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FEEDING ECOLOGY OF JUVENILE KING AND TANNER CRAB  
IN THE SOUTHEASTERN BERING SEA

Semi annual Report

to

NOAA/OCSEAP

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FEEDING ECOLOGY OF JUVENILE KING AND TANNER CRAB  
IN THE SOUTHEASTERN BERING SEA

INTRODUCTION

Under the overall aim of the National Oceanic Atmospheric Administration/Minerals Management Service (NOAA/MMS) to determine how petroleum contaminants may reach and impact the commercially valuable crab resources of the southeastern Bering Sea, the main objectives of this project are to determine the food requirements of juvenile red king crab, Paralithodes camtschatica, and tanner crab, Chionoecetes bairdi, in the waters north of the Alaska Peninsula and to synthesize this trophodynamic information with other information to assess potential impacts of Outer Continental Shelf (OCS) development. To achieve these objectives we undertook several tasks: the location and collection of crabs; shipboard experiments on stomach clearance rates; 24-h trawling to determine a diel feeding chronology and daily ration; determination of the carapace size - stomach volume relationships; visual examination of stomach contents; calculation of diet composition; and construction of a food requirements schedule. Also, an immunoassay will be applied to detect prey types ordinarily not detectable by conventional gut analysis and to determine whether juvenile crabs depend on soft-bodied prey. Table 1 lists our tasks along with our general approach and the present status.

CRUISE OPERATIONS

We collected king and tanner crab by trawl and SCUBA diving during three cruises in 1982 along the north Aleutian Shelf. The NOAA ship Miller Freeman conducted the June and August cruises; the NOAA ship Discoverer, conducted

Table 1. Tasks in studying the feeding ecology of juvenile king and tanner crabs.

Task	Cruise	Shipboard	Laboratory	Status
1. Location and collection of crabs	Jun Aug Ott	TV tows Diver sled tows Trawling		Cruises done, approximate distribution patterns indicated
2. Carapace size/stomach volume relationship	Jun	Dissection and measurement	Regression analysis	Equations obtained for king and Bairdi crab
3. Clearance rate				
a. All items	Jun Aug	Hold crabs alive and sacrifice at intervals	% stomach fullness Dry weight Regression analysis	Equations obtained for king crab
b. Specific items	Aug	Feed specific items to starved crab, hold and sacrifice at intervals	% stomach fullness Dry weight Regression analysis	Equations obtained for five items
4. Observation of feeding behavior	Aug	Feed captive crabs	Cine movies	Description of how crab handle food
5. <b>Diel</b> feeding chronology	Jun Aug Ott	24-h trawling in area of high density	% stomach fullness Dry weight Graphical analysis	Done for king crab from June, <b>lab</b> work in progress for king crab from Aug Insufficient samples for <b>Bairdi</b> crab from Jun, Aug, Ott, and king crab from Ott
6. Visual examination of gut contents	Jun Aug Ott	Collection of crabs at peak feeding time	Visual examination Volume/weight Number of prey item	In progress for king crab Bairdi crab will need to be done by immunoassay
7. Immunoassay	Jun Aug Ott	Collection of crab Collection and preparation of prey items	Immunoassay	Prey items cleared and frozen
8. Diet composition	Jun Aug <b>Oct</b>	Crab collection	Calculation with correction from clearance rates and immunoassay	Awaits completion of #6 & #7

the October cruise. In June the study area extended from Cape **Sarichef** on **Unimak** Island to Cape Seniavin. In August the study area was extended to Port Heiden. In June we sampled depths up to 70 m along 17 transect lines. In August and October we concentrated collection efforts in areas of high abundance indicated from previous cruise results.

Our approach was first to locate an area of high crab density and then to collect crabs in that area around the clock to gain samples for determining the **diel** feeding chronology and daily ration. To locate crab we towed an underwater video camera and trawled with an 18-foot try net seaward of 20 m, then towed a diver sled and did try net trawling shoreward of 20 m. To collect the smallest king crab and potential prey items, we conducted boat-tended drift diving with standard SCUBA among the rocks from 1 to 20 m around Amak Island. To collect potential prey items for the immunoassay we took bottom grabs. We also used diving and bottom grabs to obtain large numbers of prey items for the clearance rate experiment. CTD casts provided data on depth profiles of temperature and salinity. Table 2 summarizes our ship operations.

We processed the trawls for catch statistics and samples for several different analyses. With a deck scale, we weighed the total trawl and then sorted out all the crabs and any specimens needed as prey items in the immunoassay. We noted the predominant fish species and the presence of invertebrate species other than crab. We weighed individual king crab to the nearest g, measured their carapace length (CL) and width (CW) to the nearest mm, and noted its shell condition. After measuring, we either gave **ovigerous** females to **Dr. Dave Armstrong** of the University of Washington for further analysis or returned them to the sea. For trawls with more than 10 king crabs, we flash froze the crabs and then measured them during subsequent

Table 2. Ship operations accomplished during NOAA/OCSEAP cruises RP-4-MF-82A, LEG I, June, 1982; RP-4-MF-82A, LEG III, August, 1982; RP-4-DI-82B-LEG 1A, October, 1982.

<u>Operation</u>	Number per cruise		
	Jun 82	Aug 82	Ott 82
Try net trawls	93	198	72
Diver sled tows	16	0	0
Drift dives (no sled)	8	19	5
TV tows	18 (8.3 h)	4 (3 h)	Ø
Grabs	20	35	18
CTD'S	18	75	75

laboratory analyses. For smaller trawls we measured the crabs as they were frozen. During the 24-h trawling on the June and August cruises, we set aside portions of juvenile king crab from **large** catches for specific shipboard analyses or experiments. During the experiments or later analysis we also measured the crabs as above. Because most Bairdi crabs in the trawls in the trawls were less than **20 mm CW**, we did not measure them individually but counted and weighed all the **Bairdi crab >20 mm CW** in a trawl before freezing.

## MATERIALS AND METHODS

### CARAPACE SIZE/MAXIMUM STOMACH VOLUME RELATIONSHIP

On the June cruise we examined king and Bairdi crab to determine equations relating the carapace size to the stomach volume generally following Hill (1976). These equations are necessary to calculate stomach fullness by volume in later analyses. After noting wet weight, sex, carapace length, carapace width, and shell condition, we carefully dissected the carapace away from the body of a thawed crab. We removed muscle and other tissue from the outside of the stomach and tied off the stomach at the **oesophagus** and between the foregut and the midgut posterior to the filter chamber. We then cut the **oesophagus** and intestinal tract and lifted out the tied off stomach still containing its contents. In a graduate we measured the volume displaced by the stomach with its contents to the nearest 0.5 ml (0.1 ml for smaller stomachs). With a syringe we injected clean seawater into the stomach through the cut end of the filter chamber. We stopped injection when the stomach wall became smooth and taut and water began to leak along the syringe. In a graduate we measured the displacement volume of the stomach with its contents plus injected water. We then opened the

stomach, washed the contents into formalin, and measured the displacement volume of the stomach wall alone. We calculated the maximum stomach volume by subtracting the volume of the stomach wall alone from the volume of the stomach with contents and injected water. We then did regression analysis to relate carapace size to the maximum stomach volume. As a measure of carapace size, we used carapace length for king crab and carapace width for Bairdi crab following National Marine Fisheries Service (NMFS) practice because length for king crab and width for Bairdi crab are the more accurate measurements.

#### STOMACH CLEARANCE RATES

For juvenile king crabs we determined stomach clearance rates for the total stomach contents naturally present and for specific prey items fed to starved crabs. To determine how quickly the naturally-present stomach contents fell, we set aside juvenile king crabs from large catches in June and August, froze a portion immediately, and held the rest without food in a live tank at ambient seawater temperature (8 - 9°C). At prespecified time intervals after capture we froze subsamples of the captured crabs. During holding in June, we siphoned the live tank periodically to remove feces and regurgitated shell. In August, we held the crabs in baskets that separated the crabs from any regurgitated or defecated material.

Crabs isolated in June were analyzed with those for the carapace size/stomach volume relationship. We measured the volume of stomach contents by subtracting the displacement volume of the stomach wall alone from that of the intact, tied-off stomach with its contents. Dividing the resulting volume by the maximum stomach volume and multiplying by 100, gave the percentage stomach fullness by volume. Determination of clearance rates by

plotting this percentage of stomach fullness was confounded by the large volumes of clear liquid that **still** occurred in stomachs after solid material disappeared. Consequently, we modified our analysis of captive crabs in August and reanalyzed stomachs preserved in June.

