Zn sorption or uptake by the particles and their "biomass" will determine how much ^{65}Zn remains in solution. The herbivorous zooplankton feeding on the particles transform them into fecal pellets, which removes some ^{65}Zn from the plume. In the head end of the plume near the mouth of the Columbia River, the high SA particles, both fecal pellets and sediment, are delivered to the continental shelf. Possibly, the infauna select fecal pellet Zn in preference to Zn bound to more inorganic particles. At some distance downcurrent, the flux of ^{65}Zn to the bottom decreases because of the removal of ^{65}Zn by biological processes and sedimentation and because dilution of plume water with sea water downcurrent implies a lower SA for the particulate material settling out as well as for that consumed by the herbivores. With distance downcurrent, SA in the

¹¹ Soluble Zn is that fraction which passes through 0.45 μ pore-size filter.

pelagic food web would decrease less rapidly relative to the infauna owing to its transport by the current system. The patterns of ^{65}Zn SA in the pelagic and benthic food webs shown in Table 5 are in general agreement with these hypothesized mechanisms. This exercise has indicated a number of processes for which we have no estimates of rates. Thus, a dynamical description of this complex system is not possible at this time.

Owing to the central role of phytoplankton in the introduction of ^{65}Zn into both pelagic and detrital food webs, the study of factors affecting their uptake of Zn must receive the highest priority. Experiments by Bernhardt and Zattera (1969) demonstrated that ^{65}Zn is not necessarily accumulated at the same rate as its stable isotope if they are in different physico-chemical forms. Piro et al. (1972), reported that the physico-chemical form of Zn added to sea water will affect its distribution among complexed, ionic, and particulate fractions. They found that adding ionic Zn to sea water increases the concentration of ionic and particulate Zn fractions, while the concentration of the complexed fraction remains constant. On the other hand, with the addition of complexed ^{65}Zn , ^{65}Zn became distributed among all fractions in the same proportion as the stable element. These results suggest that the ^{65}Zn SA that is available for sorption to phytoplankton or other particles is not necessarily the same as the ^{65}Zn SA measured for a given volume of sea water. Evidence for the occurrence of this phenomenon in the Columbia River plume is seen in

Table 7, which shows the results of analyses for ^{65}Zn SA in surface samples of sea water at the VMN station. The difference in mean ^{65}Zn concentrations between the filtered and unfiltered samples is highly significant ($P < 0.01$). This difference could result from incomplete coprecipitation of the particulate phase in the unfiltered samples or from the ship's drift in a possibly high ^{65}Zn gradient during the 1.5-hour sampling period. The ^{65}Zn SA of the water is about one order of magnitude lower than that of the copepods caught at the same station and also lower than that of nearly all fauna in Table 5. This is especially surprising because the VMN station is located near the head of the plume, where ^{65}Zn specific activity should be high. Part of the difference could be explained by the copepods retention of ^{65}Zn from the winter before, when reactor output was double that of July (Figure 4). However, physical decay, turnover, and advection should have diminished this possible source of bias.

Geographical Patterns of ^{65}Zn Specific Activity in Benthic Fishes

In Table 5, the different species of benthic fishes found at different stations is, in part, related to different depths of capture and sediment types. Much of the difference in species composition between NH-23 and the BCF stations is explained by the use at the BCF stations of the pelagic trawl, which captures a greater proportion of larger, more mobile fishes than the otter trawl used at NH-23. Also, fishes having more pelagic habits, such as Merluccius productus, were captured by positioning the pelagic trawl into scattering layers with the aid of a depth-telemetry system. Although differences in species com-

Table 7. Zinc-65 Specific Activity of Surface Seawater at the VMN Station, 7 July 1970.¹

Sample	pCi ⁶⁵ Zn/l uncorrected ²	pCi ⁶⁵ Zn/l corrected ³	Total Zn Concentration (ppb) ⁴	nCi ⁶⁵ Zn/g Zn uncorrected	nCi ⁶⁵ Zn/g Zn corrected
Unfiltered #1	0.126 ± 9.31%	0.173	8.15	15.5	21.2
Unfiltered #2	0.111 ± 10.5%	0.152	8.89	12.5	17.1
Filtered #1:					
soluble ⁵	0.0865 ± 13.5%	0.119	14.5	5.97	8.21
particulate	0.109 ± 5.81%	0.109	----	----	----
Sum		0.228			
Filtered #2:					
soluble	0.0958 ± 8.05%	0.132	8.91	10.8	14.8
particulate	0.0776 ± 17.7%	0.0776	----	----	----
Sum		0.220			

¹ From Vanderploeg and Pearcy (In preparation).

