

Section 8

PATTERNS OF ENERGY FLOW: A CONCEPTUAL MODEL

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8.1 SUMMARY

This section attempts, by means of a conceptual model, to quantify energy flow through the **biota** of the NAS nearshore zone. Data used in development of the model are from samples collected during the present study (May, July, September, and January), from other studies in the southeastern Bering Sea (primarily PROBES), and from the general literature.

Pelagic primary production (phytoplankton) is by far the major source of energy to the invertebrate and vertebrate food web; **eelgrass** carbon reaches these consumers in **insignificant** amounts. Further, the estimated primary productivity far exceeds its estimated consumption by herbivores, both planktonic and benthic; the "excess" is possibly exported from the system and/or attenuated through benthic meiofaunal pathways.

A far greater proportion of the annual primary productivity is consumed by the benthos than by the zooplankton, but because the benthos are relatively inefficient producers, approximately equal amounts of zooplankton and benthos enter the vertebrate food web.

The measured availability of zooplankton was insufficient to feed the estimated abundance of zooplankton consumers. This undoubtedly represents some level of error in estimation, but at any rate suggests that the zooplankton are heavily cropped by the consumers. We postulate that this intensive predation on the zooplankton might depress their population growth, their standing stocks in summer, and ultimately their annual production, resulting in a phytoplankton biomass that is largely **ungrazed** in the water column, and ultimately settles or is exported.

Predation upon the benthos also appears to be intense. Though less well supported by measurements, it is possible that this predation is also sufficient to curtail standing stocks and annual productivity of the **infauna** and the epifauna.

The herbivorous invertebrates, both planktonic and benthic, thus appear to be (because of their scarcity) a weak link in the efficient transfer of primary production to the **vertebrate** community. Further, if the model we have constructed is valid, appreciable fluctuations in

abundance of these herbivores might affect the ability of the vertebrates to acquire sufficient food when they forage in the NAS **nearshore** area.

8.2 INTRODUCTION

The conceptual model described in this section depicts the flow of energy through the **biota** of the **NAS**. The area considered (approximately 8363 km²) extends along the coast between Cape Mordvinof and Cape Seniavin, and from shore to the 50 m contour. The purpose of this model is to (1) quantify the major pathways by which biological energy flows from primary producers to vertebrates, (2) identify the key components in the food web, (3) describe the seasonal variability in 1 and 2, and (4) illustrate the relative importance of **eelgrass** detritus in this food web. Energy flow is considered for sampling periods in May, July, September, and January, and an annual summary model is produced.

8.3 METHODS

Many sources of information were used in the development of this model. Primary productivity levels on the NAS have been estimated by **Schell** and Saupe (Section 3.0, this report). Secondary productivity and food consumption by zooplankton were estimated by applying data obtained during the PROBES study and other relevant studies to this study's estimates of standing crop and **taxonomic** composition of the zooplankton. Secondary productivity and food consumption by the benthos were estimated by applying relevant productivity and respiration values obtained in the literature to our estimates of standing crop. The distributions and abundances of birds and marine mammals were determined through aerial surveys during each month of the year (Sections 6.0 and 7.0, this report). Feeding habits of each species *were* determined from data collected in the field (Section 6.0, this report) or from the literature. Feeding rates *were* determined from the literature. Distributions and abundances of fishes determined during five cruises in this study (Section 5.0; this report) were integrated with data found in the literature. Fish feeding habits were determined from data collected during this study (Section 5.0; this report) and feeding rates were taken from the literature.

Estimates used in constructing the energy flow model are subject to appreciable error. A subjective evaluation of the suspected accuracy of the data used in model construction shows considerable variability in data quality, as follows:

	<u>Quality of Data (1 = poor to 5 = good)</u>		
	Standing Crop	Productivity	Feeding
Zooplankt on	4	3	3
Infauna	4	1	1
Benthic orustaoea	1	1	1
Forage fish	2	NA ¹	4
Demersal fish	3	NA	4
Other fish	2	NA	4
Seabirds	4	NA	2
Marine mammals	4	NA	2

¹NA means not applicable.

Some major sources of inaccuracy are described below. The peak in zooplankton standing crop may have been missed in our sampling, and zooplankton productivity data from the nearby PROBES study area may not be applicable in all cases to the **NAS**. Standing crop of **infauna** is well described from sampling conducted during this study and by Cimberg et al. (1984), but there are no data on feeding rates, productivity, or seasonal variability in standing crop. Data on feeding rates and productivity of **infauna** and benthic **crustacea** are little more than an educated **guess**. The standing crop of benthic orustacea is not well described. The abundances of forage fishes are not well described because of sampling limitations. Abundances of **seabirds** and marine mammals are well described through the monthly aerial surveys. Feeding habits of **seabirds** and fishes are well documented for some species and circumstances but not for others. Feeding habits of marine mammals are extrapolated from other areas, and thus are known only in a general way.

Estimates of average consumption rates for vertebrates have been extracted from the literature, and these may not always reflect actual consumption because nutritional requirements vary with activity (e.g., migration, resting, reproduction). Feeding rates for some species and circumstances are unknown. For instance, in the case of gray whales, the amount of feeding that actually occurs during their migration through the NAS is unknown.

All computations were done on an IBM AT microcomputer using the Lotus 123 spreadsheet.

8.3.1 Zooplankton

For each of six Miller Freeman cruises (May and September 1984; January, April, May, and July 1985), wet weight biomass of each **taxon** of zooplankton in each oblique Bongo net tow was converted to an equivalent biomass of carbon using values shown in Appendix 8.1. For each cruise, respiration was estimated using **Ikeda's (1985)** equation (see Appendix 8.2 for details). Growth, ingestion and assimilation were estimated using **Dagg et al.'s (1982)** and **Vidal and Smith's (1986)** data describing the spring bloom in the nearby PROBES study area (Appendix 8.2). **Vidal and Smith (1986)** suggested a weight-specific growth rate of 10 to 15% for the period June to October; we used the lower figure for this time period and a figure of **15%** for the April/May spring bloom period.

Separate consumption estimates were made for herbivores (copepods, pteropods, euphausiids) and **for** carnivores (chaetognaths, hyperiid amphipods). Jellyfish were also treated separately because they consume both carnivorous and herbivorous zooplankton. Data were interpolated for months between cruises in order to produce annual estimates.

8.3.2 Benthos

Infaunal animals collected in grab samples were grouped according to their mode of feeding, and wet weights were converted to carbon using the values shown in Appendix 8.1. Biomasses of crustaceans in the grabs (mainly amphipods), starfish and crangoniids in trawls, and mysids in epibenthic sleds were also converted to carbon-equivalent biomasses. The

values for respiration ($0.3 \mu\text{l O}_2/\text{mg dry wt/hr}$), for assimilation (0.64) , and for productivity-to-biomass ratios (1.17) used by Walsh and McRoy (1986) for the **infauna** of the middle Bering Sea shelf were used in most cases. The productivity-to-biomass ratio of 2, determined for northern Bering Sea amphipods (Thomson 1984), was used to estimate productivity of **crustacea**. Productivity and consumption by mysids were estimated in the same manner as for zooplankton (Appendix 8.2).