For June and August crabs, we determined the dry weight of the stomach contents and the volume of solid material. After **determining** sex, wet weight, and carapace length, of thawed crabs from August, we removed the stomachs and transferred their contents to graduated and tared centrifuge tubes. After 1 h of settling, we recorded the total volume of liquid and solids and the volume of solids alone. We had determined that settling for 16 h did not change the **volume** noted after 1 h. After noting the volumes and the occurrence of sand, flocculent, soft tissue, or hard parts, we dried the stomach contents to constant weight. We calculated the percentage of the maximum stomach volume occupied by solid material and standardized the dry weight by dividing it by the crab's wet weight. We did graphical analysis and model **fitting** to determine the clearance rates. We similarly reanalyzed stomach contents preserved in June, 'except that the addition of preservative precluded measurement of total volume including the liquid.

To determine stomach clearance rates for specific prey items we held, without food, a portion of the crabs from large trawls taken during the 24-h trawling operation in August. After 7-12 days without food and after determining sex, wet weight, carapace length and width, and shell condition, we tagged individual juvenile king crab and placed them into individual containers with seawater **to** be given a specific prey item. Seven days after isolation we examined the stomachs of 5 crab and confirmed that all were empty except for liquid.

To individual crabs, we presented one of the following: shrimp, juvenile gadoid fish (2-3 cm long), barnacles, small mussels (>2 cm long), shucked and diced clam (siphon, foot, and adductor), tube worms still in sand tubes, and snails. We had seen these or similar prey species in crab stomachs except for mussels. We used whole mussels because we could not obtain a large enough number of the small clams we would have preferred.

The protocol was as follows: we transferred a tagged and measured crab from isolation to an individual container with seawater. After 0.5 h of acclimation, we added a known number and volume of a specific prey item. We checked the containers every 10 to 15 min. If a crab had eaten more than half the food, we removed the crab and determined by formal randomization whether to freeze the crab immediately or transfer it to isolation for a prespecified time interval before freezing. Any crabs that had not eaten within 1.5 h after food introduction did not enter the analysis for that food. After removing a crab, we recovered and measured the volume of the remaining food to confirm that the crab had indeed ingested the food.

The live tank had flowing seawater at 0.0 to 0.3°C above ambient sea surface temperature (8 to 9°C). After 1.5 h, seawater in the static feeding containers rose less than 0.9°C. The bottom temperature at capture varied between 5 and 6°C. We fed the crabs during daylight hours.

In the laboratory, we removed the stomachs from thawed crabs and transferred the contents to graduated and tared centrifuge tubes. We noted the total volume of liquid and solids and that of solids alone before drying the contents to constant weight. We calculated and analyzed the data for specific items in the same manner as described above for all items naturally present.

## SHIPBOARD OBSERVATIONS OF FEEDING BEHAVIOR

In addition to observations of feeding behavior made during the presentation of specific prey items, we also filmed feeding behavior of juvenile king crab held on shipboard in a large glass-fronted aquarium with flowing ambient seawater. We made special note of how crabs handled prey items during ingestion.

## DIEL FEEDING CHRONOLOGY

Our approach was to find an area of high crab density and then to trawl continuously around the clock for the time available to us. Generally, two or three trawls took place within 2 h, and we pooled the samples taken within each 2-h period of the 24-h cycle. For this effort we had only 24 h available to us in June, but 72 h in August and October.

We originally intended to plot the percentage of stomach fullness by volume against time of day to indicate peak feeding time and, consequently, in June we used stomachs analyzed for the carapace size/maximum stomach volume relationship to give additional data on stomach fullness. We determined the volume of the stomach contents by first measuring the displacement volume of the intact stomach with its contents and then subtracting the displacement volume of the stomach wall alone. The contents volume divided by the maximum stomach volume calculated from carapace length and multiplied by 100 gave percentage stomach fullness by volume. We then plotted stomach fullness against time of day and examined the plot for periods of high fullness.

Because the above method proved inadequate due to high volumes of liquid in otherwise empty stomachs, we reanalyzed the stomachs preserved in June. We transferred the stomach contents to graduated and tared centrifuge tubes,

centrifuged the contents to separate the solid material, and recorded the volume of **solid** materials. We then dried the stomach contents to constant weight. We calculated the percentage of maximum stomach volume occupied by solids and standardized the dry weight of stomach contents by division by the wet weight of the crab. We examined plots of these two variables against time of day for times of high stomach contents. Currently, we are analyzing crabs frozen in August in a similar manner.

#### THE FREQUENCY OF NEWLY-DISCOVERED PREY AS A FUNCTION OF THE NUMBER OF STOMACHS EXAMINED

To determine the optimal number of stomachs to examine in detail for dietary composition, we examined 25 stomachs from one station where we collected 192 juvenile king crabs. Following **Vesin** et al. (1981) we plotted the number of newly discovered prey items against the number of additional stomachs examined.

#### CURRENT RESULTS WITH DISCUSSION

##### LOCATION AND COLLECTION OF JUVENILE CRABS

We found that juvenile crabs of the different species varied in geographical location of high density and in size class distribution. In June, August, and October, we obtained no juveniles of the tanner crab, Chionoecetes **opilio**, and only minimal numbers of adults. In June we took only 56 adult **Opilio** crabs, 50 of which came in on trawl at the extreme western end of the study area near **Unimak** Pass. The study area does not appear to contain juvenile **Opilio** crabs.

Juvenile king crab were concentrated off Port **Moller** and Cape **Seniavin**. In June, August, and October only adult king crab occurred to the west. Off

Port **Moller**, juvenile king crab were deeper in August (56 to 75 m) than in June (55 to 65 m). In contrast to the hundreds of juvenile king crab taken off Port **Moller** in June and August, only one juvenile king crab was taken in October. Within the 3.5 days available in October we were unable to find juvenile king crab.

Diver sled tows covered the areas shoreward of 20 m in June but sighted no pods or solitary king crab or tanner crab. The high-energy sandy nearshore areas along the north side of the Alaska Peninsula do not appear to offer good habitat for juvenile crab. Divers did find juvenile king crab less than 20 mm CL in the rocks at approximately 18 m near Amak Island.

TV tows off Cape **Seniavin** and Port **Moller** revealed that juvenile king crab occurred on sand bottoms with large numbers of **ascidians** and sponges growing on the tubes of large tube worms. The crabs were not aggregated or podded, but solitary. All TV tows occurred during daylight.

Most of the juvenile king crab were between 50 and **80** mmCL. One-year-old king crab (>20 mm CL) were found only around Amak Island by divers and in two rocky areas, one off Nelson Lagoon and one off Amak Island, where the try nets were torn and we picked the small crabs off the net mesh. Of king crabs less than 20 mm CL, we have one from June, eight from August, and one from October. Aside from one at 28 mm and one at 36 mm, the remaining king crab are above 48 mm CL.

Bairdi crab were most abundant near Amak Island being found at 55-65 m in June, 65-75 m in August, and over 80 m in October. We have perhaps 2,000 Bairdi crab less than 20 mm CW, but probably less than 50 greater than 20 mm CW.

The lack of juvenile king crab off Port **Moller** in October was unexpected but may have been related to oceanographic events. In October warm water

(>7°C) extended to the 75-m **isobath** due to storms with west winds in September. The crabs may have moved in response to the extension of the warm water mass. The smaller shift of juvenile king and **Bairdi** crab from 65 m in June to 75 m in August may also have been due to a seaward extension of warm water in August. A more systematic effort would be necessary to demonstrate definitely that the juvenile crabs migrate seaward and shoreward before the frontal zone of a warm water mass.

#### CARAPACE SIZE - MAXIMUM STOMACH VOLUME RELATIONSHIP

In June, 262 of the 319 king crabs (33 to 129 mm CL) that we dissected had intact stomachs and were used in the regression analysis. The following power function proved to relate the maximum stomach volume,  $V$ , in ml, to the carapace length,  $L$ , in mm:

$$v = 2.22 \times 10^{-5} L^{2.87}$$

$$\text{or } \ln V = -10.716 + 2.87 \ln L.$$

The  $R^2$  was 76.6%. Equations for the separate sexes did not differ significantly so that we pooled data from both sexes to produce the above equation. Shell condition was also not a significant variable.

For **Bairdi** crab the following power function related maximum stomach volume,  $V$ , in ml to carapace width,  $W$ , in mm:

$$v = 2.68 \times 10^{-5} W^{2.69}$$

$$\text{or } \ln V = -10.527 + 2.69 \ln W.$$

Ninety-two out of 133 crabs (27-153 mm CW) were successfully dissected and entered the analysis. The  $R^2$  was 79.8%.