² Large volume (200 l) coprecipitation with Fe(OH)₃.

³ 73% extraction efficiency based on extraction of ionic ⁶⁵Zn added to seawater.

⁴ APDC extraction. Analysis by atomic absorption spectrophotometry using method of additions.

⁵ Fraction passing through 0.45 μ pore-size filter.

position exist among many stations, the fishes may be grouped by feeding habits, and members of the same group should have approximately the same SA's, assuming no migration. This would appear to be reasonable in view of the small effect of proximate factors on ^{65}Zn SA suggested by the last chapter. Table 8 shows the feeding habits of benthic fishes in Table 5. In Table 9, the fishes are grouped by trophic position.

The fishes at a given location integrate the time history of ^{65}Zn SA in their prey. Under conditions of constant or quasi-constant ^{65}Zn input, the cycle of ^{65}Zn SA of the prey at a given location integrated over the year and divided by the number of samples provides an estimate of "average" ^{65}Zn specific activity available to the fish from its prey at that location. As a corollary, if these integrated prey specific activities are plotted for different locations on the continental shelf, the result is a pattern of ^{65}Zn specific activities that is roughly proportional to the ^{65}Zn specific activities in the fish. Deviations between the pattern of integrated SA's of the prey and the pattern of its benthic fish predator would imply migration of the fish, assuming that proximate factors are unimportant.¹² Unusually different SA values for members of the same feeding group would also imply migration. Thus, the information from Table 5 should allow us to deduce the migratory behavior of some of the fishes. Since the migratory habits of some of them are already known, these fishes will serve as a check on the

¹² The validity of this method depends on the sizes of α and λ . If α or λ is very large--which is not the case here--, marked seasonal SA patterns would appear in response to seasonal patterns of ^{65}Zn SA in their prey.

Table 8. Feeding Habits of Benthic Fishes ¹

<u>Fishes</u>	<u>Feeding Habits</u>
<u>Asterotheca pentacantha</u>	Small crustacea
<u>Atheresthes stomias</u>	<u>Pandalus jordani</u> , euphausiids, fishes
<u>Citharichthys sordidus</u>	Euphausiids, shrimps, amphipods, crab larvae
<u>Eopsetta jordani</u>	Shrimps, pelagic fishes, euphausiids
<u>Eptatretus stouti</u>	Large fishes
<u>Glyptocephalus zachirus</u>	Polychaetes, amphipods
<u>Isopsetta isolepis</u>	Gastropods, polychaetes, pelecypods
<u>Lyopsetta exilis</u>	<u>Pandalus jordani</u> (small), euphausiids
<u>Merluccius productus</u>	Euphausiids, pelagic fishes, <u>Pandalus jordani</u> ²
<u>Microstomus pacificus</u>	Polychaetes, ophiuroids
<u>Ophiodon elongatus</u>	Pelagic and benthic fishes ³
<u>Parophrys vetulus</u>	Polychaetes, amphipods, pelecypods
<u>Raja stellulata</u>	Crustacea, benthic fishes, cephalopods
<u>Sebastes entomelas</u>	Pelagic fishes, euphausiids? ⁴
<u>Sebastes flavidus</u>	Pelagic fishes, euphausiids ⁵
<u>Sebastolobus alascanus</u>	Fishes, <u>Pandalus jordani</u> , cephalopods
<u>Thaleichthys pacificus</u>	Euphausiids
<u>Xenopyxis latifrons</u>	Small crustacea

¹ The feeding habits without annotation are taken from Table 3 or from Percy and Vanderploeg (1972).

² Based on 54 stomachs; Alverson and Larkins (1969) and Gotshall (1969) reported a similar diet.

³ According to Phillips (1959) and Clemmens and Wilby (1961).

⁴ One fish; Pereyra, Percy, and Carvey (1969) reported a similar diet for four fish.

⁵ Seven fish; Pereyra et al. (1969) reported a similar diet for 22 fish.

