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Caloric Content of Oceanic Zooplankton and Fishes for Studies of Salmonid Food Habits and Their Ecologically Related Species

by

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Abstract

The caloric content of zooplankton, squid, and fish were tabulated from values given in the literature. Cnidaria (4091 cal/g ash-free dry weight) and Ctenophora (3240 cal/g ash-free dry weight) had the lowest caloric value of the organisms surveyed. Pelagic polychaetes (*Tomopterus helgolandica* 7518 cal/g ash-free dry weight), copepods (*Chiridius armatus* 7698 cal/g ash-free dry weight), mysids (*Boreomysis arctica* 8525 cal/g ash-free dry weight), arrow worms (*Sagitta elegans* 7546 cal/ ash-free dry weight), and euphausiids (*Meganyctiphanes norvegica* 8574 cal/g ash-free dry weight) had a high caloric value. Caloric content varied with season of the year (*T. helgolandica* Dec. and April, *Illex illecebrosus* winter and summer, *Metridia longa* Dec. and April), and whether the sample included females with eggs (*Euchaeta norvegica, Diaptomus siciloides, Boreomysis arctica, Oncorhynchus nerka*). Among the fishes, herring (*Clupea harengus harengus*) and lake char (*Salvelinus namaycush*) had a high caloric content, 5994 cal/g dry weight, and 7103 cal/g dry weight. The caloric content of the Pacific salmon (*Oncorhynchus* spp.) ranged from 3345 cal/g dry weight to 6227 cal/ g dry weight.

Introduction

Species of zooplankton, squid, and fish have been shown to comprise the prey organisms of oceanic Pacific salmonids (*Oncorhynchus* spp.; Brodeur 1990; Davis 1990; Ito 1964; Ishida et al. 1991, 1992; and Nagasawa et al. 1993; NMFS 1993). Information on the caloric content of prey organisms can be used to evaluate the quality of salmonid diets, and to determine the role of species ecologically related to Pacific salmonids. The purpose of this report was to compile literature values for the caloric content of oceanic species that are fed upon by salmonids, or are representative of taxonomic groups known to be fed upon by salmonids.

Methods

I summarized literature values for caloric content of organisms that are prey of Pacific salmonids during the oceanic phase of their life-history. However, not all salmonid prey organisms have had their caloric content measured. In cases where the caloric value of particular prey organisms has not been determined, I included data from taxonomically related groups. Caloric content was summarized as calories per gram of fresh weight (FW), dry weight (DW), and ash-free dry weight (AFDW). Most authors determined caloric content from bomb calorimetry. In cases where the caloric content was reported in joules, I changed the value to calories using the following conversion factor: 1 joule=0.2388 calories. When the data were available, I included information on the season or month of the year when the organism was collected, the age, sex, or body part used to make the caloric determination, and the sample area where the organism was collected. Supplementary information on the percentage of water, protein, lipid, and carbohydrate was included because caloric content can be estimated knowing the composition, and these relationships: protein is approximately 4.80 kcal/g, lipid is approximately 9.45 kcal/g, and carbohydrate is approximately 4.10 kcal/g (Brett and Groves 1979).

Results and Discussion

Cnidaria (4091 cal/g AFDW) and Ctenophora (3240 cal/g AFDW) had the lowest caloric value of the organisms surveyed (Table 1). Pelagic polychaetes (*Tomopterus helgolandica* 7518 cal/g AFDW), copepods (*Chiridius armatus* 7698 cal/g AFDW), mysids (*Boreomysis arctica*

8525 cal/g AFDW), arrow worms (*Sagitta elegans* 7546 cal/ AFDW), and euphausiids (*Meganyctiphanes norvegica* 8574 cal/AFDW) all exhibited high caloric content (Table 1.) Caloric content varied with season of the year (*T. helgolandica* Dec. and April; *Illex illecebrosus* winter and summer; *Metridia longa* Dec. and Apr), and whether the sample includes females with eggs (*Euchaeta norvegica, Diaptomus siciloides, Boreomysis arctica, O. nerka,*). Samples that include females with eggs are among the highest estimates of caloric content (Table 1). Among the fishes, herring (*Clupea harengus harengus*) and lake char, (*Salvelinus namaycush*) had a high caloric content, 5994 cal/g DW, and 7103 cal/g DW (Table 1). The caloric content of the Pacific salmon ranged from 3345 cal/g DW to 6227 cal/ g DW.

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Table 1. Caloric content of zooplankton, squid, and fish. These zooplankton include species that are prey of Pacific salmonids (*Oncorhynchus* spp.) or representative of taxonomic groups that are salmonid prey organisms. General distribution is the distribution of the organisms, if known. A: Atlantic Ocean, NA: North Atlantic Ocean, P: Pacific Ocean, NP: North Pacific Ocean, Ind: Indian Ocean, Ac: Arctic Ocean, subAc: Subarctic, WW: world-wide, temp: temperate, F: freshwater. Caloric content is summarized as calorie per g (cal/g) wet weight (WW), dry weight (DW) and ash-free dry weight (AFDW). Season is the time of year when the organism was collected. Sample area is where the organisms were collected. Comments such as the percentages of protein (prot), lipid, carbohydrate (carbo), organic material (org), and total organic material (torg) as a portion of wet or dry weight are also listed when available.