These equations differ substantially in mathematical form from that given by Cunningham (1969) and cited and used by Jewett and Feder (1982) for adult king crab. The equation appearing in Jewett and Feder (1982) has a typographical error and is really a second order quadratic. Thus, Jewett and Feder's equation is only a good fit over a specific size range and for king crabs below 70 mm CL actually gives increasing stomach volumes for decreasing carapace lengths. Most allometric relationships in crustaceans are power functions so that we were not surprised that regression analysis confirmed a power function relating carapace size and stomach volume. We submit that the power functions presented here are more appropriate models than quadratic best fit given by Cunningham (1969) and used by Jewett and Feder (1981).

From the carapace size of crabs analyzed in the laboratory, we used the above equations to calculate the maximum stomach volume. We then used the calculated maximum stomach volume in calculations of percentage stomach fullness and other statistics.

#### STOMACH CLEARANCE RATES

##### Clearance Rate for all Items Naturally Present

In June we held 85 captured juvenile king crab, 61.3 ( $\pm 6.6$  SD) mm CL, without food and sacrificed them at intervals of  $t = 0, 1, 2, 4, 8, 12, 16, 24, 40, 72,$  and 121 h. In August we sacrificed 58 juvenile king crabs, 64.3 ( $\pm 8.1$ ) mm CL, at  $t = 0, 8, 12, 24,$  and 48 h. In June we determined the percentage stomach fullness on shipboard using the total volume of the stomachs with contents minus the volume of the stomach wall and we anticipated that this stomach fullness plotted against time after isolation would give an exponential decay curve describing the passage of food from the stomach. Unfortunately, large amounts of liquid still present in otherwise

empty stomachs confounded this method for determination of clearance rates. In fact, the volume of liquid actually increased with time after isolation (Table 3), and otherwise empty stomachs contained enough liquid to maintain 25 to 30% stomach fullness after 130 h. Consequently, for the August samples we determined the volume of solid material in the stomach and the dry weight of the stomach contents. When this approach proved successful, we then reanalyzed stomachs preserved in June in a similar manner.

Both the volume of solids and the dry weight of stomach contents fell exponentially with time after isolation (Figure 1, Table 4). We found a two-compartmental model for the volume of solids and a three-compartmental model for the loss of dry weight. The exponential decay curves are needed to calculate daily ration following Elliott and Persson (1978). Dry weight of stomach contents proved to be a better measure of stomach clearance rates than volume.

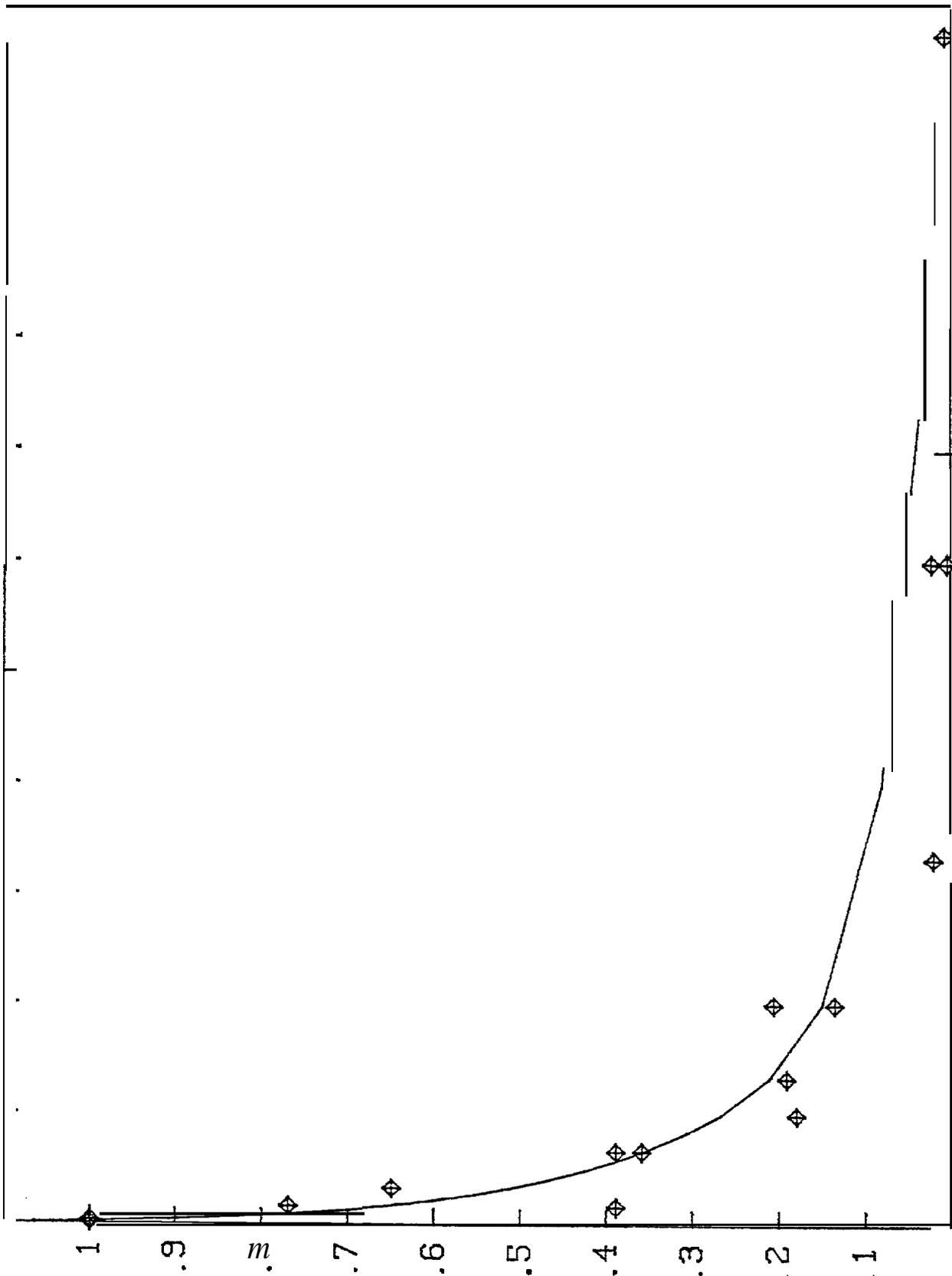
Evidence for several compartments rather than one in the exponential decay curves comes from two sources: information concerning variation in gut residence times of different materials (Hill, 1976; Carter and Steele, 1982) and graphical analysis of our data. Whereas many models of stomach clearance assume a one-compartmental exponential decay curve, it is not reasonable to accept the implication of a one-compartmental model that all the materials in the stomach are digested and passed out at the same rate. From Hill (1976) and Carter and Steele (1982), we know that in the stomachs of crabs and lobsters soft tissue is lost in hours while hard parts from bivalves and echinoderms remain for days. Thus knowing that clearance rates do vary among different tissues, it is reasonable to expect that a decay curve for the loss of contents from stomachs containing a mixture of materials would be the cumulative result of different clearance rates for the different materials

Table 3. Stomach fullness as a function of time after isolation. Stomach fullness is expressed as the percentage of maximum stomach volume occupied by the total or liquid portion of stomach contents.

Time after isolation (h)	Stomach fullness by volume %	
	Total contents	Liquid contents
0	48.3	30.1
8	30.9	22.0
12	23.7	16.2
24	24.9	24.4
48	28.3	28.3

Figure 1. Decay curve for the clearance of all items naturally present in the stomachs of juvenile king crab. The proportion of the initial value for grams dry weight of stomach contents per grams crab wet weight vs. the time in hours after isolation.

PROPORTION INITIAL DRY WT



2 24 36 48 60 72 84 96 108 120 132 144 156 168 180 192 200

TIME (HRS) AFTER ISOLATION  
ITEMS NATURALLY PRESENT

Table 4. Clearance rates for all items naturally present in the stomachs of juvenile king crab. V = proportion of the initial value for the volume of **solids** as a percentage of maximum stomach volume. This average initial value of solids volume was 23.1 ( $\pm$  2.4 SD) %. W = proportion of the initial value for the gram dry weight of stomach contents per gram crab wet weight. The average **initial** value for the dry weight was 2.91 ( $\pm$  1.51) mg dry weight/g crab wet weight. T = time in hours after isolation.  $\bar{T}$  = mean life, the reciprocal of the decay constant.

Bas is	No. of time intervals	Equati on	R <sup>2</sup>	$\bar{T}$ in the compartments	Time (h) to 10% of initial	Time (h) to 5% of initial
Vol ume	14	$V=0.191e^{-1.190T}+0.856e^{-0.0930T}$	87.9	0.84 10.8	23.2	30.6
Dry wei ght	18	$W=0.287e^{-1.134T}+0.551e^{-0.148T}+0.226e^{-0.0217T}$	93.1	0.88 6.8 46.1	38.0	69.5

initially present in different proportions. The king crab stomachs examined for this analysis contained flocculent, sand, soft tissue, and fragments from small bivalve and gastropod shells and sand dollar tests. Our finding **multicompartmental** exponential models for stomach clearance meets this reasonable expectation.