Table 9. Feeding Groups of Benthic Fishes

<u>Feeding Groups</u>	<u>Description of Feeding Habits</u>
Group I <u>Thaleichthys pacificus</u>	Pelagic crustacea of low trophic level
Group II <u>Asterotheca pentacantha</u> <u>Citharichthys sordidus</u> <u>Lyopsetta exilis</u> <u>Merluccius productus</u> <u>Xenopyxis latifrons</u>	Mostly pelagic organisms of low trophic level
Group III <u>Atheresthes stomias</u> <u>Eopsetta jordani</u> <u>Raja stellulata</u> <u>Sebastes entomelas</u> <u>Sebastes flavidus</u> <u>Sebastolobus alascanus</u>	Pelagic organisms of medium trophic level or combination of benthic and pelagic organisms
Group IV <u>Ophiodon elongatus</u>	Pelagic and benthic fishes
Group V <u>Glyptocephalus zachirus</u> <u>Isopsetta isolepis</u> <u>Microstomus pacificus</u> <u>Parophrys vetulus</u>	Infauna
Group VI <u>Eptatretus stouti</u>	Large fishes

method. In the previous chapter, in order to calculate the α of Lyopsetta exilis, we assumed that it did not migrate. These geographical data may help to assess the validity of this assumption. Also, before the effect of geography on the relative importance of the detrital and pelagic food webs in conveying ^{65}Zn SA to the fishes can be evaluated by examining the ^{65}Zn SA's of the fishes themselves, their migratory habits should be known. Finally, the migratory habits of the fishes are of great interest to fisheries biologists.

Information on the spatial distribution of ^{65}Zn SA in a few Group V fishes, the infauna feeders, is available in Table 5. As already discussed, ^{65}Zn SA in benthic invertebrates decreases at about the same rate with increasing distance north or south of the Columbia River mouth.¹³ Moreover, the strong north-south gradient in ^{65}Zn SA seen in the infauna will simplify our interpretation. The geographical pattern of SA of Glyptocephalus zachirus closely follows the SA pattern of the infauna. The ^{65}Zn SA of G. zachirus at Station 12 (see Figure 16) of 54.0 nCi/g drops to 21.1 nCi/g at Station 10 to the north. To the south of Station 12, it drops abruptly to 15.4 nCi/g at Station 18 and, moving still southward, drops to 8.90 nCi/g at NH-23. On the basis of these data, G. zachirus, of an age corresponding to the weights of fish captured in Table 5, does not migrate very far north or south. The same

¹³ Caution would seem necessary in interpreting these geographical patterns derived from one season. However, the nearly constant ^{65}Zn SA of the infauna at NH-23 during spring-fall of 1970 (Figure 6) argues against strong seasonal patterns. Furthermore, ^{65}Zn SA should decrease with distance north or south of the river mouth regardless of the seasonal nature of the input.

conclusion applies to Microstomus pacificus on the basis of the data at Stations 12, 18, and NH-23. The high specific activities of Parophrys vetulus at Station 12 and of Isopsetta isolepis at Station 5 indicate that these fishes have not recently strayed far from the Columbia River mouth.

Of the Group V fishes, the migratory behavior of two have been studied by other workers. As discussed earlier, M. pacificus, although possessing a bathymetric migration associated with spawning, does not migrate north or south, a fact which agrees with the results suggested by the SA data. P. vetulus is known to have a north-south spawning migration (Forrester, 1969; Pattie, 1969). Some are known to migrate hundreds of miles, a characteristic more common of mature females (Forrester, 1969). Using the length-maturity data of Harry (1959), three out of the four P. vetulus analyzed were smaller than the length at which 50% of the females were mature. Since sex of the fish was not distinguished, immaturity and/or maleness may explain the lack of migratory behavior deduced from the SA data. In addition, only a fraction of mature females are likely to migrate (Forrester, 1969; Pattie, 1969).

The seasonal concentrations of ^{65}Zn in mixed plankton that Seymour and Lewis (1964) reported will serve to indicate the geographical pattern of relative "average" SA's of pelagic prey on the continental shelf (Table 6). The total ^{65}Zn concentration over the year may be considered approximately proportional to the "average" ^{65}Zn SA available to benthic

fishes that prey on low trophic level pelagic organisms.¹⁴ According to Table 6, the ^{65}Zn SA should be higher in the fishes near the river mouth and lower to the north and south and may be higher in pelagic-feeding benthic fishes over Washington's continental shelf than in fishes over Oregon's continental shelf. Interpretation of the data for the fishes that prey on the pelagic food web is more difficult than for Group V fishes because the north-south gradients of ^{65}Zn SA in the pelagic food web averaged over the year are less well defined (Table 6). This would imply low resolution for deducing migration.