Organism or Group	General Distribution	cal/G WW	cal/G DW	cal/G AFDW	% Ash (of DW)	% Water (of WW)	Season	Maturity, Stage, or Sex	Sample Area	Reference	Comments
COELENTERATES											
Cnidaria											
Medusae		60		4513				whole	NW Atlantic	Steimle et al. 1985	
Medusae				4091						Steimle et al.1985*	
Hybocodon prolifera	A-P-Ac		3400	6210	45.4	94.9	Aug-Sep	whole	Arctic	Percy et al. 1981	% prot=27.0, % lipid=17.6, % carbo=0.8, % org=54.7 (of DW)
Aglantha digitale	A-P-Ac		1990	4890	58.5	95.6	Aug-Sep	whole	Arctic	Percy et al. 1981	% prot=21.9, % lipid=6.5, % carbo=0.7, % org=41.5 (of DW)
Aglantha digitale	A-P-Ac				39.2	94.2	Jun-Aug	whole	Bering Sea	Ikeda 1972	% prot=56.5, % lipid=3.0, % carbo=0.8, % chitin=0.5 (of DW)
Aurelia aurita	A-P-Ac									Larson et al. 1989*	lipid=0.4 % of DW
Aurelia aurita	A-P-Ac					96				Larson et al. 1989*	lipid=0.3% of DW
Cyanea capillata	A-P-Ac					96				Larson et al. 1989*	lipid=0.6 % of DW
Rhizostoma sp.										Larson et al. 1989*	lipid=1% of DW
Spirocodon saltatrix						96				Larson et al. 1989*	lipid=0.3% of DW
Stomolophus sp.	A-P					96				Larson et al. 1989*	lipid=0.5% of DW
Ctenophora											
Beroe cucumis	A-P-Ac		1350	4590			Dec		NE Atlantic	Norrbin et al. 1984	% org=29.4 of DW
Beroe cucumis	A-P-Ac		1360	3855	66.4	96.7	Aug-Sep	whole	Arctic	Percy et al. 1981	% prot=8.8, % lipid=5.2, % carbo=0.7, % org=33.8 (of DW)
Beroe cucumis	A-P-Ac						Aug	whole	Arctic	Clarke et al. 1987	% lipid=0.06 of FW
Beroe cucumis	A-P-Ac						May-Oct		NE Pacific	Lee 1974	lipid=13% of DW
Pleurobrachia pileus	A		680	3240			Dec		NE Atlantic	Norrbin et al. 1984	% org=20.9 of DW
Pleurobrachia pileus	A						May-Oct		NE Pacific	Lee 1974	lipid=9% of DW
Pleurobrachia pileus	A									Larson et al. 1989*	lipid=1.7% of DW
Bolinopsis infundibulum	A-P		780	3510			May		NE Atlantic	Norrbin et al. 1984	org=22.2% of DW
Bolinopsis infundibulum	A-P						Aug	whole	Arctic	Clarke et al. 1987	lipid=0.47% of FW
Bolinopsis infundibulum	A-P									Larson et al. 1989*	lipid=0.5% of DW
Mertensia ovum	A-P-Ac		1920	4430	56.2	95.5	Aug-Sep	whole	Arctic	Percy et al. 1981	% prot=21.9, % lipid=9.9, % carbo=0.6, % org=43.9 (of DW)
Ctenophores		49	1324	4003	68.3	97.2	Dec-Mar	whole	NW Atlantic	Thayer et al.1973	average value for mixed species, Class Tentaculata
Ctenophores				3756						Steimle et al. 1985*	
Ctenophores						95.8				Reeve et al. 1978*	AFDW=28.5% of DW; org=3% of DW
Coelenterates		494	2886	5882				whole		Cummins et al. 1971	grand mean
Coelenterates			3481	4109						Griffiths 1977	

Table 1. Continued.