Graphical analysis indicated the number of compartments in the specific decay curves with which we dealt. If the appropriate model for the exponential decay had only one compartment, then plotting natural logarithm of the dependent variable, e.g., the dry weight, against time would give a straight line. For a two-compartmental model such a plot would show a straight line falling to an inflection point where another straight line of shallower slope would continue. Similarly, for a three-compartmental model the plot would show three straight lines meeting at two inflection points. For clearance rates of all items naturally present and of specific prey items we made such plots to indicate the appropriate number of compartments and to estimate starting values for a reiterative curve fitting program. We then used the FIT program developed by **Battelle** Pacific Northwest Laboratories for evaluating the parameters of **multicompartmental** exponential decay curves.

Beyond 48 h the volume of solids had fallen below the minimum measurable volume so that we did not use volume data beyond 48 h. If we had been able to measure smaller volumes, we suspect that a three-compartmental exponential model would also have described the volume decay curve. In contrast to volume, the dry weight of stomach contents did not fall below our minimum measurable amount. The coefficient and decay constant for the "first compartment in the volume curve agree well with those in the dry weight curve. Also, the parameters of the second compartment in the volume curve approximates a combination of the parameters of the second and third

compartments of the dry weight curve. Given this good agreement, the better measurements for dry weight than solids volume with extremely low stomach contents, and the better fit of the dry weight curve, dry weight of stomach contents is the better basis for determining clearance rates. Similarly, dry weight also proved a better measure for determining clearance rates for specific prey items and the diel feeding chronology described in the next sections.

The parameters of the exponential model have definite biological meaning. The decay constants and their reciprocals, the mean life,  $\bar{T}$ , indicate how long material remains in a given compartment. Thus from Table 4, material remains in the first compartment less than 1 h; in the second compartment, about 7 h; in the third, 46 h. The coefficients also can be interpreted. Because the dry weight is expressed as a proportion of the standardized dry weight initially present,  $W = 1.000$  at  $T = 0$  by definition. Note that the coefficients of the three compartments in Table 4 sum to 1.064. In exponential models for specific prey items discussed in the next section, the coefficients also sum to one. The coefficients represent, then, the proportion of the total dry weight that is in each compartment at  $T = 0$ . There are three possible biological interpretations of the coefficient. Under the first interpretation, the coefficients represent the proportions at  $T = 0$  of different classes of material (either tissue types, e.g., soft tissue, hard tissue, or prey types, e.g., worms, crustaceans, molluscs) that are digested and passed out at different rates. Under this first interpretation then we would assign soft tissue to the first compartment and observe that soft tissue was slightly less than 30% of the original material and had essentially disappeared after 0.9 h, the mean life of the compartment. Similarly, we would assign the hard tissue to the third

compartment and note that this third compartment constitutes 23% of the material originally present and has a mean life of 46 h. Under the second interpretation, the compartments are seen to represent processes, such as, digestion and active passage of indigestible material, rather than kinds of materials or tissues. Here the compartments might represent first, the digestion of soft tissue, secondly, the digestion of more refractory material, and thirdly, the clearance of indigestible material. Under the third interpretation the compartments are seen to represent some combination of process and material.

More experimental work would be necessary to confirm one or the other of these interpretations, but we present them because all three have practical implications. If we can indeed interpret the compartmental coefficients as indicating the proportion of tissue type initially present, or the predominant digestive process, then we have a potential method for estimating the time at which the crabs fed from a decay curve such as in Figure 1 and Table 4. A high proportion (high coefficient) in the first compartment would indicate recent feeding whereas a low proportion in the first compartment would indicate feeding at a more remote time in the past.

#### Clearance Rates for Specific Prey Items

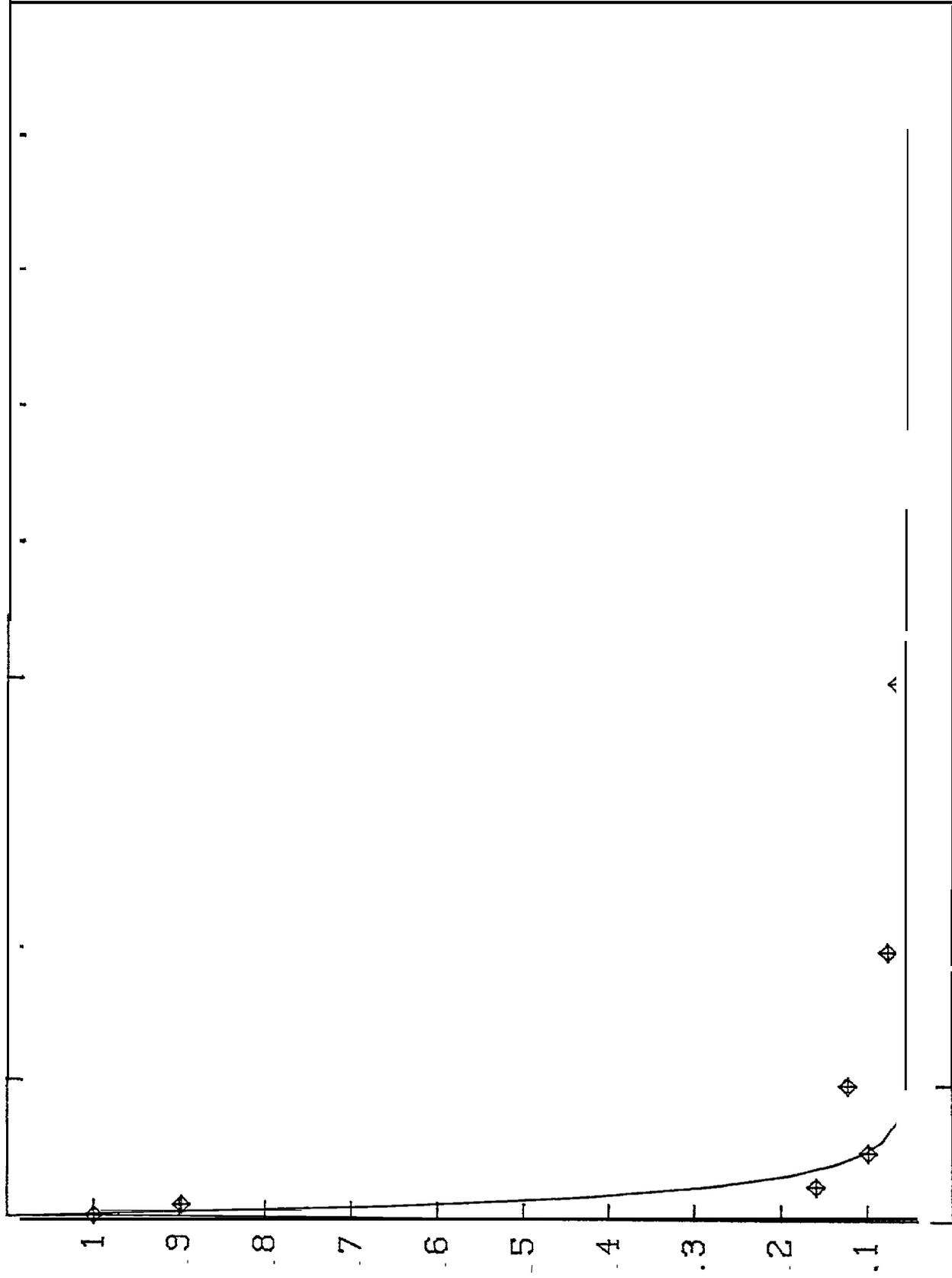
On shipboard starved juvenile king crabs fed readily on shucked and diced clam, juvenile fish, shrimp and barnacles, less readily on tube worms, only slightly on mussels, and not at all on snails even after we cracked the snail shells. For mussels and snails we did not have enough samples to determine clearance rate. The clearance rate for tube worms is based on much fewer data points than those for the other items and, therefore, should be considered tentative.

For the proportion of the initial grams dry weight of stomach contents per gram crab wet weight, we found one-, two-, and three-compartmental exponential decay curves (Figures 2-5, Table 5). As described in the previous section, we used graphical analysis to indicate the number of compartments and **Battelle's** FIT program to evaluate the parameters. Because the small number of crabs consuming tube worms only allowed us to follow the clearance of stomach contents to 12 h, we suspect that the exponential decay model for tube worms (Table 5) may have shown more than one compartment if it had been followed longer. An example of how the individual compartments combine to give the overall decay curve appears in Figure 5.