Enough geographical data are available to infer the migratory behavior of some of the Group II fishes. The ^{65}Zn specific activities of the Merluccius productus at Station 12 are very low relative to other members of Group II, especially in view of the high SA of the anchovies found in M. productus stomachs. Also, at Station 10 the SA of M. productus is lower than the Group V Glyptocephalus zachirus. These results suggest that M. productus has immigrated from some distant area where SA is very low in the prey. M. productus, abundant over the continental shelf and slope (< 800 m) from Vancouver Island to Baja California, is known to migrate (Alverson and Larkins, 1969). The adults occupy the northern part of the range in spring-fall and the

¹⁴ Probably there is a difference between species composition of the plankton hauls and the prey the fishes eat. In fact, these hauls made with a one-half meter net with No. 6 mesh (215 μ aperture) sometimes contained phytoplankton. Implicitly assumed is that the prey and plankton have similar geographic patterns of ^{65}Zn SA.

southern part in the winter. Percy and Naidu (1970) observed that the ^{65}Zn SA's of M. productus increased dramatically from low levels off California to high levels off Oregon and Washington, where highest levels were observed near the Columbia River mouth. Thus, the migration of M. productus inferred from its low ^{65}Zn SA relative to other Group II fishes is substantiated by its known migratory habits and by the data of Percy and Naidu, which shows that fishes that initially enter Oregon-Washington waters each summer have low ^{65}Zn SA's.

The ^{65}Zn SA of Lyopsetta exilis is high at Station 12 and low at NH-23, which would be expected if L. exilis did not migrate north or south. Note that in an earlier chapter, in order to calculate the α of L. exilis, we assumed that it did not migrate. This result does not, however, rule out a bathymetric migration. The ^{65}Zn SA of Citharichthys sordidus is low relative to L. exilis. Furthermore, it is lower than the Group III Eopsetta jordani. Possibly C. sordidus has a north-south migration.

The ^{65}Zn SA's for the 175-447 g Sebastolobus alascanus at Station 18 ranges between 12.2-15.7 nCi/g, which is not appreciably different from the range for the 214-553 g S. alascanus of 12.3-14.3 nCi/g at NH-23. This unexpectedly small difference may have occurred because the north-south gradients for integrated SA's may be less pronounced in higher trophic level pelagic prey than in lower trophic level pelagic prey. This follows from the lag time between attaining highest SA's in the lower and higher trophic levels. Highest ^{65}Zn SA's in the higher

trophic levels would probably occur downcurrent of lower trophic levels during a particular season. Migration can probably be ruled out, because S. alascanus is a very bony, heavy-bodied fish.

It would appear that the methods described above for determining the migratory behavior of fishes from SA data are valid in view of the agreement between migratory behavior known for some of the fishes and their behavior as deduced from the SA data. Either migration or its absence was suggested for some of the species for which there was no literature available.

Having discussed the fishes' migration, the effect of geographical position on the pelagic and detrital food webs in conveying ^{65}Zn to the fishes may be deduced from the SA's of fishes themselves. The spatial relations of ^{65}Zn in low trophic level pelagic prey and infauna are paralleled in their non-migratory predators. Interestingly, the data on benthic fishes would suggest that the detrital food web near the river mouth is possibly even more important than the pelagic food web in conveying ^{65}Zn to the fishes than implied by the ^{65}Zn SA's of the prey collected in July 1970. The decreasing role of the detrital food web with distance away from the source is suggested also by the data for benthic fishes.