8.3.3 Seabirds and Marine Mammals

The results of aerial surveys (Sections 6.0 and 7.0, this report) were used to estimate the abundances of **seabirds** and marine mammals. Body weights of **seabirds** were estimated using actual weights of birds collected during this study and from the literature. Weights of marine mammals were taken from the literature. Consumption rates of birds and mammals were taken from the literature (Appendix 8.3) and feeding habits were taken from the literature and from data collected in the field (Sections 6.0 and 7.0, this report) and the literature.

8.3.4 Fish

The standing crops, consumption rates, and **timing** of fish occurrence in the study area are shown in Appendix 8.4. Dietary information was collected in the field (Section 5.0, this report).

8.4 RESULTS

8.4.1 Zooplankton

Estimated ingestion rates of phytoplankton by herbivorous zooplankton ranged from $164 \text{ mg C/m}^2/\text{mo}$ in September to $2037 \text{ mg C/m}^2/\text{mo}$ in July; the total annual consumption rate was estimated to be $5380 \text{ mg C/m}^2/\text{yr}$ (Table 8.1). These figures are very low compared with primary production levels of 30 to $60 \text{ g C/m}^2/\text{mo}$ and an annual estimate of $225 \text{ g C/m}^2/\text{yr}$ (Section 3.0, this report). Thus, it appears that, as in the case of many shallow

Table 8.1. Estimated average standing crop and rates of production and consumption for zooplankton on the NAS, Alaska. See Appendix 8.2 for methods of calculation.

	Monthly estimates (mg C/m ² /mo)*					Annual Estimates (mg C/m ² /yr)*
	Jan	April	May	July	Sept	
Herbivores						
Standing crop	28.2	33.9	47.1	284.4	21.9	72.2
Respiration	27.2	28.1	70.2	390.5	34.9	1141.7
Growth	0	152.5	212.0	853.2	65.7	2301.1
Winter storage	0	21.7	30.2	182.3	14.0	465.6
Total assimilated	0	202.4	312.4	1426.0	114.6	3766.6
Fecal production	0	86.7	133.9	611.2	49.1	1614.3
Total ingestion	0	289.1	446.2	2037.2	163.8	5380.9
Carnivores						
Standing crop	47.4	22.8	23.1	36.0	8.1	28.7
Respiration	42.6	17.0	19.3	39.5	9.9	320.7
Growth	0	102.6	104.0	108.0	24.3	550.4
Winter storage	0	13.4	13.6	21.2	4.8	94.4
Total assimilated	0	133.1	136.8	168.6	39.0	802.6
Fed production	0	33.3	34.2	42.2	9.7	200.7
Total ingestion	0	166.3	171.0	210.8	48.7	1003.3
Jellyfish						
Standing crop	32.4	24.0	19.5	33.9	273.9	90.2
Respiration	7.6	4.7	4.5	10.1	92.4	229.2
Growth	0.0	3.6	2.9	3.4	27.4	76.6
Winter storage	0.0	4.0	3.3	5.7	46.0	125.0
Total assimilated	0.0	12.3	10.7	19.2	165.8	430.8
Fecal production	0.0	1.4	1.2	2.1	18.4	47.9
Total Ingestion	0.0	13.7	11.8	21.4	184.2	478.7

* For **standing crop**, mg C/m²; annual estimate is average of monthly estimates.

northern seas, much of the primary productivity was not utilized by the zooplankton and was therefore, available to the benthos.

The estimated consumption of zooplankton by carnivorous zooplankton and jellyfish accounts for about 1500 of the 2900 mg C/m² annual growth (production) by the herbivores and carnivores (Table 8.1), leaving about 1400 mg C/m² available for higher trophic levels.

On the NAS, the highest zooplankton biomass (thus, probably highest production) was found in the July sampling period, but the peak in biomass could have occurred in June, when sampling was not conducted. On the outer shelf and slope of the southeastern Bering Sea, Vidal and Smith (1986) found that zooplankton biomass and production peaked in mid-May. On the middle shelf, they found that both biomass and production were increasing in early June when their sampling ended; the timing of the peaks in growth and biomass were unknown. If the peak did occur in June on the NAS, then total annual productivity of herbivores could be as high as 5 g C/m². This is far lower than the 40-50 g C/m²/yr produced by herbivores on the outer shelf and slope, or the 30 g C/m²/yr produced on the middle shelf (Vidal and Smith 1986).

8.4.2 Benthos

Because most of the phytoplankton was not utilized by the zooplankton, it presumably sank and became directly available to benthic filter- and surface deposit-feeders as a high-quality food source. Consumption by filter- and deposit-feeding benthos, based on application of respiration, production and assimilation estimates to biomass, was about 136 g C/m²/yr (Table 8.2). This is over half of the estimated 225 g C/m²/yr produced annually by the phytoplankton.

Most of the annual production by deposit and filter feeders appears to be consumed within the benthic invertebrate food chain (Table 8.2). The estimated net availability of all benthos to higher trophic levels is about 1500 mg C/m²/yr (production of filter feeders, deposit feeders and carnivores less consumption by invertebrate carnivores), which is approximately equal to the zooplankton available (see previous Section 8.4.1).

Table 8.2. Estimated annual respiration, growth and consumption by the benthos on the NAS, Alaska. See **Section 8.3.2** for methods of calculation.

	Average Standing Crop (mg C/m ²)	Annual Carbon Budget (mg C/m ² /yr)				
		Respiration	Production	Total Assimilated	Fecal Production	Total Consumption
Filter and deposit feeders						
Filter feeders	393	1359	459	1817	1022	2839
Surf. dep. feeders	3267	76575	3812	80386	45217	125604
Deposit feeders	437	1833	510	2343	1318	3661
Other	331	519	386	906	509	1415
Crangonids	9	47	18	65	37	102
Other crustacea	229	680	458	1138	640	1778
Mysids*	10	67	44	156	67	222
Total	4676	81080	5686	86811	48810	135621
Carnivores						
Infaunal carnivores	606	2307	707	3014	1696	4710
Starfish	20	62	23	85	48	132
Total	626	2369	730	3099	1743	4843

*See **Appendix 8.2** for methods of calculation; 'total assimilated' includes winter storage.

8.4.3 Flow of Primary Organic Matter

Over 50% of the estimated total organic input (carbon fixed by primary production) to the NAS cannot be accounted for (Table 8.3). A similar surplus of carbon appears to occur on the outer shelf, according to Walsh and McRoy (1986). On the outer shelf, however, zooplankton consumption of phytoplankton may be far higher than the 68 g C/m² estimated by these authors (see Vidal and Smith 1986).

There are three possible fates for this apparent surplus of organic carbon detritus on the NAS, as follows: (1) it is exported from the area, (2) it is consumed by bacteria, and (3) consumption by the benthos is higher than estimated. Evaluations of these possibilities follow.