A comparison of the equations in Table 5 shows that the overall clearance rates, the number of compartments, and the relative size and mean life of the compartments clearly varied with prey type. The diced clam represented soft tissue with no hard parts and had by far the fastest clearance rate. The decay model for diced clam shows that the first compartment contains almost 100% of the material and has a very low mean life, 2.0 h. In contrast to clam, the other three items showed substantial amounts of material in their second and third compartments and lower clearance rates due primarily to longer mean life in the second and third compartments. Shrimp with an exoskeleton but no heavily calcified parts had two compartments whereas barnacles and juvenile fish with calcified parts (barnacle plates and fish bone) had three compartments. Note that the decay constants in the first compartments (Table 5) are quite comparable for shrimp and barnacles but are much higher for clam and fish. If the first compartment represents digestion of soft tissue, we might expect shrimp and barnacles with their crustacean exoskeleton to have similar decay constants

Figure 2. Exponential decay curve for stomach contents in juvenile king crab fed diced clam. The dependent variable is the proportion of the grams dry weight of stomach contents per gram crab wet weight at time = 0. See Table 5 for equations.

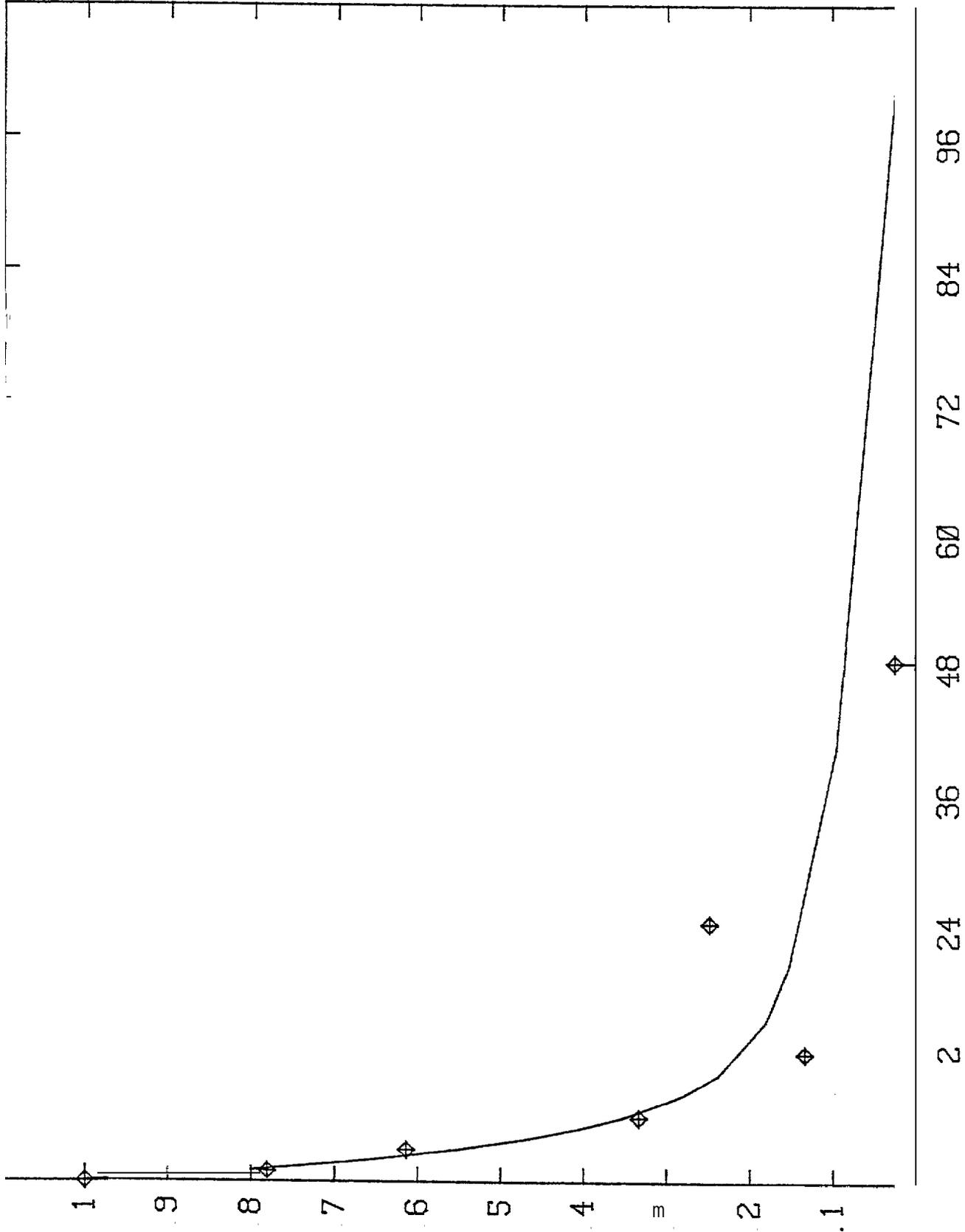
PROPORTION INITIAL DRY WT



2 24 48 60 72 84 96  
TIME (HRS) AFTER FEEDING  
DICED CLAM

Figure 3. Exponential decay curve for stomach contents in juvenile king crab fed shrimp. The dependent variable is the proportion of the grams dry weight of stomach contents per gram crab wet weight at time = 0. See Table 5 for equations.

PROPORTION INITIAL DRY WT



TIME (HRS) AFTER FEEDING  
SHRIMP

Figure 4. Exponential decay curve for stomach contents of juvenile king crab fed barnacles. The dependent variable is the proportion of grams dry weight of stomach contents per gram crab wet weight at time = 0. See Table 5 for equations.

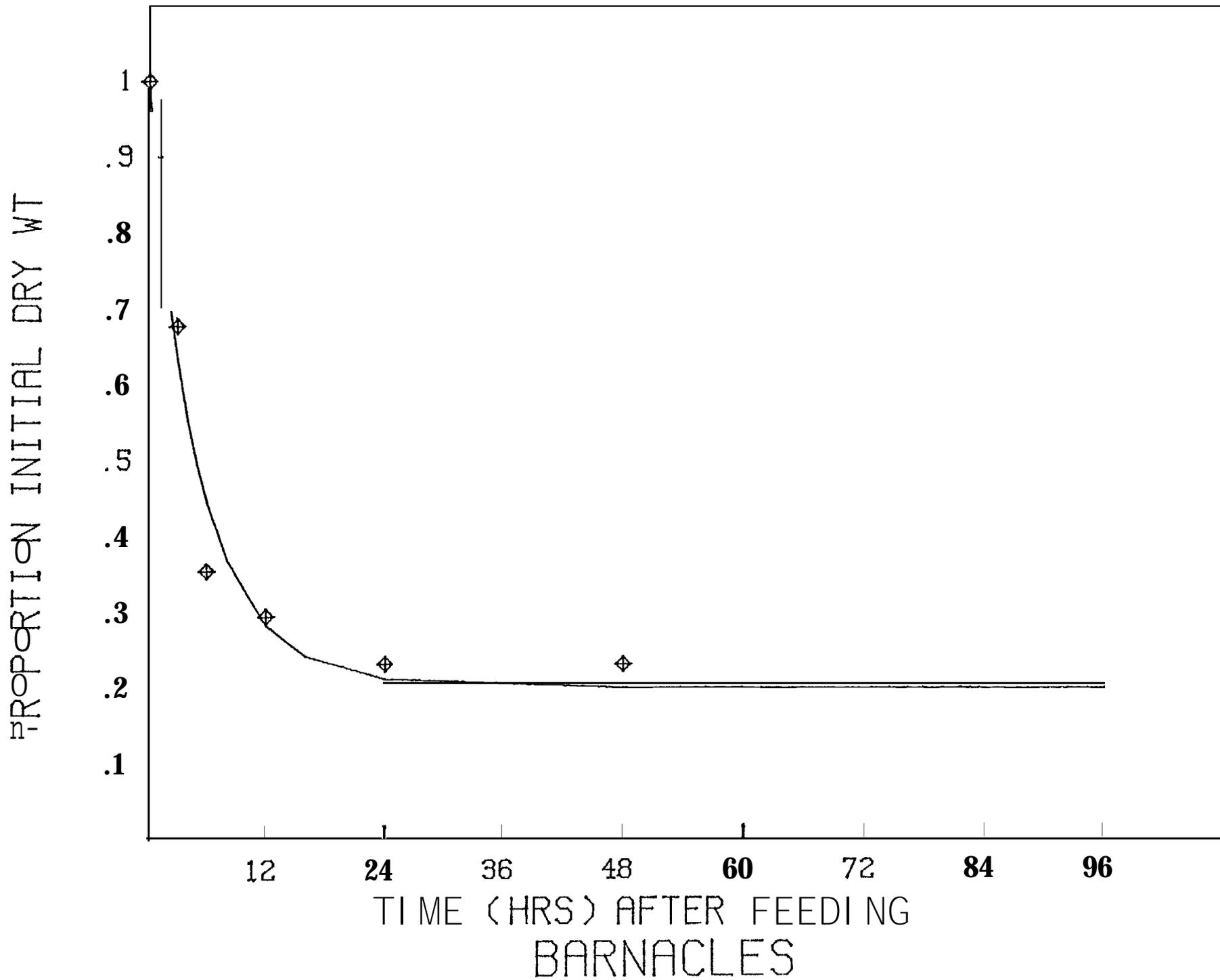


Figure 5. Exponential decay curve for stomach contents of juvenile king crab fed juvenile fish. The dependent variable is the proportion of grams dry weight of stomach contents per gram crab wet weight at time = 0. Decay curves for each compartment are plotted individually and labelled with roman numerals. See Table 5 for equations.