BIBLIOGRAPHY

- Alexander, G. V. and R. H. Rowland. 1966. Estimation of zinc-65 background levels for marine coastal waters. *Nature* 210(5032):155-157.
- Alverson, D. L. and H. A. Larkins. 1969. Status of knowledge of the Pacific hake resource. *Calif. Coop. Fish. Invest. Rep.* 13:24-31.
- Baptist, J. P. and C. W. Lewis. 1969. Transfer of ^{65}Zn and ^{51}Cr through an estuarine food chain, p. 420-430. In: D. J. Nelson and F. C. Evans, ed., *Proceedings of the Second National Symposium on Radioecology*. U.S. Atomic Energy Comm. CONF-670503.
- Barnes, C. A. and M. C. Gross. 1966. Distribution at sea of Columbia River water and its load of radionuclides, p. 291-302. In: *Disposal of radioactive wastes into seas, oceans, and surface waters*. Intern. Atomic Energy Agency, Vienna.
- Barraclough, W. E. 1964. Contribution to the marine life history of the eulachon Thaleichthys pacificus. *J. Fish. Res. Bd. Canada* 21(5):1333-1337.
- Baxter, J. L. 1967. Summary of biological information of the northern anchovy Engraulis mordax Girard. *Calif. Coop. Fish. Invest. Rep.* 11:110-116.
- Bernhard, M. and A. Zattera. 1969. A comparison between the uptake of radioactive and stable zinc by a marine unicellular alga, p. 389-398. In: D. J. Nelson and F. C. Evans, ed., *Proceedings of the Second National Symposium on Radioecology*. U.S. Atomic Energy Comm. CONF-670503.
- Best, E. A. 1963. Movements of petrale sole, Eopsetta jordani (Lockington), tagged off California. *Pac. Mar. Fish Comm. Bull.* 6:23-35.
- Bevington, P. R. 1969. *Data reduction and error analysis for the physical sciences*. McGraw-Hill, New York. 336 p.
- Bowen, V. T., J. S. Olsen, C. L. Osterberg, and J. Ravera. 1971. Ecological interactions of marine radioactivity, p. 200-222. In: *Radioactivity in the marine environment*. National Academy of Sciences.
- Brinton, E. 1967. Vertical migration and avoidance capability of euphausiids in the California current. *Limnol. Oceanogr.* 12:451-483.

- Butler, T. H. 1964. Growth, reproduction, and distribution of pandalid shrimps in British Columbia. *J. Fish. Res. Bd. Canada* 21(6):1403-1452.
- Carey, A. G., Jr. 1969. Zinc-65 in echinoderms and sediments in the marine environment off Oregon, p. 380-388. In: D. J. Nelson and F. C. Evans, ed., *Proceedings of the Second National Symposium on Radioecology*. U.S. Atomic Energy Comm. CONF-670503.
- Carey, A. G., Jr. 1972. Zinc-65 in benthic invertebrates off the Oregon coast, p. 833-844. In: A. T. Pruter and D. L. Alverson, ed., *The Columbia River estuary and adjacent ocean waters*. Univ. of Washington Press, Seattle.
- Carey, A. G., Jr. and N. Cutshall. 1972. Zinc-65 specific activities from Oregon and Washington continental shelf sediments and benthic invertebrate fauna. In: *Symposium on the Interaction of Radioactive Contaminants with the Constituents of the Marine Environment*, Seattle, Washington, 10-14 July 1972 (in press). Intern. Atomic Energy Agency, Vienna.
- Carey, A. G., Jr., W. G. Pearcy, and C. L. Osterberg. 1966. Artificial radionuclides in marine organisms in the northeast Pacific Ocean off Oregon, p. 303-319. In: *Disposal of radioactive wastes into seas, oceans, and surface waters*. Intern. Atomic Energy Agency, Vienna.
- Clemmens, W. A. and G. V. Wilby. 1961. Fishes of the Pacific coast of Canada. *Fish. Res. Bd. Canada Bull. No. 68*, Ottawa. 443 p.
- Collins, C. A. and J. G. Pattullo. 1970. Ocean currents above the continental shelf off Oregon as measured with a single array of current meters. *J. Mar. Res.* 28(1):51-68.
- Cutshall, N. 1972. Research Associate, School of Oceanography, Oregon State University. Personal communication.
- Cutshall, N., W. C. Renfro, D. W. Evans, and V. G. Johnson. 1971. Zinc-65 in Oregon-Washington continental shelf sediments. In: *Proceedings of the Third National Symposium on Radioecology*, Oak Ridge, Tennessee, 10-16 May 1971 (in press). U.S. Atomic Energy Comm.
- Davis, G. E. and C. E. Warren. 1968. Estimation of food consumption rates, p. 204-225. In: W. E. Ricker, ed., *Methods for assessment of fish production in fresh waters*. Blackwell Scientific Publications, Oxford and Edinburgh.