1. Export from the NAS. The residence time of water in the NAS area is on the order of 10 to 20 days (*Section 2.0*, this report). Thus, a significant portion of the primary production could be exported to the middle shelf or, likely to a much lesser extent, to the coastal domain of inner Bristol Bay (see Walsh and McRoy (1986) and Walsh et al. (1985) for a discussion of the possible fate of this material).
2. Consumption by bacteria. Based on data provided by Griffiths et al. (1983), microbial respiration in Port Moller is about 100 g C/m²/yr, end in the St. George Basin it is about 10 g C/ m²/yr. Thus, it appears that a high proportion of the unused detritus could enter a bacterial/meiofaunal food chain.
3. Increased consumption by benthos. The productivity-to-biomass ratio of the NAS benthos was assumed to be 1.17, the figure used by Walsh and McRoy (1986). Given the food availability and warm bottom temperatures in these shallow waters in summer (3°C in May to 9.5°C in September), productivity of the benthos could be much higher than estimated. A higher rate of productivity would require a higher rate of consumption.

Table 8.3. Sources and fate of primary production through the lower **trophic** levels of the southeastern Bering Sea (**g C/m²/yr**). Except where noted, data are from Tables 8.1 and 8.2.

	Outer Shelf*	Middle Shelf*	North Aleutian Shelf
Phytoplankton production	162	166	225
Consumption by herbivorous zooplankton	68	36	5
To detritus pool	<u>94</u>	<u>130</u>	<u>220</u>
Detritus pool			
Phytoplankton not consumed	94	130	220
Zooplankton fecal pellets	20	8	2
Rivers and eelgrass			30**
Total	<u>114</u>	<u>138</u>	<u>252</u>
Detritus consumption			
Infaunal benthos	11	138	135
Meiofauna	29	22	22*
Total	<u>40</u>	<u>160</u>	<u>157</u>
Total detritus accumulation			
Not consumed	74	-22	95
Infaunal fecal production	5	50	51
Total	<u>79</u>	<u>28</u>	<u>144</u>

* from Walsh and **McRoy** (1986).

** From **Schell** and Saupe (this report).

On the NAS, all three of these factors likely account for the apparent surplus of carbon, but the relative importance of these factors remains unknown.

8.4.4 Seabirds and Marine Mammals

Estimated annual prey consumption by **seabirds** and marine mammals is shown in Table 8.4. In terms of biomass, benthic **crustacea**, **infauna**, fish and plankton appeared to be consumed in approximately equal quantities by

Table 8.6. Estimated annual consumption by seabirds and marine mammals on the NAS, Alaska. Crustacea eaten by surface and mid-water feeders are planktonic; those eaten by benthic feeders are benthic. See Appendix.8.3 and Section 8.3.3 for methods of calculation.

	Feeding Type*	Prey Consumed (mg C/m ² /yr)				Total
		Crustacea (Plankton, Benthos)	Fish	Benthic		
				Invertebrates	Otter	
Seabirds						
Shearwater-dark	S	100.32	3.60	0.00	3.47	107.40
Glaucous winged gull	S	13.49	22.75	5.43	9.27	50.95
Black-legged Kittiwake	S	1.76	17.84	0.00	0.35	19.95
Northern fulmar	S	0.04	0.51	0.00	0.15	0.70
New gull	S	0.14	0.48	0.07	0.00	0.68
Jaeger	S	0.13	0.10	0.00	0.10	0.32
Tern	S	0.04	0.17	0.00	0.00	0.21
Phalarope	S	0.19	0.00	0.00	0.00	0.19
Bonapartes gull	S	0.00	0.00	0.00	0.00	0.01
Fork-tailed storm-petrel	S	0.00	0.00	0.00	0.00	0.01
Sabine's gull	S	0.00	0.00	0.00	0.00	0.00
Auklet	M	13.66	1.54	1.37	0.51	17.08
Murre	M	0.00	10.68	0.00	0.00	10.68
Comorant	M	0.15	7.87	0.00	0.35	a.37
Tufted puffin	M	0.01	0.35	0.05	0.02	0.44
Loon	M	0.08	0.29	0.02	0.00	0.38
Red-breasted merganser	M	0.06	0.19	0.00	0.00	0.25
Alcid	M	0.00	0.05	0.01	0.01	0.07
Horned puffin	M	0.01	0.05	0.00	0.00	0.06
Murrelet	M	0.02	0.02	0.00	0.00	0.04
Grebe	M		0.03	0.00	0.00	0.04
Scoter	B	0.00	1.30	65.85	1.50	74.68
King eider	B	0.29	0.00	23.07	0.01	23.37
Steller's eider	B	0.46	0.00	19.26	0.60	20.32
Duck	B	1.79	0.30	3.08	0.00	5.97
Oldsquaw	B	1.30	0.50	0.19	1.34	3.33
Common eider	B	0.57	0.00	1.20	0.07	1.85
Harlequin duck	B	0.00	0.00	0.15	0.01	0.16
Pigeon guillemot	B	0.00	0.00	0.00	0.00	0.01
Marine Mammals						
Steller's sea lion	M	0.00	89.81	0.00	0.00	89.81
Harbor seal	M	0.52	9.89	0.00	0.00	10.41
Small (minke) whale	M	0.34	0.30	0.00	0.03	0.67
Harbor porpoise	M	0.00	0.15	0.00	0.15	0.31
Pac. white-sided dolphin	M	0.01	0.17	0.00	0.05	0.23
Dall porpoise	M	0.01	0.03	0.00	0.15	0.19
Grey whale	B	84.07	0.00	0.86	0.86	as.70
Sea otter	B	8.96	0.05	55.52	0.47	65.01
Walrus	B	0.05	0.00	0.99	0.00	1.04
Summary						
Seabirds						
Surface feeders		116	45	6	13	180
Mid-water feeders		14	21	1	1	37
Benthic feeders		10	2	114	4	130
Total		141	69	121	18	348
Marine Mammals						
Mid-water feeders		1	100	0	0	102
Benthic feeders		93	0	57	1	152
Total		94	100	57	2	253
Total by surface feeders		116	45	6	13	180
Total by mid-water feeders		15	121	1	1	139
Total by benthic feeders		104	2	171	5	282
Grand total		235	169	178	19	601

* S = surface feeders; M = mid-water feeders; B = benthic feeders.

birds and mammals on the **NAS**, as shown below:

	Plankton	Benthos		Fish	Other
		Crustacea	Infauna		
Total consumption (mg C/m ² /yr)	131	104	178	169	19

An approximately equal biomass was consumed by **seabirds** and by marine mammals. For birds and marine mammals, pelagic (surface and mid-water) feeders consumed an amount similar to that eaten by benthic feeders. **Major** consumers were shearwaters, Steller sea lions, gray whales, sea otters, **scoters**, and glaucous-winged gulls. Together, these six species accounted for an estimated **79%** of consumption by **seabirds** and marine mammals.

Table 8.5. Estimated annual consumption by fish on the NAS, Alaska. See Appendix 8.4 and Section 8.3.4 for methods of calculation.