Organism or Group	General Distribution	cal/G WW	cal/G DW	cal/G AFDW	% Ash (of DW)	% Water (of WW)	Season	Maturity, Stage, or Sex	Sample Area	Reference	Comments
POLYCHAETES											
Tomopteris helgolandica			5278	7518			Dec		NE Atlantic	Norrbin et al. 1984	org=70.2% of DW
Tomopteris helgolandica			4407	6278			Apr		NE Atlantic	Norrbin et al. 1984	org=70.2% of DW
Tomopteris septentrionalis							May-Oct		NE Pacific	Lee 1974	Lipid=22% of DW
Tomopteris septentrionalis					15.1	89.9	Jun-Aug	whole	Bering Sea	Ikeda1972	% prot=73.8, % lipid=8.1, % carbo=1.7, %chitin=1.3 (of DW)
Polychaetes			3641							Griffiths 1977	
Polychaetes		1094	3792	5218	28	70		whole	NW Atlantic	Steimle et al. 1985	mostly epibenthic species
Polychaetes		640		4695						Steimle et al. 1985*	
Polychaetes		673	3388			80			NW Atlantic	Steimle et al. 1985*	mean value
Polychaetes		849	4798	6070	21.1	79.3		whole	NW Atlantic	Thayer et al. 1973	average values for 3 species
Polychaetes				5502						Steimle et al. 1985*	
PTEROPODS											
Clione limacina limacina	A-P-Ac			5878	9	89.1	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	mean values; prot=33.4%, lipid=13.3% (of DW)
Clione limacina limacina	A-P-Ac				28.2	88.6	Jun-Aug	whole	Bering Sea	Ikeda 1972	% prot=52.7, % lipid=17.5, % carbo=0.5, % chitin=1.1 (of DW)
Clione limacina	A-P-Ac		3680	6030	38.2	93.2	Aug-Sep	whole	Arctic	Percy et al. 1981	% prot=39.7, % lipid=20.7, % carbo=0.8, % org=60.9 (of DW)
Clione limacina	A-P-Ac						May-Oct		NE Pacific	Lee 1974	Lipid=31 % of DW
Limacina helicina helicina	A-P-Ac	958	4585	5006	8.4	79.1	Jun-Jul	whole	Bering Sea	Nishiyama 1977	% prot=52.4, %lipid=25.4 (of DW)
Limacina helicina helicina	A-P-Ac				28.5	75	Jul	whole	N Pacific	Omori 1969	north of 30° N
Limacina retroversa	A-Ac			5026	29.5					Phillipson 1964	
Cavolinia longirostris	A-P				39.3		Aug	whole	N Pacific	Omori 1969	north of 30° N
Pteropods				5442	8.7	84.1	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=42.9, %lipid=19.4 (of DW)
SQUIDS											
Illex illecebrosus	A	1695	5254	5636	7	69		whole	NW Atlantic	Steimle et al. 1985	Illex spawns in winter
Illex illecebrosus	A			5875			winter	whole	NW Atlantic	Steimle et al. 1985	Illex spawns in winter
Illex illecebrosus	A			5397			summer	whole	NW Atlantic	Steimle et al. 1985	Illex spawns in winter
Loligo pealei	A	1337	4872	5110	8	72		whole	NW Atlantic	Steimle et al. 1985	Loligo spawns late spring
Loligo pealei	A			4991			winter	whole	NW Atlantic	Steimle et al. 1985	Loligo spawns late spring
Loligo pealei	A			5540			spring	whole	NW Atlantic	Steimle et al. 1985	Loligo spawns late spring
Loligo pealei	A			5134			summer	whole	NW Atlantic	Steimle et al. 1985	Loligo spawns late spring
Loligo pealei	A			5230			fall	whole	NW Atlantic	Steimle et al. 1985	Loligo spawns late spring
Loligo brevis	A	1051	5743	6342	9.4	81.7	Dec		NE Atlantic	Thayer et al. 1973	
Ornastrephes bartrami	WW-temp			5318	6.4					Phillipson 1964	originally called Stenoteuthis sp. in this article
Squids				5578	9.2	85.2	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	mean values; % prot=63.3, % lipid=15.8 (of DW)
COPEPODS											
Copepods				5512	8.8	80.8	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	mean values; % prot=56.6, % lipid=20.1 (of DW)
Neocalanus cristatus	NP			5428	10.5	84.6	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=56.5, % lipid=16.9 (of DW)
Neocalanus cristatus	NP				1.7	80.8	Mar	stage IV & V	Sea of Japan	Nakai 1955	% prot=53.4, % lipid=36.1 (of DW)
Neocalanus cristatus	NP				2.1	83.3	Jul	stage V	N Pacific	Omori 1969	north of 30° N
Neocalanus cristatus	NP				3.4	84.5	Dec	stage V	N Pacific	Omori 1969	north of 30° N
Neocalanus cristatus	NP				2.9	66.1	May	stage V	N Pacific	Omori 1969	north of 30° N
Neocalanus cristatus	NP				14	84.2	Jun-Aug	stage V	Bering Sea	Ikeda 1972	% prot=50.2; % lipid=31.7, % carbo=0.6, % chitin=3.5 (of DW)
Neocalanus plumchrus	NP			5680	8.8	80.8	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=56.5, % lipid=20.1 (of DW)
Neocalanus plumchrus	NP				1.7	82.7	Mar-May	stages II, III, IV, V	Sea of Japan	Nakai 1955	% prot=44.1; % lipid=44.2 (of DW)
Neocalanus plumchrus	NP						May-Oct		NE Pacific	Lee 1974	lipid=47 % of DW
Neocalanus plumchrus	NP				1.9	72.3	Jul	female	N Pacific	Omori 1969	north of 30° N
Neocalanus plumchrus	NP				5.4	82.8	Jun-Aug	stage V	Bering Sea	Ikeda 1972	% prot=53.5; % lipid=38.0, % carbo=0.9, % chitin=2.2 (of DW)
Calanus finmarchicus	NA		6437	7020			Dec	whole	NE Atlantic	Norrbin et al. 1984	% org=91.7 of DW
Calanus finmarchicus	NA			5914			Jan-Dec	adult female		Cummins et al. 1971*	
Calanus finmarchicus	NA			7380				adult female		Cummins et al. 1971*	
Calanus finmarchicus	NA			6369	10.8					Phillipson 1964	
Calanus finmarchicus	NA				3.3		Nov	stage V		Mayzaud et al. 1975	% prot=44.5, % lipid=44.4 (of DW)
Calanus helgolandicus	NA			5400				whole		Cummins et al. 1971*	
Calanus helgolandicus	NA				2.8	83.8	Jan & May	mixed; mostly females	Sea of Japan	Nakai 1955	% prot=75.2, % lipid=8.1 (of DW)
Calanus hyperboreus				7432				adult female		Cummins et al. 1971*	
Paracalanus parvus	WW not Ac				2.9	84.1				Cummins et al. 1971*	% prot=70.1, % lipid=19.1 (of DW)
Calanus pacificus	NP				4.4	80.3	Apr	stage V	N Pacific	Omori 1969	north of 30° N
Calanus pacificus	NP				2.9	78.8	Nov	stage V	N Pacific	Omori 1969	north of 30° N

Table 1. Continued.