- Dawes, B. 1930-31. Growth and maintenance in the plaice (Pleuronectes platessa L.). J. Mar. Biol. Assoc. U.K. 17:103-174, 877-947.
- Demory, R. L. 1972. Aquatic Biologist, Oregon Fish Commission Research Laboratory, Newport, Oregon. Personal communication.
- Draper, N. R. and H. Smith. 1966. Applied regression analysis. Wiley, New York. 407 p.
- Eberhardt, L. L. and R. E. Nakatani. 1968. A postulated effect of growth on retention time of metabolites. J. Fish. Res. Bd. Canada 25(3):591-596.
- Eberhardt, L. L. and R. E. Nakatani. 1969. Modeling the behavior of radionuclides in some natural systems, p. 87-109. In: D. J. Nelson and F. C. Evans, ed., Proceedings of the Second National Symposium on Radioecology. U.S. Atomic Energy Comm. CONF-670503.
- Edwards, R. R. C. 1967. Estimation of the respiratory rate of young plaice (Pleuronectes platessa L.) in natural conditions using zinc-65. Nature 216(5122):1335-1337.
- Ege, R. and A. Krogh. 1914. On the relation between the temperature and the respiratory exchange in fishes. Int. Rev. ges. Hydrob. 7: 48-55.
- Evans, D. W. and N. H. Cutshall. 1972. Effects of ocean water on the soluble-suspended distribution of Columbia River radionuclides. In: Symposium on the Interaction of Radioactive Contaminants with the Constituents of the Marine Environment, Seattle, Washington, 10-14 July 1972 (in press). Intern. Atomic Energy Agency, Vienna.
- Forrester, C. R. 1969. Results of English sole tagging in British Columbia waters. Pac. Mar. Fish. Comm. Bull. 7:2-10.
- Foster, R. F. 1959. Radioactive tracing of the movement of an essential element through an aquatic community with special reference to radiophosphorous. Publ. Staz. Zoologica Napoli 31(suppl.):34-69.
- Foster, R. F., I. L. Ophel and A. Preston. 1971. Evaluation of human radiation exposure, p. 240-260. In: Radioactivity in the marine environment. National Academy of Sciences.
- Fowler, S. W. and L. F. Small. 1972. Sinking rates of euphausiid fecal pellets. Limnol. Oceanogr. 17(2):293-296.

- Fowler, S. W., L. F. Small, and J. M. Dean. 1971. Experimental studies on elimination of zinc-65, cesium-137 and cerium-144 by euphausiids. *Marine Biology* 8(3):224-231.
- Frederick, L. C. 1967. Dispersion of the Columbia River plume based on radioactivity measurements. Doctoral dissertation. Corvallis, Oregon State University. 134 numb. leaves.
- Gerking, S. D. 1955. Influence of rate of feeding on body composition and protein metabolism of bluegill sunfish. *Physiol. Zool.* 25(4): 267-282.
- Gotshall, D. W. 1969. Stomach contents of Pacific hake and arrowtooth flounder from northern California. *Calif. Fish and Game* 55(1):75-82.
- Gross, M. G., B. Morse, and C. A. Barnes. 1969. Movement of near-bottom waters on the continental shelf off the northwestern United States. *J. Geophys. Res.* 74(28):7044-7047.
- Hagerman, F. B. 1952. The biology of the Dover sole Microstomus pacificus. *Calif. Fish and Game Fish. Bull.* 85:1-48.
- Hancock, D. 1972. Instructor, School of Oceanography, Oregon State University, Corvallis, Oregon. Personal communication.
- Harry, G. Y. 1959. Time of spawning, length at maturity, and fecundity of the English, Petrale, and Dover soles (Parophrys vetulus, Eopsetta jordani, and Microstomus pacificus, respectively). *Ore. Fish. Comm. Res. Briefs* 7(1):5-13.
- Hoss, D. E. 1964. Accumulation of zinc-65 by flounder of the genus Paralichthys. *Trans. Am. Fish. Soc.* 93(4):364-368.
- Johannes, R. E. and M. Satomi. 1966. Composition and nutritive value of fecal pellets of a marine crustacean. *Limnol. Oceanogr.* 11:191-197.
- Kevern, N. R. 1966. Feeding rate of carp estimated by a radioisotopic method. *Trans. Am. Fish. Soc.* 95(4):363-371.
- Kolehmainen, S. E. and D. J. Nelson. 1969. Balances of ^{137}Cs , stable cesium, and the feeding rates of bluegill (Lepomis macrochirus Raf.) in White Oak Lake. Oak Ridge National Laboratory, Tenn. ORNL-4445. 114 p.