	Consumption of prey (mg C/m ² /yr)				Total
	Plankton	Fish	Benthic Crustacea	Infaunal Benthos	
Pelagic feeders					
Salmon adults	14	0	0	0	14
Salmon juveniles	3	3	0	0	6
Herring/capelin	260	0	0	0	260
Sand lance	2617	0	26	1	2667
Other forage fish	13	13	4	24	32
Total	2907	16	31		2978
Benthic feeders	2060	2491	3299	3057	10907
Grand total	4967	2507	3330	3081	13885

8.4.5 Fish

Estimated annual consumption of various types of prey by fish is shown in Table 8.5. Benthic crustacea (3.3 g C/m²/yr), zooplankton (5 g C/m²/yr), infauna (3.1 g C/m²/yr), and fish (2.5 g C/m²/yr) were consumed in approximately equal quantities. In all, fish consume more than an order of magnitude more prey than do birds and marine mammals (14 g C/m²/yr vs. 0.6 g C/m²/yr). Demersal fish (pollock, cod, and flatfish) consumed considerably more than the pelagic feeders (Table 8.5). Most of the pelagic feeding was by the sand lance and by the large pulse of herring and capelin that passes through the study area in midsummer.

8.4.6 Summary and Discussion

Two important aspects of food webs on the NAS need to be summarized. First, we need an overview of the prey groups important in the diets of the important vertebrates--fish, birds, and mammals. Second, we need to examine discrepancies within the energy flow model we have built, for example to see whether estimated biomasses of prey consumed exceed the estimated availability of the prey.

Table 8.6 summarizes the estimated biomasses of the various prey groups consumed by fish, birds, and marine mammals on the NAS. Several points are noteworthy. Nearly half (46%) of the total biomass consumed was benthic; half of this was epibenthic (mostly decapods and amphipods). The other half of the total consumed was either zooplankton (35%) or fish that eat mainly zooplankton (19%); the major zooplankton groups consumed were copepods and euphausiids (Table 8.6).

The energy flow model does not always "balance"; that is, the amount of energy estimated to be available to consumers does not always approximate the amount estimated to be consumed (Tables 8.7 and 8.8). Beginning at the lower end of the food web, we see that the estimated primary productivity far exceeds its estimated consumption by herbivores (Table 8.3). The "excess" primary productivity may have been exported or consumed by bacteria (which were *not* sampled). Alternatively, benthic herbivore biomasses or productivity may have been underestimated.

Another discrepancy relates to the zooplankton. The measured availability of the zooplankton was not sufficient to feed the zooplankton consumers (Table 8.7). Based on vertebrate diets and on estimated

Table 8.6. Estimated consumption of major prey by fish, **seabirds** and marine mammals on the NAS, Alaska.

Prey Taxa	Consumption					
	Birds and marine mammals		Fish		Total	
	mg	C/m²/yr %	mg	C/m²/yr %	mg	C/m²/yr %
Plankton						
Copepods	4	0.7	2264	16.3	2268	15.7
Euphausiids	117	19.4	1275	9.2	1392	9.6
Mysids			864	6.2	864	6.0
Other zooplankton	10	1.7	563	4.1	573	4.0
Total	131	21.8	4967	35.8	5098	35.2
Nekton						
Squid	3	0.5			3	0.0
Sand lance	63	10.5	1247	9.0	1310	9.0
Other fish	106	17.6	1259	9.1	1365	9.4
Total	172	28.6	2507	18.1	2679	18.5
Infauna						
Bivalves	159	26.4	310	2.2	469	3.2
Gas tropods	5	0.8			5	0.0
Echinoderms	12	2.0	1015	7.3	1027	7.1
Polychaetes	3	0.5	1333	9.6	1336	9.2
Other infauna			424	3.1	424	2.9
Total	179	29.7	3081	22.2	3260	22.5
Benthic Crustacea						
Decapods	9	1.5	1002	7.2	1011	7.0
Amphipods	84	14.0	1375	9.9	1459	10.1
Other Crustacea	10	1.7	953	6.9	963	6.6
Total	103	17.1	3330	24.0	3433	23.7
Other	17	2.8		0.0	17	0.1
Total	602	100.0	13885	100.0	14486	100.0

biomasses of **vertebrates**, we calculate that 5.1 g **C/m²** of zooplankton was consumed by vertebrates annually (Table 8.7). The total measured availability of zooplankton, however, was estimated to be only about 1.5 g **C/m²/yr** (Table 8.7 and Section 8.4.1). If the peak of zooplankton biomass and growth occurred in June (when no sampling was done) rather than in July, and was relatively similar in magnitude to that occurring on the middle and outer shelf areas, then zooplankton availability might be

Table 8.7. Comparison of estimated prey availability vs consumption by vertebrates on the NAS.

	Monthly availability and consumption (mg C/m ² /mo)				Estimated Annual (mg C/m ² /yr)
	Jan	May	July	Sept	
Zooplankton					
Herbivores					
Standing crop	28	47	284	22	72
Production	0	212	853	66	2301
Carnivores					
Standing crop	47	23	36	8	29
Production	0	104	108	24	550
Grass availability	76	386	1282	120	2952
Consumption by invertebrates					
by carnivorous zooplankton	0	171	211	49	1003
by jellyfish	0	12	21	184	479
Total	0	183	232	233	1482
Net availability	76	203	1049	0	1470
Consumption by vertebrates					
Birds and marine mammals	10	26	<1	2	131
Fish	36	448	1071	338	4968
Total	46	474	1071	340	5099
Nsh					
Standing crop	882	1992	3550	1902	1898
Consumption by wrtebrates					
Birds and marine mammals	11	24	10	14	169
Fish	44	353	353	342	2507
Total	55	377	363	356	2676
Benthos					
Availability					
Standing crop	*	*	*	*	5302
Productivity	*	*	*	*	6416
Gross availability	*	*	*	*	11718
Consumption by benthos	*	*	*	*	4843
Net benthic availability	*	*	*	*	6875
Consumption by vertebrates					
Birds and marine mammals	17	43	3	34	282
Fish	112	895	908	867	6411
Total	129	938	911	901	6693

* Data are insufficient for monthly estimates.

Table 8.8. Estimated biomasses of major food web components on the NAS, Alaska, in terms of how **much** is available and how much is consumed. Discrepancies between the amount available and the amount consumed suggest sampling biases or net influx or export of components.

Food Component	Food Biomass (g C/m /yr)						Difference (Biomass and % of Availability)	
	Available	Consumed				Total	Surplus	Deficiency
		Zoopl.	Benthos	Fish	Birds/Mamm.			
Primary Production ¹	225.0	5.0	157.0	0.0	0.0	161.0	64 (28%)	
Zooplankton	7.9	1.5		5.0	0.1	6.6		3.6 (120%)
Benthos	11.7	0.0	6.4	3.5	0.3	11.5	0.2 (2%)	
Fish	1.9	0.0	0.0	2.5	0.2	2.7		0.8 (42%)
Birds & Mammals	0.03	No Significant		Consumers		0.0	0.03 (100%)	

¹Largely phytoplankton; eelgrass contribution to higher levels in the food web is negligible.

greater than the amount estimated by as much as $1.0 \text{ g C/m}^2/\text{yr}$, but would still be less than estimated consumption.