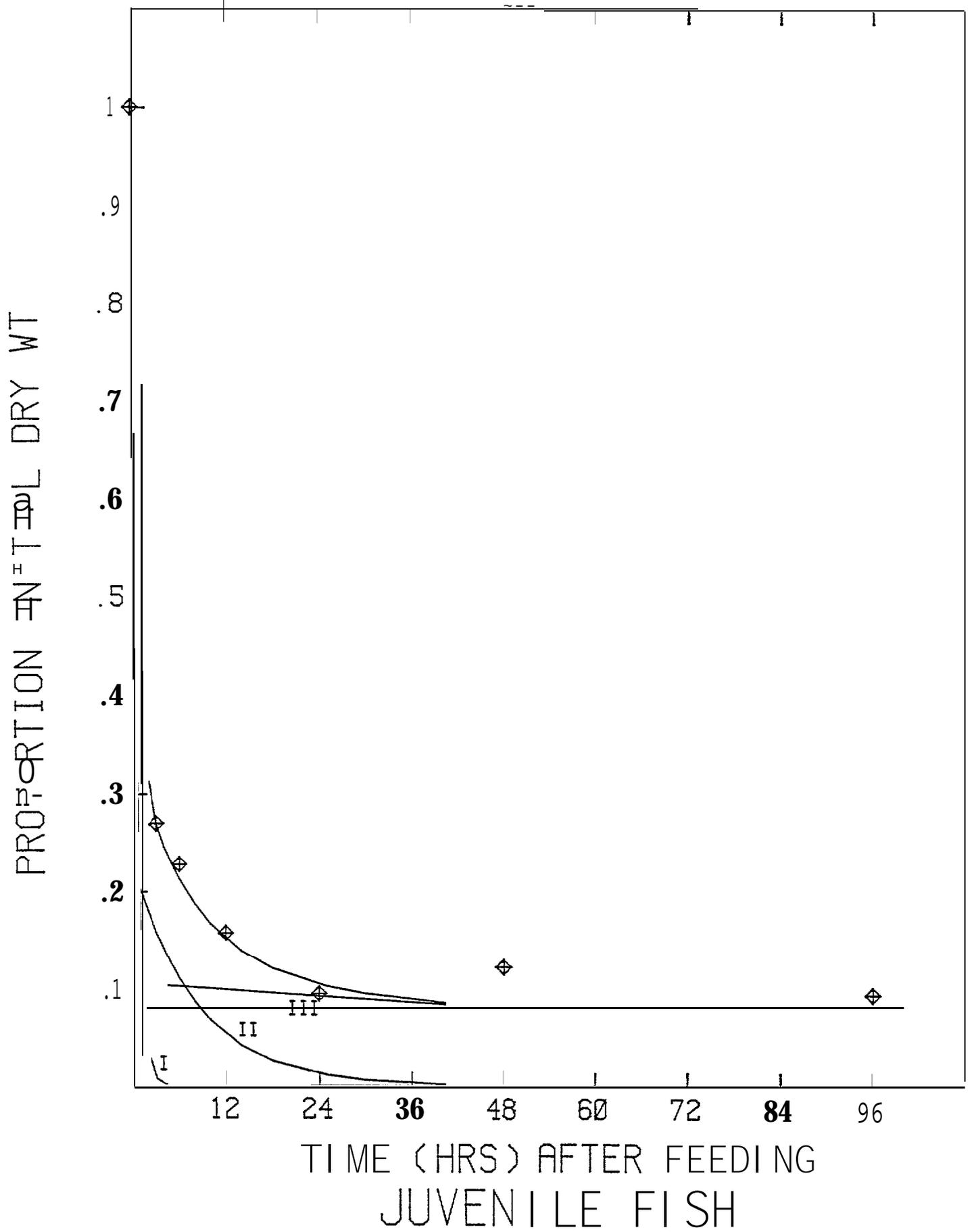


Table 5. Stomach clearance rates for specific prey items fed to juvenile king\_crab. W = proportion of initial g dry weight/g crab wet weight, T = time in h after feeding or isolation,  $\bar{T}$  = mean life, the reciprocal of the decay constant.

Prey	Avg. dry Wt (g) @ t = 0	Equation	R <sup>2</sup>	$\bar{T}$ by (h) compartment	Time (h) to 10% of initial	Time (h) to 5% of initial
Diced clam	0.425	$W=1.003e^{-0.494T}+0.0518e^{-0.0000022T}$	92.9	2.0 4.5X10 <sup>5</sup>	6.1	asymptotic to 5% @ 11 h
Shrimp	0.212	$W=0.763e^{-0.0271T}+0.233e^{-0.0224T}$	96.6	3.69 44.5	37.5	68.5
Barnacles	0.180	$W=0.598e^{-0.225T}+0.192e^{-0.128T}+0.200e^{-0.000033T}$	97.6	4.45 7.84 3.0x10 <sup>4</sup>	asymptotic to 20% @ 48 h	
Juvenile fish	0.525	$W=0.666e^{-1.518T}+0.229e^{-0.121T}+0.106e^{-0.0058T}$	99.8	0.66 8.23 172.0	26.5	129.5
Tube worm	0.502	$W=0.912e^{-0.204T}$	99.5	4.9	10.8	14.2

when compared to each other but have slower decay constants when compared with unexposed soft tissue.

If the coefficients for each compartment represent the proportions of tissue types present at  $T = 0$ , then we see that for barnacles and fish 20% and 10%, respectively, of the ingested material have very long stomach residence time. For lobsters, Homarus americanus, Carter and Steele (1982) found that barnacle plates and bivalve shells remain in the stomach for 180 days. Because we followed the stomach clearance for only 4 days in the king crab, the third compartment for barnacles appears almost indefinite (mean life  $\sim 1000$  d). Even so, our estimate for barnacles is not totally unimaginable given Carter and Steele's (1982) findings.

Determinations of diet composition are biased in favor of those items with long stomach residence times (Peterson and Bradley, 1979) and we shall use our findings concerning clearance rates for specific prey items to correct our diet composition following Peterson and Bradley (1979). The occurrence of multi-compartmental models makes it inappropriate to use mean life, the reciprocal of the decay constant, as a measure of stomach residence time because we know of no legitimate way to combine the mean lives from several compartments into one number. Instead we shall take the time required from the dry weight to fall to 5% of initial value as a measure of stomach residence time. Such estimates can be readily calculated from the exponential equations and appear in Table 5. We would estimate the stomach residence time of prey items we did not feed to the crabs by their similarity to those we did.

Estimating an appropriate residence time for shell fragments appears problematic but a reasonable estimate is possible. Carter and Steele (1982) found that shell fragments remained in lobster stomachs 90 to 180 d (2160 to

4320 h). Hill (1976) observed no decrease in the weight of shell fragments in the stomachs of the crab, Scylla serrata, during 8 days of observations while soft tissue fell to 5% of its initial level in 12 h and fishbone, to >5% in about 3.5 days (-84 h). We found barnacle tissue reaching 5% of its initial dry weight at  $3.0 \times 10^4$  h (1250 days). Hard tissue, such as barnacle plates and molluscan shell fragments, appear to remain indefinitely in crab stomachs. Hill suggests that crabs regurgitate the shell rather than pass it to the lower digestive system. We have seen captive blue crab, Callinectes sapidus, and Dungeness crab, Cancer magister, periodically regurgitate shell when held on an ad libitum diet of blue mussels. During shipboard holding of juvenile king crab we also observed regurgitated shell and sand dollar test fragments. We suggest that shell fragments and other hard tissue remain indefinitely in crab stomachs accumulating to a threshold volume at which point the crab regurgitates the entire volume at one time. If SO, our problem becomes one of determining the time frame within which the regurgitation will normally occur. During shipboard holding of juvenile king crab without food, regurgitated shell appeared 4 days after capture and occurred each night until the crabs were used in an experiment at 12 days after isolation. Five crabs sacrificed 7 days after isolation had no visible shell fragments, but we did not determine a dry weight of stomach contents for these individuals. Both Hill's (1976) data and our own indicate shell fragments have a longer stomach residence time than fish bone. In light of the available information, a stomach residence time for hard tissue such as shell fragments appears to be more than 5.4 days and could be on the order of 135 days for crustaceans continuing to feed on soft tissue. The shipboard observations on regurgitation and visual examination of the stomachs would indicate a residence time between 4 and 7 days, Our exponential model would

indicate one of 1250 days. The harmonic mean of these four estimates is 10.7 days. This latter value is used in our example of how we shall use the residence time data to correct the diet composition (Table 7).