Organism or Group	General Distribution	cal/G WW	cal/G DW	cal/G AFDW	% Ash (of DW)	% Water (of WW)	Season	Maturity, Stage, or Sex	Sample Area	Reference	Comments
Calanus gracilis	Ac				7.4	78.8	Jun-Aug	whole	Bering Sea	Ikeda 1972	% prot=48.6; % lipid=40.9, % carbo=1.0, % chitin=2.1 (of DW)
Pseudocalanus elongatus	temp				2.3	87.7	Mar	mixed, mostly females	Sea of Japan	Nakai 1955	% prot=71.5, % lipid=17.3 (of DW)
Eucalanus bungii	NP						May-Oct		NE Pacific	Lee 1974	lipid=40 % of DW
Eucalanus bungii bungii	NP				3.9	88	Jul	female	N Pacific	Omori 1969	north of 30° N
Eucalanus bungii bungii	NP				18.3	88.7	Jun-Aug	whole	Bering Sea	Ikeda 1972	% prot=52.5, % lipid=25.4, % carbo=1.1, % chitin=2.7 (of DW)
Rhincalanus nasutus	A-P-Ind				3.4	86.5	Apr	whole	N Pacific	Omori 1969	north of 30° N
Acartia clausi					3.3	87.9	Apr	mixed, mostly females	Sea of Japan	Nakai 1955	% prot=82.6, % lipid=5.8 (of DW)
Metridia longa			6489	7030			Dec	whole	NE Atlantic	Norrbin et al. 1984	% org=92.3 of DW
Metridia longa			7151	7559			Apr	whole	NE Atlantic	Norrbin et al. 1984	% org=94.6 of DW
Metridia okhotensis					2.7	81.2	Jul	female	N Pacific	Omori 1969	north of 30°N
Euchaeta japonica	NP				2.1	79.6	Jul	mixed juveniles & adults	Sea of Japan	Nakai 1955	% prot=51.8, % lipid=33.7 (of DW)
Euchaeta norvegica			6464	6950			Dec	whole	NE Atlantic	Norrbin et al. 1984	% org=93.0 of DW
Euchaeta norvegica			6299	6651			Dec	males	NE Atlantic	Norrbin et al. 1984	% org=94.7 of DW
Euchaeta norvegica			6898	7494			Dec	females	NE Atlantic	Norrbin et al. 1984	% org=92.0 of DW
Euchaeta norvegica			6927				Apr	egg sack	NE Atlantic	Norrbin et al. 1984	
Euchaeta norvegica			6566	7060			Apr	stage V	NE Atlantic	Norrbin et al. 1984	% org=93.0 of DW
Euchaeta norvegica			7020	7565			Apr	females with eggs	NE Atlantic	Norrbin et al. 1984	% org=92.8 of DW
Euchaeta norvegica			6595	7107			Apr	females	NE Atlantic	Norrbin et al. 1984	% org=92.8 of DW
Pareuchaeta birostrata					2.1	81.5	Apr	female	N Pacific	Omori 1969	north of 30°N
Pareuchaeta sarsi					2.1		Nov	egg	N Pacific	Omori 1969	north of 30°N
Chiridius armatus			7175	7698			Dec	females	NE Atlantic	Norrbin et al. 1984	% org=93.2 of DW
Chiridius armatus			5980	6550			Apr	females	NE Atlantic	Norrbin et al. 1984	% org=91.3 of DW
Chiridius armatus			6127	6674			Apr	females	NE Atlantic	Norrbin et al. 1984	% org=91.8 of DW
Diaptomus articus				5468			Jun	adult reproductive males		Cummins et al. 1971*	500 animals, 2.34 mm length
Diaptomus articus				5526			Jun	adult nonreproductive females		Cummins et al. 1971*	550 animals, 2.80 mm length
Diaptomus sicilioides				5334			Jul	adult reproductive males		Cummins et al. 1971*	8500 animals, 0.75 mm length
Diaptomus sicilioides				5643			Jul	adult nonreproductive females		Cummins et al.1971*	12,500 animals, 0.95 mm length
Diaptomus sicilioides			5605	5849	4.3		Aug-Nov	adult nonreproductive females		Cummins et al. 1971*	
Diaptomus sicilioides			5877	6149	4.6		Aug-Nov	adult females with eggs		Cummins et al. 1971*	
Diaptomus leptopus				5396			Jun	adult reproductive females		Cummins et al. 1971*	3000 animals, 1.45 mm length
Diaptomus leptopus				5436			Jun	adult nonreproductive females		Cummins et al. 1971*	2100 animals, 1.70 mm length
Diaptomus sp.		550								Cummins et al. 1971*	
Diaptomidae		550	5741	5883				whole		Cummins et al. 1971	grand mean
Diaptomidae				5868				females with eggs		Cummins et al. 1971	grand mean
Gaetanus columbiae							May-Oct		NE Pacific	Lee 1974	lipid=28% of DW
Heterorhabdus tanneri	NP						May-Oct		NE Pacific	Lee 1974	lipid=43 % of DW
Candacia columbiae	NP				3.3	86.8	Aug		N Pacific	Omori 1969	north of 30°N
EUPHAUSIIDS											
Thysanoessa spp.				5414	9	75.7	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=58.8, % lipid=14.7 (of DW)
Thysanoessa raschii	A-P			5861			Jun-Jul	whole	Bristol Bay	Nishiyama 1977	
Thysanoessa raschii	A-P						Sep		NE Atlantic	Falk-Petersen 1981*	lipid=23.0 % of DW
Thysanoessa raschii	A-P				20.1		Sep-Apr	0-group	NE Atlantic	Falk-Peterson 1981	% prot=48.4, % lipid=27.6 (of DW)
Thysanoessa raschii	A-P				14.2		Jun-Apr	I-group	NE Atlantic	Falk-Peterson 1981	% prot=41.4, % lipid=37.5 (of DW)
Thysanoessa raschii	A-P				10.9	82.2	Jun-Aug	whole	Bering Sea	Ikeda 1972	% prot=78.6, % lipid=7.2, % carbo=0.5, % chitin=2.8 (of DW)
Thysanoessa inermis	A-P-Ac		6005	6430	6.7	73.9	Aug-Sept	whole	Arctic	Percy et al. 1981	% prot=43.9, % lipid=52.4, % carbo=0.3, % organic=93.4 (of DW)
Thysanoessa inermis	A-P-Ac				11.8		Feb-May			Falk-Petersen 1981*	% prot=52.3, % lipid=22.3 (of DW)
Thysanoessa inermis	A-P-Ac				19		Jul-Apr	0-group	NE Atlantic	Falk-Petersen 1981	% prot=46.9, % lipid=31.7 (of DW)
Thysanoessa inermis	A-P-Ac				11.9		Jul-Apr	I-group	NE Atlantic	Falk-Petersen 1981	% prot=33.9, % lipid=47.6 (of DW)
Euphausia pacifica	P	1138	4904	5592	12.3	76.8	Jun-Jul		Bristol Bay	Nishiyama 1977	% prot=59.3, % lipid=16.0 (of DW)
Euphausia pacifica	P				7.1	84.9	Feb	mixed females and males	Sea of Japan	Nakai 1955	% prot=79.3, % lipid=2.7 (of DW)
Euphausia pacifica	P						May-Oct		NE Pacific	Lee 1974	% lipid=19 of DW
Euphausia pacifica	P						May-Oct	juveniles	NE Pacific	Lee 1974	% lipid=26 of DW
Euphausia pacifica	P				8	79.8	Jul		N Pacific	Omori 1969	north of 30° N
Euphausia pacifica	P				8.5	79.3	Jul	juveniles	N Pacific	Omori 1969	north of 30° N
Euphausia krohni	A			5251	8.4					Phillipson 1964	