On the middle shelf a high biomass of zooplankton is maintained until October (Vidal and Smith 1986). From April to October, productivity of the herbivores is about $40\text{-}50 \text{ g C/m}^2$ on the outer shelf and about 30 g C/m^2 on the middle shelf. Water exchange between the NAS and offshore waters is rapid and all of the water in the NAS is exchanged every 10-15 d (see Section 2.0, this report). About $12.6 \text{ mg C/m}^2/\text{d}$ or $2.7 \text{ g C/m}^2/\text{yr}$ of zooplankton could be imported from offshore areas. This value is equivalent to herbivore production in the NAS and would increase net zooplankton availability to $4.2 \text{ g C/m}^2/\text{yr}$, a figure that is close to the total consumption of $5.1 \text{ g C/m}^2/\text{yr}$.

Net benthic prey availability to vertebrates (total benthic production less consumption by invertebrate predators) was about $6.8 \text{ g C/m}^2/\text{yr}$. Total consumption of benthos by vertebrates was approximately equivalent to that available (Table 8.7).

Among the infauna, polychaetes, bivalves, and echinoderms were consumed in approximately equal quantities (Table 8.6) that are equivalent to 20%-120% of the standing crop (or productivity). (Standing crop of polychaetes was 1.1 g C/m^2 and of bivalves was 2.4 g C/m^2 ; productivity = $1.17 \times$ standing crop).

Estimated consumption of benthic amphipods and decapods far exceeded their standing crops or productivity (consumption was estimated at $3.4 \text{ g C/m}^2/\text{yr}$; standing crop was 248 mg C/m^2 and productivity was $500 \text{ mg C/m}^2/\text{yr}$; Table 8.2). It would appear that availability of benthic crustacea was underestimated. In order to balance their availability with consumption, the productivity-to-biomass ratio would have to be 14 (unlikely), or biomass has been underestimated by a factor of 7 (likely).

Total consumption of fish by predators was about $2.7 \text{ g C/m}^2/\text{yr}$ (Table 8.6). However, the total standing crop of fish was estimated to be only 1.9 g C/m^2 (annual average, Table 8.9), and a good deal of this biomass consisted of cod, pollock, and flatfish too large to be consumed by seabirds and other fish. About half the fish consumed by seabirds and marine mammals consisted of sand lance (Table 8.6); the estimated consumption of sand lance by all vertebrates was about $1.3 \text{ g C/m}^2/\text{yr}$. The average estimated biomass of sand lance, however, was only 485 mg C/m^2 and

Table 8.9. Standing crop of invertebrates and vertebrates on the NAS, Alaska. Standing crop of vertebrates has been weighted to account for the time present in the area.

	Standing Crop (mg C/m ²)				Annual Average
	Jan	May	July	Sept	
Zooplankton					
Herbivores	28	47	284	22	72
Carnivores	47	23	36	8	29
Jellyfish	32	20	34	274	90
Benthos					
Filter feeders	393	393	393	393	393
Deposit feeders	4283	4283	4283	4283	4283
Carnivores	626	626	626	626	626
Fish					
Pelagic feeders	0	228	1786	138	535
Benthic feeders	882	1764	1764	1764	1363
Birds					
Pelagic feeders	1	3	1	1	2
Benthic feeders	1	1	0	1	1
Mammals					
Pelagic feeders	7	15	1	1	7
Benthic feeders	0	67	0	40	17
All vertebrates					
Pelagic feeders	8	246	1788	140	543
Benthic feeders	884	1831	1764	1806	1381

the maximum was 1742 mg C/ m² (in July). Thus, there is a discrepancy between estimated availability of fish and estimated fish consumption by other vertebrates, especially in the case of sand lance. This discrepancy is likely attributable to underestimates of the standing stocks of forage fish on the NAS.

0.5 DISCUSSION

At the onset of this study, four hypotheses were generated to address study objectives. The results of the conceptual energy flow model assist in addressing two of these hypotheses.

Hypothesis 1 : Organic materials and nutrients derived from lagoons contribute significantly to food webs of fish, birds and marine mammals in adjacent marine waters. This hypothesis is not supported by the data. In the study area as a whole, input of eelgrass detritus is small relative to primary productivity (see Table 8.3 and Section 3.0, this report). Despite this, the eelgrass could theoretically important to vertebrates, because it becomes available to the benthos as detritus, and as demonstrated in this section, the benthos supplies about half the food for vertebrates. However, the benthos probably feeds mainly on settled phytoplankton because phytoplankton is underutilized by the zooplankton and this provides a continuous (for seven months) supply of high quality organic matter directly to the benthos. In contrast, eelgrass must be degraded by bacteria before it is of use to most benthic invertebrates. Indeed, results of stable and radio-isotope studies (Section 3.0, this report) show that very little of the eelgrass is ultimately incorporated into the benthic invertebrate food chain.

Hypothesis 2: The greatest vertebrate biomass and the largest number of vertebrate species in the study area depend mainly on a marine phytoplankton-epibenthos food chain. This hypothesis is partly invalidated by the data. It is true that marine phytoplankton provides the great majority of carbon fixed. But

on the whole, total consumption by vertebrates appears to be more or less equally divided between zooplankton and benthos. Furthermore, about half of the benthos biomass consumed by vertebrates is **infauna**, so only about a fourth at most of the vertebrate food supply is from the epibenthos.

The flow of biological energy on the NAS is summarized in Figure 8.1. Primary productivity by phytoplankton is probably lower on the outer and middle shelf areas of the southeastern Bering Sea than it is on the NAS, but total biomass of phytoplankton consumed by herbivorous zooplankton, and the standing stocks of eooplankton, appear to be an order of magnitude higher in the offshore waters than on the NAS (Table 8.10; Walsh and McRoy 1986). As a consequence, the production of zooplankton was also an order of magnitude higher on the outer and middle shelf (30-45 g C/m²/yr; Vidal and Smith 1986) than on the NAS (2.9 g C/m²/yr; this study).

The major difference in zooplankton between nearshore and offshore waters was that, in nearshore waters, biomass remained low in the presence of an abundant food supply. Differences in the seasonal dynamics of predation among areas may account for this. Walsh and McRoy (1986) estimated that total predation on zooplankton was 11.4 g C/m² on the outer shelf and 5.5 g C/m² on the middle shelf. These predation rates are much lower than the zooplankton availability (production 30.45 g C/m², see above). In May, July, and September on the NAS, estimated predation on zooplankton was equivalent to its estimated availability. In addition to continuous predation by demersal and forage fish, predation by the millions of shearwaters present in May and June was followed by a large pulse of herring and capelin that was, in turn, followed by an inundation of the area by jellyfish prior to September. This constant predation may not allow zooplankton biomass to accumulate, and thus, may limit the secondary productivity.