#### SHIPBOARD OBSERVATIONS OF FEEDING BEHAVIOR

On shipboard, juvenile king crabs selectively ingested only certain parts of some prey. Crabs ate the fleshy portions of the shrimp and juvenile fish, leaving the heads. Similarly, crabs ingested little of the barnacle plates and mussel shell. Crabs scrapped the soft tissue from the hard parts with the palps and then dropped the cleaned hard parts. Only small fragments of plate or shell were ingested. Previously we have seen similar selective feeding on soft tissue and discarding of hard parts by the Dungeness crab, Cancer magister (Pearson et al., 1979, 1981). The implication of the selective ingestion observed in the king crab is that in actively selecting soft tissue and rejecting hard tissue, the crab is not ingesting prey items in proportion to the occurrence of hard parts of those items in the stomach. For example, juvenile king crab could well be consuming more clams than the presence of shell fragments indicates. We shall have to use the immunoassay with more prey items than originally thought to examine the diet composition for this bias.

#### DIEL FEEDING CHRONOLOGY

For juvenile king crab we have analyzed all the samples for the diel feeding chronology from June but have not yet completed analyzing those from August. In June we did not obtain adequate numbers of king crab at every hour of the day, but in August we obtained at least 25 crabs in each 2-h period of the 24-h cycle. In October we collected only one juvenile king

crab >20 mm CL. Consequently, our best estimate of the diel feeding chronology will come from the August samples. For tanner crab our sample sizes for crabs greater than 15 mm CW are inadequate.

For juvenile king crab in June the volume of solid material in the stomach averaged 18% of the maximum stomach volume, and the dry weight of the stomach contents, 1.630 mg dry weight/g crab wet weight (Table 6). Because of the low sample size and consequent high variance, there was no significant difference with time of day for the volume of solid stomach contents or the dry weight. Ignoring those times of day with less than 10 samples there was a decrease in stomach fullness during the day but again not a significant one. We await the results for August before drawing any conclusions. During the photoperiods of June, a nocturnal feeding rhythm present at other seasons may break down. The nocturnal rhythm suggested for adult king crab by Tarverdieva (1978) was based on sampling done in September.

We shall use the diel feeding chronologies coupled with the clearance rate data to calculate daily rations for June and August after Elliott and Persson (1978).

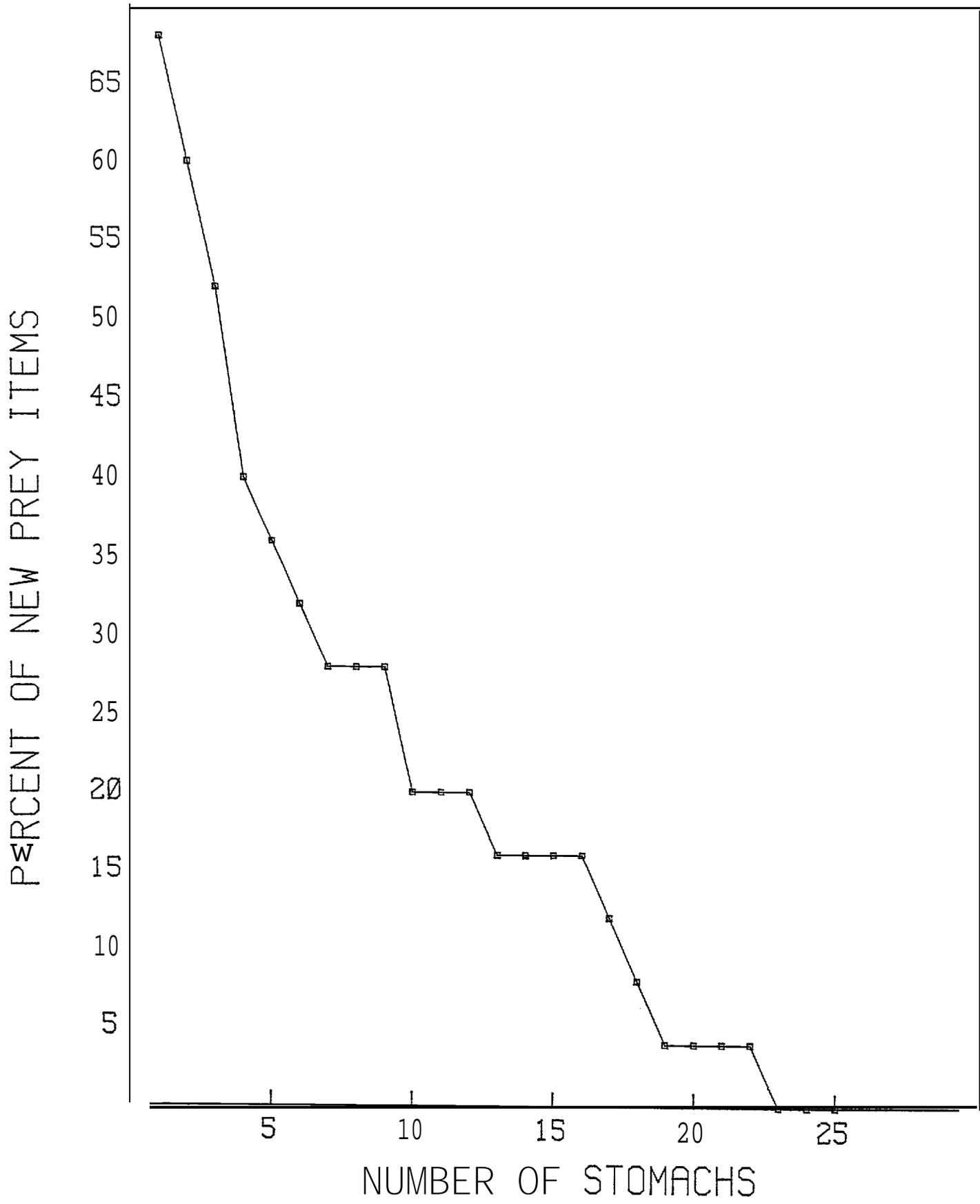
#### THE FREQUENCY OF NEWLY-DISCOVERED PREY AS A FUNCTION OF THE NUMBER OF STOMACHS EXAMINED

Following Vesin et al. (1981), we determined the frequency of newly-discovered prey as a function of the number of stomachs examined. In 25 stomachs of juvenile king crab from a single station we observed a total of 25 prey items. Examination of 19 stomachs gave 95% of the total number of prey items (Figure 6). Thus, 19 is the optimal number of stomachs to examine per sampling unit. Vesin et al. (1981) found that for capelin (Mal lotus villosus) examining beyond 10 to 15 stomachs added no new information that influenced overall estimates of diet composition,

Table 6. Diel feeding chronology from June, 1982, for juvenile king crab ( $\leq 90$  mm CL). Mean carapace length 64.5 ( $\pm 8.8$ ) mm.

Time of day	N	Volume of solids as % maximum stomach volume $\bar{x} \pm SD$		mg dry weight stomach contents/ per g crab wet weight $\bar{x} \pm SD$	
0100	4	6.8	3.0	0.635	0.230
0300	1	7.5		1.195	
0500	28	17.3	12.9	1.845	1.480
0700	18	21.1	13.3	1.742	1.030
0900	1	2.7		<b>0.539</b>	
1100	2	7.9	4.3	0.776	0.027
1300	24	16.6	14.5	1.346	1.310
1500	7	20.5	9.9	1.863	<b>1.010</b>
1700	4	11.4	7.3	1.176	1.030
1900	8	18.5	10.5	1.596	0.695
2100	22	20.2	14.7	1.723	<b>1.210</b>
2300	31	18.8	15.6	1.772	1.380
Overall	150	17.9	13.5	1.630	1.240

Figure 6. The frequency of newly discovered prey items as a function of the number of stomachs examined. Examination of 25 stomachs of juvenile king crab from one station gave a total of 25 prey items.