Table 1. Continued.

Organism or Group	General Distribution	cal/G WW	cal/G DW	cal/G AFDW	% Ash (of DW)	% Water (of WW)	Season	Maturity, Stage, or Sex	Sample Area	Reference	Comments
Meganyctiphanes norvegica	A-P	940	4945			81	Feb-Dec	whole	NW Atlantic	Tyler 1973	
Meganyctiphanes norvegica	A-P	958	5040			81	Jan-Dec	whole	NW Atlantic	Tyler 1973	
Meganyctiphanes norvegica	A-P			5230	16					Phillipson 1964	
Meganyctiphanes norvegica	A-P	812	4633	5946	22	82		whole	NW Atlantic	Steimle et al. 1985	
Meganyctiphanes norvegica	A-P		7562	8574			Dec		NE Atlantic	Norrbin et al. 1984	% org=88.2 of DW
Meganyctiphanes norvegica	A-P		6181	6861			Dec		NE Atlantic	Norrbin et al. 1984	% org=90.1 of DW
Meganyctiphanes norvegica	A-P		5913	6563			Dec		NE Atlantic	Norrbin et al. 1984	% org=90.1 of DW
Meganyctiphanes norvegica	A-P				16.1		Jan-Nov		NE Atlantic	Falk-Petersen 1981*	% prot=56.6, % lipid=17.2 (of DW)
Meganyctiphanes norvegica	A-P				13.6		Nov-May		NE Atlantic	Falk-Petersen 1981*	% prot=56.5, % lipid=18.4 (of DW)
Meganyctiphanes norvegica	A-P				11.5		Jul-Jul ??		NE Atlantic	Falk-Petersen 1981*	% prot=61.1, % lipid=17.5 (of DW)
Meganyctiphanes norvegica	A-P				17		Nov-Jul	0 & I-group	NE Atlantic	Falk-Petersen 1981	% prot=40.2, %lipid=37.0 (of DW)
Meganyctiphanes norvegica	A-P				14.5		Jan-Jul	I & II-group	NE Atlantic	Falk-Petersen 1981	% prot=35.3, % lipid=37.3 (of DW)
Tessarabrachion oculatus	P				8.1	78.7	Jul		N Pacific	Omori 1969	north of 30° N
Euthemisto sp.				5515	8.9					Phillipson 1964	
Euphausiids				5554	10.9	76.3	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=59.4, % lipid=15.5 (of DW)
AMPHIPODS											
Parathemisto pacifica				4556	20.8	82.8	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=54.8, % lipid=8.9 (of DW)
Parathemisto libellula				4458	23.4	80.9	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=50.4, % lipid=10.4 (of DW)
Parathemisto libellula			4920	5915	18	77.6	Aug-Sep	whole	Arctic	Percy et al. 1981	% prot=47.5, %lipid=26.2, %carbo=1.3, % organic=82.3 (of DW)
Euthemisto libellula					21.1	80.6	Jun-Aug	whole	Bering Sea	Ikeda 1972	% prot=49.4, % lipid=21.6, % carbo=3.1, % chitin=4.8 (of DW)
Parathemisto japonica					13.4	81.6	Jul	juvenile	N Pacific	Omori 1969	north of 30°N
Parathemisto abyssorum			4733	5815			Apr		NE Atlantic	Norrbin et al. 1984	% org=81.4 of DW
Parathemisto gaudichaudi				5138			Jul	adults	NE Atlantic	Williams et al. 1979	
Parathemisto sp.					9.3	83.6	Mar-Jun	females	Sea of Japan	Nakai 1955	% prot=48.7, % lipid=39.6 (of DW)
Hyperoche medusarum			5420	6345	14.8	79.9	Aug-Sep	whole	Arctic	Percy et al. 1981	% prot=35.9, %lipid=27.2, %carbo=2.9, % organic=85.3 (of DW)
Hyperia galba		860	4442	5898	26	80		whole	NW Atlantic	Steimle et al. 1985	
Hyperia galba							May-Oct		NE Pacific	Lee 1974	% lipid=19 of DW
Euprimno abyssalis							May-Oct		NE Pacific	Lee 1974	% lipid=26 of DW
Cyphocaris challengeri					10	78	Jul		N Pacific	Omori 1969	north of 30°N
Gammaridea		810	4050	5362				whole, mixed size & sex		Cummins et al. 1971	grand mean
Gammaridea		1409	2627	4895	52	49		whole	NW Atlantic	Steimle et al. 1985	
Amphipods		1058	3761			72	Jun-Oct	whole, mixed size & sex	NW Atlantic	Brawn et al. 1968	
Amphipods		934	4002	4878						Cummins et al. 1971	grand mean
Amphipods				4517	17.8	82.2	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=53.0, % lipid=9.5 (of DW)
ISOPODS											
Isopoda				4439						Cummins et al. 1971	grand mean
MYSIIDS											
Boreomysis arctica	A		6201	7618			Dec		NE Atlantic	Norrbin et al. 1984	% org=81.4 of DW
Boreomysis arctica	A		7391	8525			Apr	females with eggs	NE Atlantic	Norrbin et al. 1984	% org=86.7 of DW
Boreomysis arctica	A		5922	6830			Apr		NE Atlantic	Norrbin et al. 1984	% org=86.7 of DW
Mysis stenolepis	A	990	4714			79	Fall-Winter	whole	NW Atlantic	Tyler 1973	
Neomysis americana	A		3845					whole	NW Atlantic	Steimle et al. 1985	
SHRIMPS											
Argis dentata		1158	4878			76	Jun-Oct	female with eggs	NW Atlantic	Brawn et al. 1968	
Argis dentata		1081	4549			76	Jun-Oct	adults, mixed sexes	NW Atlantic	Brawn et al. 1968	
Crangon septemspinosa	NA	1111	4272			74	Jan-Apr	whole	NW Atlantic	Tyler 1973	
Crangon septemspinosa	NA	981	4088			76	Nov	whole	NW Atlantic	Tyler 1973	
Pasiphaea multidentata	NA		5007	5822			Dec		NE Atlantic	Norrbin et al. 1984	
Pasiphaea pacifica	P-Ind						May-Oct		NE Pacific	Lee 1974	% lipid=21 of DW
Caridean shrimp		1098	4083	5230	21	75		whole	NW Atlantic	Steimle et al. 1985	
Pandalus montagui	NA	1291	4610			72	Aug-Dec	whole	NW Atlantic	Tyler 1973	
Pandalus montagui	NA	1320	4740			72	Jun-Oct	mixed sizes and sexes	NW Atlantic	Brawn et al. 1968	
Pandalus montagui	NA		4747	5924	24	72	Summer	adult nonreproductive female		Cummins et al. 1971	
Pandalus montagui	NA		4442	5634	26	71	Summer	adult reproductive male		Cummins et al. 1971	
Paneidean shrimp		1648	3892	4895	21	59		whole	NW Atlantic	Steimle et al. 1985	
CRAB ZOEA				5032	26.3	80.8	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=36.0, % lipid=11.0 (of DW)

Table 1. Continued.