It is also possible that predation on benthos on the NAS is very high relative to benthic productivity; this could limit benthos standing crop and productivity. Although no data are yet available for infaunal mortality rates on the NAS, in the deeper shelf waters of the southeastern Bering Sea annual mortality of bivalves generally exceeds 20% and may reach 50%, and mean age of bivalves is on the order of three to five years

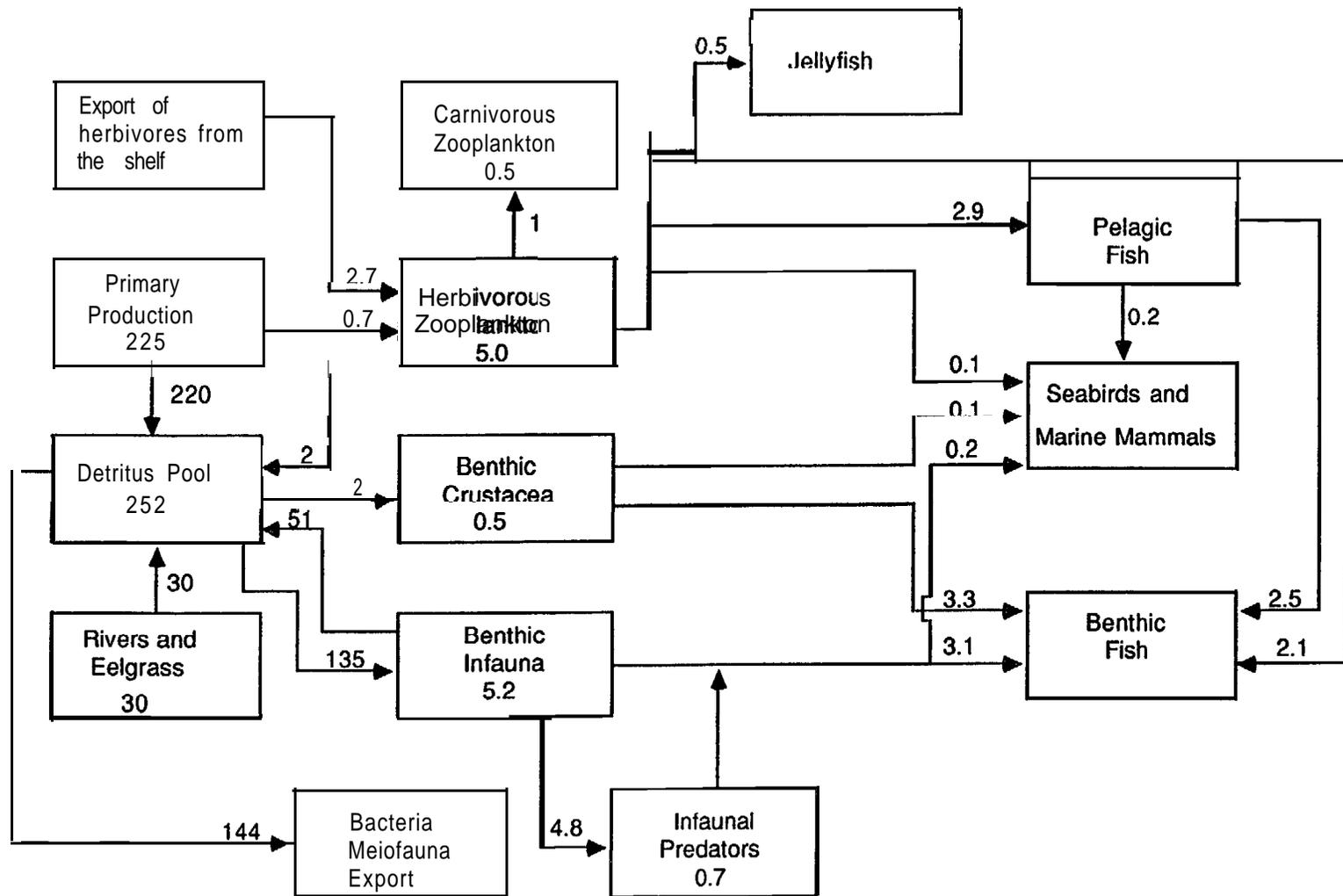


Figure 8.1 Schematic representation of energy flow (g/C/m²/yr) on the NAS. Arrows indicate the direction of flow and associated numbers indicate the annual magnitude. Numbers within boxes are estimated annual production.

(McDonald et al. 1981). In contrast, near northern Baffin Island, where predation on the benthos is negligible, mortality of bivalves (Macoma, Mya, Astarte) is about 8% per year, and mean age is about 12 years at 10-m depth and >20 years at depths of 30 to 50 m (Thomsen et al. 1986). Because of the low predation pressure in this high arctic environment, a high biomass (>1 kg/m²) develops, consisting mainly of old individuals.

Thus predation on the zooplankton and benthos of the NAS appears to be intense. Because these invertebrate resources may be cropped to their annual net production limit, any factor that causes decreased availability of invertebrates could have a serious impact on higher trophic levels.

8.6 LITERATURE CITED

- Allredge, A.L. **1984.** The quantitative significance of gelatinous zooplankton as pelagic consumers. P. **407-433.** In: M.J.R. Fasham (Ed.), Flows of energy and materials in marine ecosystems. Plenum.'
- A&well-Erickson, S. and R. Elsnor. **1981.** The energy cost of free existence for Bering Sea harbor and spotted seals. P. **869-900.** In: D.W. Hood and J.A. Calder (**Eds.**), The eastern Bering Sea shelf: Oceanography and resources, Vol. II. **OMPA/NOAA**, Seattle. **1339** p.
- Brown, S.G. and C.H. **Lockyer.** 1984. Whales. P. **717-781.** In: R.M. Laws (Ed.), Antarctic Ecology. Vol. 2. Academic Press, **London.** 850 p.
- Bushev, S.G. 1986. Feeding of minke whales, Balaenoptera acutorostrata in the Antarctic. Rep. Int. Whal. Comm. **36:241-245.**
- Cimberg, R., D. Costa and P. **Fishman.** 1984. Ecological characterization of shallow **subtidal** habitats in the North Aleutian Shelf. U.S. Dept. Commer., NOAA, OCSEAP. Final Rep. **44(1986):437-646;**
- Dagg,** M.J. 1982. Zooplankton feeding and egg production in the southeast Bering Sea. P. **419-452.** In: PROBES: Processes and Resources of the Bering Sea shelf, Final Progr. Rep., **Vol. 1.** Off. Polar Programs, National Science Foundation. **735** p.
- Dagg, M.J., J. **Vidal,** T.E. Whitley, R.L. Iverson and J.J. Goering. 1982. The feeding, respiration and excretion of zooplankton in the Bering Sea during a spring bloom. Deep Sea Res. **29:45-63.**
- Estes, J.A. and J.F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science **185:1058-1060.**
- Fay, F.H. **1982.** Ecology and biology of the Pacific walrus, Odobenus rosmarus divergens Illiger. **U.S. Dept.** Interior, Fish Wildl. Serv., North American Fauna No. **74.** 279 p.
- Griffiths, W.B. and R.A. Buchanan. 1982. Characteristics of **bowhead** feeding areas. P. 347-455. In: W.J. Richardson (Ed.), Behavior, disturbance responses and feeding of **bowhead** whales Balaena mysticetus in the **Beaufort** Sea, **1980-81.** Rep. by LGL Ecological Research Associates, Inc., Bryan, TX, for **U.S.** Bureau of Land Management, Washington. 456 p.
- Griffiths, R.P., B.A. Caldwell, W.A. **Broich** and R.Y. Morita. **1983:** Microbial processes relating to carbon cycling in southeastern Bering Sea sediments. Mar. Ecol. Progr. Ser. **10:265-275.**
- Gilmer, T. **1983.** Alaska Peninsula-Aleutian Islands area, herring sac roe report to the Alaska Board of Fisheries, Alaska Dept. Fish & Game, Anchorage.