- Lasker, R. 1966. Feeding, growth, respiration, and carbon utilization of a euphausiid crustacean. *J. Fish. Res. Bd. Canada* 23(9):1291-1317.
- Lowman, F. G., T. R. Rice, and F. A. Richards. 1971. Accumulation and redistribution of radionuclides by marine organisms, p. 161-199. In: *Radioactivity in the marine environment*. National Academy of Sciences.
- Mann, K. H. 1965. Energy transformation by a population of fish in the River Thames. *J. Anim. Ecol.* 34:253-275.
- Mann, K. H. 1967. Cropping the food supply, p. 243-257. In: S. D. Gerking, ed., *The biological basis of freshwater fish production*. Blackwell Scientific Publications, Oxford and Edinburgh.
- Nakatani, R. E. 1966. Biological response of rainbow trout (*Salmo gairdneri*) ingesting zinc-65, p. 809-823. In: *Disposal of radioactive wastes into seas, oceans, and surface waters*. Intern. Atomic Energy Agency, Vienna.
- National Academy of Sciences-National Research Council. 1962. Disposal of radioactive waste into Pacific coastal waters. N.A.S.-N.R.C., Publ. 985. 87 p.
- O'Neil, R. V. 1971. Systems approaches to the study of forest floor arthropods, p. 441-476. In: B. C. Patten, ed., *Systems analysis and simulation in ecology*. Vol. 1. Academic Press, New York.
- Osterberg, C. L., A. G. Carey, Jr., and H. Curl, Jr. 1963. Acceleration of sinking rates of radionuclides in the ocean. *Nature* 200 (4913):1276-1277.
- Osterberg, C. L., N. Cutshall, V. Johnson, J. Cronin, D. Jennings, and L. Frederick. 1966. Some non-biological aspects of Columbia River radioactivity, p. 321-335. In: *Disposal of radioactive wastes into seas, oceans, and surface waters*. Intern. Atomic Energy Agency, Vienna.
- Osterberg, C., J. Pattullo, and W. Percy. 1964. Zinc-65 in euphausiids as related to Columbia River water off the Oregon coast. *Limnol. Oceanogr.* 9(2):249-257.
- Overton, S. W. 1971. Professor of Statistics and Forest Management, Oregon State University. Personal communication.

- Paloheimo, J. E. and L. M. Dickie. 1966. Food and growth of fishes. II. Effects of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Bd. Canada 23(6):869-908.
- Paraketsov, I. A. 1963. (On the biology of Sebastes alutus of the Bering Sea). Trvses. Nauch. Issled Inst. Okeanogr. 48:305-312. from Refzh. Biol. 1964, No. 3144, Biol. Abs. 46(9019).
- Pattie, B. H. 1969. Dispersal of English sole, Parophrys vetulus, tagged off the Washington coast in 1956. Pac. Mar. Fish Comm. Bull. 7:11-14.
- Pearcy, W. G. 1970. Vertical migration of the ocean shrimp, Pandalus jordani: a feeding and dispersal mechanism. Calif. Fish and Game 56(2):125-129.
- Pearcy, W. G. and J. Naidu. 1970. Zinc-65 in Pacific hake, p. 87-89. In: Annual progress report: Ecological studies of radioactivity in the Columbia River estuary and adjacent Pacific Ocean. Oceanography Department, Oregon State University. Ref. 70-20, RLO 1750-66.
- Pearcy, W. G., and C. L. Osterberg. 1967. Depth, diel, seasonal, and geographic variations in zinc-65 of mid-water animals off Oregon. Int. J. Oceanol. Limnol. 1(2):103-116.
- Pearcy, W. G. and H. A. Vanderploeg. 1972. Radioecology of benthic fishes off Oregon, U.S.A. In: Symposium on the Interaction of Radioactive Contaminants with the Constituents of the Marine Environment. Seattle, Washington, 10-14 July 1972 (in press). Intern. Atomic Energy Agency, Vienna.
- Pentelow, F. T. K. 1939. The relation between growth and food consumption in the brown trout (S. trutta). J. Exp. Biol. 16:446-473.
- Pequegnat, J. E., S. W. Fowler, and L. F. Small. 1969. Estimates of zinc requirements in marine organisms. J. Fish. Res. Bd. Canada 26:145-150.
- Pereyra, W. T., W. G. Percy, and F. E. Carvey, Jr. 1969. Sebastes flavidus, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Bd. Canada 26:2211-2215.