Organism or Group	General Distribution	cal/G WW	cal/G DW	cal/G AFDW	% Ash (of DW)	% Water (of WW)	Season	Maturity, Stage, or Sex	Sample Area	Reference	Comments
OSTRACODS											
Conchoecia elegans							May-Oct		NE Atlantic	Lee 1974	% lipid=17 of DW
Conchoecia elegans			6180					females with eggs	NE Atlantic	Norrbin et al. 1984	
CHAETOGNATHS											
Sagitta elegans	Ac-subAc		5860	6814			Dec		NE Atlantic	Norrbin et al. 1984	% org=86 of DW
Sagitta elegans	Ac-subAc		6716	7546			Apr		NE Atlantic	Norrbin et al. 1984	% org=89 of DW
Sagitta elegans	Ac-subAc		4272	4800			Apr		NE Atlantic	Norrbin et al. 1984	% org=89 of DW
Sagitta elegans	Ac-subAc		5035	6210	18.2	90.3	Aug-Sep	whole	Arctic	Percy et al .1981	% prot=63.3, %lipid=20.8, %carbo=0.07, % organic=81.9 (of DW)
Sagitta elegans	Ac-subAc				6.7		Nov	whole, mature	NW Atlantic	Mayzaud et al. 1975	% prot=54.2, % lipid=7.8 (of DW)
Sagitta elegans	Ac-subAc						May-Oct		NE Pacific	Lee 1974	% lipid=14 of DW
Sagitta elegans	Ac-subAc				4.8	85.9	Jul		N Pacific	Omori 1969	north of 30°N
Sagitta elegans	Ac-subAc				8	91.5	Jun-Aug	whole	Bering Sea	Ikeda 1972	% prot=84.0, % lipid=6.7,% carbo=0.7,% chitin=0.6 (of DW)
Sagitta nagae					4.2	88.4	Nov		N Pacific	Omori 1969	north of 30°N
Eukrohnia hamata	WW		5789	7218			Apr		NE Atlantic	Norrbin et al. 1984	% org= 80.2 of DW
Chaetognaths				5032	8.6	90.1	Jun-Jul	whole	Bristol Bay	Nishiyama 1977	% prot=49.9, % lipid=6.5 (of DW)
Chaetognaths				5808						Steimle et al. 1985*	
APPENDICULARIA											
Oikopleura vanhoeffeni							Feb	stage 2-4	NW Atlantic	Diebel et al. 1992	% lipid=5.1 (of DW); before spring diatom bloom
Oikopleura vanhoeffeni							May	stage1-4	NW Atlantic	Diebel et al. 1992	% lipid=7.8 (of DW); after spring diatom bloom
SALPS											
Pegea confoederata					70			aggregate, whole	N Atlantic	Madin et al. 1981	% prot=81.3, % lipid=10.2 (of torg)
Salpa cylindrica					78.1			solitary, whole	N Atlantic	Madin et al. 1981	% prot=82.5, % lipid=5.9 (of torg)
Salpa maxima					69.2			aggregate, whole	N Atlantic	Madin et al. 1981	% prot=76.9, % lipid=9.4 (of torg)
Thaliacea					73.4			adult	N Atlantic	Madin et al. 1981	% prot=81.8, % lipid=7.6 (of torg)
Salpidae		96	2125	4346	51	95		whole	NW Atlantic	Steimle et al. 1985	
FISH LARVAE											
Pleurogramus monopterigius	NP			5049	10.8	67.9	Jun-Jul	larvae	Bristol Bay	Nishiyama 1977	% lipid=12.9 of DW
Tarletonbeania crenularis taylori	NP			5204	16.7	75.2	Jun-Jul	larvae	Bristol Bay	Nishiyama 1977	% lipid=21.2 of DW
Hippoglossoides sp.				5329	10.9	77.1	Jun-Jul	larvae	Bristol Bay	Nishiyama 1977	% lipid=18.8 of DW