- Harris, R.K. 1985. Body composition (carbon, nitrogen and calories) and **energetics** of immature walleye pollock, Theranra chalcogramma (Pallas) in the southeast Bering Sea. **M.S. Thesis**, Univ. Alaska, Fairbanks, AK. 112 p.
- Hartt, A. 1966. Migration of salmon in the North Pacific Ocean and Bering Sea as determined by seining and tagging, **1959-1960**. Int. N. Pacific Fish. Comm. Bull. No. **19. 141 p.**
- Ikeda, T. 1985. Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. Mar. **Biol. 85:1-11.**
- Isakson, J., J. Houghton, D. Rogers and S. Parker. **1986**. Fish use of inshore habitats north of the Alaska Peninsula, June-September 1984 and June-July **1985**. Rep. by Dames and Moore to U.S. Dept. Commer., NOAA, OCSEAP, Anchorage, AK. **357 pp.**
- Livingston, P. and B. **Goiney**. 1984. Bibliography on daily food ration of fishes. U.S. Dept. Commer., NOAA Tech. Memo. NMFS F/NWC-63. 60 p.
- McCullough, J. 1984. Herring sac roe report, Alaska Peninsula-Aleutian Islands area. Rep. to Alaska Board Fish., Alaska Dept. Fish & Game, Div. Comm. Fish. 20 p.
- McDonald, J., H.M. Feder and M. **Hoberg**. **1981**. Bivalve mollusks of the southeastern Bering sea. P. **1155-1204**. In: D.W. Hood and J.A. Calder (**Eds.**), The eastern Bering Sea **shelf**: Oceanography and resources. Vol. 2. **BLM/NOAA**, OMPA. Univ. Washington Press, Seattle.
- Nagasawa, S. **1985**. Digestive efficiency of the chaetognath **Sagitta crassa** Tokioka, with observations on the feeding process. J. Exper. Mar. Biol. Ecol. **87:271-281.**
- Parsons, T.R., M. Takahashi and B. Hargrave. **1977**. Biological oceanographic processes, 2nd Edition. Pergamon Press, Toronto. 132 **p.**
- Peroy, J.A. and F.J. Fife. **1980**. The approximate composition and caloric content of arctic marine invertebrates from Frobisher Bay. Canadian Data Rep. of Fish and Aquat. Sci. No. 214. 35 p.
- Schneider, P., G.L. Hunt, Jr. and H.M. Morrison. 1986. Mass and energy transfer to **seabirds** in the southeastern Bering sea. **Continental Shelf Research 5:241-257.**
- Schwartz, L. **1985**. Alaska Peninsula-Aleutian Islands area, herring **sac-ro**e report. Alaska Dept. Fish & Game, Div. Comm. Fish. **18 p.**
- Shaul**, A., T. Gilmer, J. McCullough and L. Malloy. **1983** **1983** fin fishes annual report, Alaska Peninsula-Aleutian Islands areas. Alaska Dept. Fish & Game. Data Rep. 15 **p.**
- Spotte, S. and G. Adams. **1981**. Feeding rate of captive adult female northern fur seals, Callorhinus ursinus. Fish. bull. **79:182-185.**

- Stoker, S.W. 1978. Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi seas. Ph.D. Thesis, Univ. Alaska, Fairbanks. 259 p.
- Swartzman, G.L. and R.T. Hoar. **1983**. Interactions between fur seal populations and fisheries in the Bering Sea. Fish. Bull. **81:121-132**.
- Thomson, D.H. 1984. Distribution, production, and ecology of gray whale prey species. **In:** D.H. Thomson (Ed.), Feeding ecology of gray whales (Eschrichtius robustus) in the Chirikof Basin, summer 1982. U.S. Dept. Commer., NOAA, OCSEAP, Final Rep. **43(1986):209-460**.
- Thomson, D.H., **C.M** Martin and W.E. Cross. 1986. Identification and characterization of Arctic **nearshore** habitats. Can. Tech. Rep. Fish. Aquat. Sci. 1434: vii + 70 p.
- Thomson, D.H. and L.R. Martin. **1984**. Feeding ecology of gray whales in the Chirikof Basin. **In:** D.H. Thomson (Ed.), Feeding ecology of gray whales (Eschrichtius robustus) in the Chirikof Basin, summer 1982. U.S. Dept. Commer., NOAA, OCSEAP, Final Rep. **43(1986):209-460**.
- Vidal, J. and S.L. Smith. 1986. Biomass, growth, and development of populations of herbivorous zooplankton in the southeastern Bering Sea during spring. Deep-Sea Research **33**. pp. **523-556**.
- Walsh, J.J. and C.P. **McRoy**. 1986. Ecosystem analysis in the southeastern Bering Sea. Continental Shelf Research. **132:30**.
- Walsh, J.J., E.T. Premuzic, J.S. Gaffney, G.T. Rowe, G. Harbottle, R.W. Stoenner, W.L. Balsam, P.R. **Betzer** and S.A. **Macko**. 1985. Organic storage of **CO₂** on the continental slope off the mid Atlantic bight, the southeastern Bering Sea, and the Peru coast. Deep-Sea Research. **32:853-883**.

8.7 APPENDIXES

Appendix 8.1. Values used to convert wet weight of zooplankton and benthos to equivalent weight of organic carbon.

Taxon	Dry weight as a % of wet weight	Carbon as a % of dry weight	References^a
Jellyfish	4	10	1, 5
Copepods	17	46.5	2, 3
Hyperiid	19	38.4	2, 3
Euphausiid	21	46.6	2, 3
Mysid	17	43.9	2, 3
Decapod larvae	19	38.0	2, 3
Chaetognath	10	40.7	1, 2
Larvacean	10	40.7	Estimated from chaetognaths
Fish larvae	24.5	45	2, 3
Eggs	8	40	2
Nauplius	19	38	Estimated from Decapod larvae
Crangonid shrimp	18.6	29.3	4
Amphipod	15.6	47	4
Polychaete	19.8	36	4
Bivalve	6.7	41	4
Gastropod	14.6	43	4
Ophiuroid	47.9	3	4
Echinoid	32.4	4	4
Sand dollar	51.4	2	4
Holothuroid	27.4	9	4
Sipunculid	18.0	25	4

- ^a
1. Percy and Fife (1980).
 2. Harris (1985).
 3. Griffiths and Buchanan (1982).
 4. Stoker (1978).
 5. Parsons et al. (1977).