- Perkins, R. W., J. L. Nelson, and W. L. Haushild. 1966. Behavior and transport of radionuclides in the Columbia River between Hanford and Vancouver, Washington. *Limnol. Oceanogr.* 11(2):235-248.
- Phillips, J. B. 1959. A review of the lingcod, Ophiodon elongatus. Calif. Fish and Game 45(1):19-27.
- Piro, A., M. Bernhard, M. Branica, and M. Verzi. 1972. Incomplete exchange reaction between radioactive ionic zinc and stable natural zinc in seawater. In: Symposium on the Interaction of Radioactive Contaminants with the Constituents of the Marine Environment, Seattle, Washington, 10-14 July 1972 (in press). Intern. Atomic Energy Agency, Vienna.
- Reichle, D. E. 1969. Measurement of elemental assimilation by animals from radioisotope retention patterns. *Ecology* 50(6):1102-1104.
- Renfro, W. C. and C. Osterberg. 1969. Radiozinc decline in Starry flounders after temporary shutdown of Hanford reactors, p. 372-378. In: D. J. Nelson and F. C. Evans, ed., Proceedings of the Second National Symposium on Radioecology. U.S. Atomic Energy Comm. CONF-670503.
- Schonzeit, M. H. 1973. Relationships between lower trophic levels and hydrography during an upwelling season. Master's thesis. Corvallis, Oregon State University. 102 numb. leaves.
- Seymour, A. H. and G. B. Lewis. 1964. Radionuclides of Columbia River origin in marine organisms, sediments, and water collected from the coastal and offshore waters of Washington and Oregon, 1961-1963. U.S. Atomic Energy Comm. UWFL-86. 73 p.
- Small, L. F. 1972. Associate Professor of Oceanography, Oregon State University. Personal communication.
- Small, L. F., H. Curl, Jr., and W. A. Glooschenko. 1972. Effects of solar radiation and upwelling on daily primary production off Oregon. *J. Fish. Res. Bd. Canada* 29:1269-1275.
- Small, L. F. and S. W. Fowler. In preparation. Turnover and vertical transport of zinc by the euphausiid Meganycitiphanes norvegica in the Ligurian Sea.
- Small, L. F., S. W. Fowler, and S. Kečkeš. 1972. Flux of zinc through a macroplanktonic crustacean. In: Symposium on the Interaction of Radioactive Contaminants with the Constituents of the Marine Environment, Seattle, Washington, 10-14 July 1972 (in press). Intern. Atomic Energy Agency, Vienna.

- Smith, R. L., C. N. K. Mooers, and D. B. Enfield. 1971. Mesoscale studies of the physical oceanography in two coastal upwelling regions: Oregon and Peru, p. 513-535. In: J. D. Costlow, ed., Fertility of the sea. Vol. 2. Gordon and Breach, New York.
- Vanderploeg, H. A. and W. G. Pearcy. In preparation. Spatial patterns of ^{65}Zn specific activity in pelagic and benthic food webs on the continental shelf off Oregon.
- Westrheim, S. J. and A. R. Morgan. 1963. Results from tagging a spawning stock of Dover sole Microstomus pacificus. Pac. Mar. Fish. Comm. Bull. 6:14-21.
- Winberg, G. G. 1956. (Rate of metabolism and food requirements of fishes.) Nauchnye Trudy Belorusskovo Gosudarstvennovo Universiteta imeni V. I. Lenina, Minsk. 235 p. (Trans. Fish. Res. Bd. Canada, Trans. Ser. No. 194.)
- Wolfe, D. A. 1970. Levels of stable Zn and ^{65}Zn in Crassostrea virginica from North Carolina. J. Fish. Res. Bd. Canada 27(1):47-