Liparis sp.				5395	12.9		Jun-Jul	larvae	Bristol Bay	Nishiyama 1977	% lipid=20.9 of DW
Ammodytes hexapterus	NP			5598	12.2		Jun-Jul	larvae	Bristol Bay	Nishiyama 1977	% lipid=21.0 of DW
Stichaeidae				5332	13.2		Jun-Jul	larvae	Bristol Bay	Nishiyama 1977	% lipid=13.0 of DW
Larvae				4960	14.5		Jun-Jul	larvae	Bristol Bay	Nishiyama 1977	% lipid=13.3 of DW
Larvae				5207	12.3	73.8	Jun-Jul	larvae	Bristol Bay	Nishiyama 1977	mean value; % lipid=15.7 of DW
FISHES											
Ammodytes americanus	A	1624	5182	5922	12	69		adult	NW Atlantic	Steimle et al. 1985	
Tautogolabrus asapersus	A	1058	4880				Jun-Oct	whole	NW Atlantic	Brawn et al. 1968	22 cm length
Clupea harengus harengus	A	1927	6360				Jun-Oct	whole	NW Atlantic	Brawn et al. 1968	% lipid= 6.6 of DW; 14 cm length
Clupea harengus harengus	A	2531	5994	6496	8	57		whole	NW Atlantic	Steimle et al. 1985	
Sardinella aurita	A	1433	4752	5516	14	70		whole	NW Atlantic	Steimle et al. 1985	
Anchoa hepsetus	A	1385	4752	5637	16	71		whole	NW Atlantic	Steimle et al. 1985	
Scomberesox saurus	A	2030	5325	5874	9	62		whole	NW Atlantic	Steimle et al. 1985	
Scomber japonicus	NA-NP	1481	5158	5827	12	71		whole	NW Atlantic	Steimle et al. 1985	
Cyclothone alba	A-P-Ind				8.9	81.4	Aug		N Pacific	Omori 1969	north of 30° N
Engraulis japonicus	P-Ind				6.8	78.9	Aug	juvenile	N Pacific	Omori 1969	north of 30° N
Thunnus albacares	A-P		5588					muscle	NW Atlantic	Steimle et al. 1985	
Salvelinus namaycush	F	2674	7103				Apr-Nov	males	Lake Michegan	Rottiers et al. 1982	% lipid=50.5 of DW; mean length=584 mm
Salvelinus namaycush	F	2576	6999				Apr-Nov	females	Lake Michegan	Rottiers et al. 1982	% lipid=46.9 of DW; mean length=619 mm
Salvelinus namaycush	F	2059	6486				Apr-Nov	immatures	Lake Michegan	Rottiers et al. 1982	% lipid=32.1 of DW; mean length=507 mm
Salvelinus namaycush	F	2458	6885				Apr-Nov	all samples	Lake Michegan	Rottiers et al. 1982	% lipid=46.3 of DW; mean length=570 mm
Salvelinus namaycush	F	1247	5421				Apr-Nov	age 1	Lake Michegan	Rottiers et al. 1982	% lipid=18.2 of DW
Salvelinus namaycush	F	1637	6101				Apr-Nov	age 2	Lake Michegan	Rottiers et al. 1982	% lipid=25.1 of DW; mean length=304 mm
Salvelinus namaycush	F	2235	6721				Apr-Nov	age 3	Lake Michegan	Rottiers et al. 1982	% lipid=44.2 of DW; mean length=510 mm
Salvelinus namaycush	F	2652	7050				Apr-Nov	age 4	Lake Michegan	Rottiers et al. 1982	% lipid=49.7 of DW; mean length=566 mm
Salvelinus namaycush	F	2569	7014				Apr-Nov	age 5	Lake Michegan	Rottiers et al. 1982	% lipid=48.2 of DW; mean length=607mm
Salvelinus namaycush	F	2739	7140				Apr-Nov	age 6	Lake Michegan	Rottiers et al. 1982	% lipid=51.5 of DW; mean length=644 mm