Appendix 8.2. Data used in the computation of zooplankton respiration, growth, and consumption.

Respiration

Zooplankton respiration was estimated using Ikeda's (1985) equation:

$$\ln (1 \text{ O}_2/\text{indiv/h}) = 0.5254 + 0.8354 \ln (\text{mg C}/\text{indiv.}) + 0.0601 (\text{temp})$$

Mean wet weight (mg) of individuals was determined from zooplankton data taken during this study. Wet weight was converted to carbon using values shown in Appendix A.

<u>Copepods</u>	<u>Mg wet wt/indiv.</u>	<u>Other Taxa</u>	<u>mg wet wt/indiv.</u>
September	1.3	Euphausiids	17.5
January	1.8	Decapod larvae	3.6
April	1.9	Fish larvae	0.7
May	1.0	Chaetognaths	12.0
July	0.5	Mysids	12.0

Typical mid-water temperature °C (from 2.0 Physical Oceanography)

May 1984	2.75	April 1985	0.5
September 1984	9.5	May 1985	3.25
January 1984	3.5	July 1985	7.5

$$1 \mu\text{l of Oxygen} = 0.535 \text{ g carbon}$$

Growth

April-to-May weight-specific growth rate, 15%; June-to-October **weight-specific** growth rate, 10% (from Vidal and Smith 1986).

Storage for Winter

It is assumed that zooplankton feed for seven months and store food for the remaining five months when food is not available. The respiration (as above) was calculated for those five months when they do not feed (November to March). In order to assimilate and store enough food to meet demands of winter respiration, it was estimated that additional monthly food requirements during the seven months when feeding occurs were 0.64 mg **C/mg C/mo** for herbivores, 0.59 mg **C/mg C/mo** for carnivores, and 0.17 mg **C/mg C/mo** for jellyfish.

Assimilation, Fecal Production, and Total Ingestion

Food assimilated by zooplankton was calculated as the sum of respiration, growth, and winter storage. Assimilation efficiencies of 70% for herbivores (Dagg et al. 1982), 80% for carnivores (Nagasawa 1985) and 90% for jellyfish (Alldredge 1984) were used to calculate total ingestion. Fecal production was the difference between assimilation and ingestion.

Appendix 8.3. Consumption rates for vertebrates used in computation of the energy flow model.

Seabirds (from Schneider et al. 1986)

Consumption (**Kcal/bird/d**) = (a) (b) (c) (M)(0.723)

a = 1.33 Ingested/assimilation ratio

b = 2.8 Active/resting ratio

c = 78.3 **Kcal/d** at rest

M = body weight in kg

Harbor Seal (from **Ashwell-Erickson** and Elsner 1981)

Mean body weight of 67 kg with average consumption of **3935 Kcal/d**, based on the annual requirements of a population of **1000** seals using their Model I assumptions.

Walrus (from **Fay 1982**)

Total body weight 720 kg with average net food intake of **6.2% of** body weight/d.

Sea Otter (from Estes and Palmisano 1974)

Body weight of 23 kg with consumption equal to 20 to 23% of body weight/d.

Minke Whale

Average weight of about **8000** kg (Brown and **Lockyer 1984**) with daily food intake equivalent to about **3.5%** of body weight/d (**Bushev 1986**).

Gray Whale (from Thomson and Martin 1984)

Average body weight of 23,000 kg. Daily consumption while migrating is unknown. Average daily metabolic requirements are about 295,000 **Kcal/d**.

Steller's Sea Lion

Average body weight is about 636 kg. Consumption rates are unknown. However, fur seals consume from **7.5** to **14%** of body weight/d (**Swartzman and Hoar 1983**) or from 5 to 10% of body weight/d (**Spotte and Adams 1981**).

Appendix 8.4. Daily ration (% of body weight/d), standing crop (g/m^2 wet weight), and timing of fish occurrence in the study area.

Species	Daily ration (%)	Standing Crop (g/m^2)	Days in study area													
			Jan	Feb	Mar	Apr	May	Jun	Jul.	Aug	Sep	Oct	Nov	Dec		
Salmon adults	1	1.6					1	7	1							
Salmon juveniles	7	0.008							30	31	31	30				
Herring/Capelin	Spring	2						5	10							
	Summer	6							20	31						
	Summer	6									30	31				
Sand lance																
Jan	6	0.001	31	28												31
May	6	0.6			31	30	31									
July	2	15.8							30	31	31					
Sep	2	1.2										30	31	30		
Other forage fish	6	0.04						31	30	31	31	30				
Bottom fish																
Summer	4	16.0				26	31	30	31	31	30	21				
Winter	1	8.0	31	28	31	4							10	30	31	

Sources of standing crop and daily rates data for fish.

Salmon Adults

An estimated 4.5 million adult salmon migrate through the NAS on their way into Bristol Bay (see text) at a speed of 60 cm/s, which equals seven days per fish in the NAS. A daily ration of 1% (Hartt 1966) may be high because sockeye had only 12 g of food (99% euphausiids) in their stomachs at that time. An additional 1.5 million adult salmon which spawn locally in the NAS (Shaul et al. 1983) are not included here, because they presumably had stopped feeding, being so close to their spawning streams.

Salmon Juveniles

Daily ration is estimated from Livingston and Goiney (1984); abundance estimates are from Isakson et al. (1986; their transects 4, 5 and 6).

Herring/Capelin

Few herring or capelin were caught, even though some spawning occurs near Port Moller. Estimates of spawner abundance (11K-100K tons) are rough, usually based on visual estimates of schools in the Port Moller vicinity (Gilmer 1983, McCullough 1984; Schwartz 1985). A mean value (70K tons) was used. Thereafter, estimates were based on **midwater** trawl data (g/m^3) x average water depth (30 m) of the study area. Best-guess estimates are that the fish have a moderate daily ration (2%) during spawning, and 6% thereafter.

Sand Lance

Daily ration is assumed to be 6% in winter and spring when most feeding occurs, and 2% at other times. Abundance estimates per sampling period = average BPUE in **midwater** trawls (g/m^3) * average depth in the study area + average BPUE in bottom trawls (g/m^2).

Other Forage Fish

Abundance = average purse seine catch of all fish except salmon and sand lance (Isakson et al. 1986) x 3 to account for the average depth of the study area compared to the depth of the purse seine net.

Bottom Fish

Daily ration is estimated from Livingston and Goiney (1984). Summer abundance estimates from various sources vary widely (1.5-50 g/m²), depending on gear used and annual variation. The value used here is the average catch of small trawls (2.4 g/m²) and large trawls in NMFS new subsea 1 (29.3 g/m²) (see text). Winter abundance *was taken* as 1/2 summer abundance, which *is* the ration of the winter BPUE (January) to the summer BPUE (May-September) using our small trawl.