## DIET COMPOSITION

While final determination of diet composition awaits the analysis of more stomachs by visual examination and the immunoassay, we can make some preliminary comments. For juvenile king crab individual stomachs tend to contain predominantly one food type. Most of the variation in diet appears to be between individuals rather than within them. Small sand dollars, Echinorachius parma, (about 2 mm diameter) are the dominant recognizable item in many stomachs.

Table 7 gives a tentative estimate of diet composition based on the frequency of occurrence calculated from a limited number of stomachs. This table serves to illustrate how the clearance rate data **will** be applied to correct the diet composition for biasing toward prey with long stomach residence time and **will** change with more data. Note especially how prey with hard parts have a decreased percentage of occurrence in diet from that seen in the stomachs and the large increases in soft-bodied prey such as polychaetes. The immunoassay will give more information on the presence of soft-bodied animals and will, consequently, expand the number of prey items.

## PROBLEMS ENCOUNTERED AND APPROACHES

We have encountered problems in three areas: (1) we were **unable** to collect sufficient numbers of crabs in certain size classes and at certain times to accomplish some tasks, (2) our original determination of stomach fullness was confounded and additional unanticipated analyses with different techniques were required, and (3) we are encountering difficulty in working with the small amounts of material contained in the small stomachs of juvenile king and tanner crab and fear that some tasks will prove impossible with conventional methods.

Table 7. Tentative determination of diet composition of juvenile king crab in June 1982 (n = 25). Because we anticipate more analysis, please consider this table as an illustration. The average residence times are based on the clearance rates determined on shipboard.

	A Uncorrected % of occurrence in stomachs	B Average residence time h	C = A/B Relative frequency in total diet	D Corrected % of occurrence in diet
chitoderms				
<u>Echinorachius</u> <u>parma</u>	92	259 <sup>a</sup>	0.355	5.9
rustaceans (total)	44			
<u>Balanus crenatus</u>	8	259	0.031	0.5
<u>Pagurus</u> sp.	36	68.5	0.526	8.8
bivalves (total)	100			
<u>Cyclocardia</u> <u>cebricostata</u>	88	259	0.340	5.6
<u>Spisula</u> <u>polynma</u>	24	259	0.093	1.5
<u>Tellina lutes</u>	20	259	0.077	1.3
Bivalve A	4	259	0.015	0.2
B	4	259	0.015	0.2
c	12	259	0.046	0.8
D	16	259	0.062	1.0
E	8	259	0.031	0.5
astropods (total)	100			
<u>Osnopota</u> sp.	56	259	0.216	3.6
<u>Retusa obtusa</u>	4	259	0.015	0.2
<u>Soliarella</u> sp.	60	259	0.232	3.9
<u>Neverita nana</u>	16	259	0.062	1.0
Gastropod A	4	259	0.015	0.2
B	4	259	0.015	0.2
c	16	259	0.062	1.0
D	4	259	0.015	0.2
polychaetes	32	14.2	2.254	37.5
fish	8	129.5	0.062	1.0
plant matter	36	24	1.500	25.0
			6.008	

From Table 6 prey with hard parts, such as, barnacles appear to remain in the gut almost indefinitely. See also Carter and Steele (1982).

We have gaps in the size class distribution of the crabs collected. We found no juvenile C. opilio in the study area and, therefore, can not address any questions concerning juvenile Opilio crabs. For C. bairdi, we lack sufficient numbers of crabs above 20 mm CW for a credible diel feeding chronology for any of the three cruises. Because of the extremely small size of the Bairdi crab we do have, determination of the diet composition can probably only be accomplished with the immunoassay. We have only 10 juvenile red king crab below 40 mm CL and for these small juveniles the immunoassay is also probably the only practical technique. For juvenile king crab above 40 mm CL we have only one from October, but quite sufficient numbers from August for a credible diel feeding chronology and other analyses. Our strategy will be to concentrate on these samples. The diel feeding chronology completed for June appears in the Results section above. Given the uneven size distribution of our samples, we propose using the immunoassay to obtain frequency of occurrence data for the Bairdi crab and the king crab below 40 mm CL. We further recommend that red king crab below 40 mm CL that may be collected during the upcoming 1983 NOAA/MMS cruises in the North Aleutian Basin, be flash frozen for analysis by our immunoassay.

In our analyses for clearance rates, diel feeding chronologies, and daily rations, our original determination of stomach fullness proved inadequate because of substantial volumes of liquid in otherwise empty stomachs. As prescribed in the Results section, in analyzing more stomachs and reanalyzing preserved stomachs, we used dry weight as our basic measurement. This change in technique was successful but did entail a larger effort than we originally anticipated. Consequently we have devoted more labor and material to these necessary tasks than originally planned and are somewhat behind schedule.

We are encountering difficulty in working with the small amounts of material contained in juvenile crab stomachs. For king crabs of 20 mm CL and Bairdi crab of 20 mm CW, maximum stomach volumes are 0.1 and 0.08 ml, respectively. The stomachs are rarely full to the maximum volume and one can readily see that the total volumes of stomach contents, not to mention volumes for individual prey items, are at and below the minimums that can be measured accurately. For crabs less than 30 mm CL or CW, we feel the immunoassay is the only really practical analysis.

For crabs from 30 to 80 mm CL, there still remain difficulties for conventional techniques of stomach contents. In crab stomachs, shells and tests are finely ground to a powder and often mixed with sand so that the number of individuals can not be determined. Indeed, during the clearance rate determination we observed that particle size fell rapidly with time and is, therefore, a potential indicator of when the animal fed. Moreover, the volume and weights for individual prey items approach the minimum measurable. To obtain sufficient volumes and weights we shall have to pool to higher taxa, for example, we would measure the volume and weight of all the gastropod rather than each individual species. We also intend using the immunoassay and the conventional visual examination on the same set of samples to obtain a comparison of frequency of occurrence data.

#### CURRENT AND PLANNED ACTIVITIES

We are now completing the diel feeding chronology for August based on dry weight measurements. From the diel feeding chronology we shall determine the daily ration and the peaks of feeding activity. We shall concentrate analyses for diet composition by visual examination of stomach contents on samples from the feeding activity peaks. The clearance rate data will

correct the diet composition based on visual examination for bias toward prey with long residence times. Data from the yet-to-be-funded immunoassay will not only lengthen the list of prey items but also probably change their relative frequencies in the diet. We shall obtain caloric equivalents for prey types from the literature. The data on caloric values, diet composition, and daily rations will be combined to yield a schedule of food requirements for juvenile crabs.

When the immunoassay is funded, we intend to **apply** the immunoassay and continual visual analysis to the same stomachs and thereby obtain a direct comparison of the results of both methods.

#### TENTATIVE CONCLUSIONS AND RECOMMENDATIONS

Juvenile red king crab, Paralithodes camtschatica, were concentrated off Port Moller whereas juvenile tanner crab, Chionoecetes bairdi, were concentrated in the Amak Island Black Hill Region. Both species were in deeper water in August, 1982 than in June, 1982.

A power law can be described in the relationship between carapace size and maximum stomach volume in both king and tanner crab. Sex and shell condition did not affect the relationship. Our model differs substantially from that currently used by other workers.

Shipboard experiments showed that the clearance of contents from the stomachs of juvenile king crab was best described by **multicompartmental** exponential decay models. Stomach residence time calculated from these models showed considerable variation with prey type. Soft tissue, such as shucked clam, clears in 11 h while hard tissue, such as barnacle plate, remains in the stomach almost indefinitely ( $10^4$  h) unless regurgitated.

In June, 1982, juvenile king crab had daily means of 18% for the volume of solids as percentage of maximum stomach volume and 1.630 mg dry weight of stomach contents per gram crab wet weight. Because some times of day in June had inadequate sample sizes, determination of peaks in feeding activity awaits analysis of the more complete set of samples from August, 1982.

While final determination of diet composition requires further analysis and the yet-to-be-funded immunoassay, application of the stomach residence times estimated from the clearance rate models to preliminary estimates of diet composition shows that relative frequencies of prey items actually in the diet as opposed to observed in stomachs are quite sensitive to residence time.

Because of a real paucity of red king crab below 50 mm CL in our collection, we recommend that during the 1983 NOAA/MMS study of red king crab distribution in the North Aleutian Basin any crabs below 50 mm CL collected be flash frozen immediately after capture and made available to us for stomach content analysis with the immunoassay. Available information indicates that crabs in their first and second years may differ substantially in food habits from older juveniles. Given such differences, a clear picture of the food habits of the smallest king crabs should rest on more than 10 samples.

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