Table 1. Continued.

Organism or Group	General Distribution	cal/G WW	cal/G DW	cal/G AFDW	% Ash (of DW)	% Water (of WW)	Season	Maturity, Stage, or Sex	Sample Area	Reference	Comments
Oncorhynchus mykiss	F	1180				71.5		adult muscle		Exler 1987	rainbow trout
Oncorhynchus mykiss	F					71.5		adult muscle		Sabry 1990	rainbow trout; % prot=20.5, % lipid=3.4 (of WW)
Oncorhynchus nerka	F	1292	3345	3479	3.81	61.4	Oct	breeding females	Kamchatka	Cummins et al. 1971*	kokanee
Oncorhynchus nerka	NP-F	1369	3446	3580	3.73	60.3	Aug-Sep	breeding females	Kamchatka	Cummins et al. 1971*	
Oncorhynchus nerka	NP-F	1943					Jun-Jul	muscle; maturing female	Bristol Bay	Nishiyama 1977	% muscle=67.5, % gonad=7.5% (of BW); length>30 cm
Oncorhynchus nerka	NP-F	1881					Jun-Jul	muscle; maturing male	Bristol Bay	Nishiyama 1977	% muscle=67.5, % gonad=7.5% (of BW); length>30 cm
Oncorhynchus nerka	NP-F	2910					Jun-Jul	gonad; maturing female	Bristol Bay	Nishiyama 1977	% muscle=67.5, % gonad=7.5% (of BW); length>30 cm
Oncorhynchus nerka	NP-F	1150					Jun-Jul	gonad; maturing male	Bristol Bay	Nishiyama 1977	% muscle=67.5, % gonad=7.5% (of BW); length>30 cm
Oncorhynchus nerka	NP-F	1680			1.18	70.2		adult muscle		Exler 1987	
Oncorhynchus keta	NP-F	1597	3606	3745	3.72	55.7	Aug-Sep	breeding females	Kamchatka	Cummins et al. 1971*	
Oncorhynchus keta	NP-F	1200			1.18	75.4		adult muscle		Exler 1987	
Oncorhynchus keta	NP-F					73.3		adult muscle	British Columbia	Sabry 1990	% prot=23.1, % lipid=3.7 (of WW)
Oncorhynchus gorbuscha	NP-F	1687	4043	4187	3.44	58.3	Aug-Sep	breeding females	Kamchatka	Cummins et al. 1971*	
Oncorhynchus gorbuscha	NP-F	1565	3599	3732	3.56	56.5	Sep	breeding females	Murmansk	Cummins et al. 1971*	
Oncorhynchus gorbuscha	NP-F	1160				76.4		adult muscle		Exler 1987	
Oncorhynchus gorbuscha	NP-F					71.5		adult muscle	British Columbia	Sabry 1990	% prot=20.4, % lipid=6.7 (of WW)
Oncorhynchus kisutch	NP-F	1931	6227				Apr-Nov	male	Lake Michegan	Rottiers et al. 1982	% lipid=28.6 (of DW); mean length=602 mm
Oncorhynchus kisutch	NP-F	1866	6157				Apr-Nov	female	Lake Michegan	Rottiers et al. 1982	% lipid=26.4 (of DW); mean length=576 mm
Oncorhynchus kisutch	NP-F	1664	6003				Apr-Nov	immature	Lake Michegan	Rottiers et al. 1982	% lipid=20.23 (of DW); mean length=503 mm
Oncorhynchus kisutch	NP-F	1818	6123		6.51	70.8	Apr-Nov		Lake Michegan	Rottiers et al. 1982	mean; % lipid=25.0 (of DW); mean length=560 mm
Oncorhynchus kisutch	NP-F	1381	3446	3592	4.07	59.9	Oct	breeding females	Kamchatka	Cummins et al. 1971*	
Oncorhynchus kisutch	NP-F	1460				72.6		adult muscle		Exler 1987	
Oncorhynchus kisutch	NP-F					72.6		adult muscle	British Columbia	Sabry 1990	% prot=20.0, % lipid=4.6% (of WW)
Oncorhynchus tshawytscha	NP-F	1363	3649	3740	2.45	62.6	Aug	breeding females	Kamchatka	Cummins et al. 1971*	
Oncorhynchus tshawytscha	NP-F	1800				73.12		adult muscle		Exler 1987	
Oncorhynchus masou	NP-F	1719	3767	3905	3.55	54.4	Aug-Sep	breeding females	Kamchatka	Cummins et al. 1971*	
Oncorhynchus masou	NP-F	1566	3464	3588	3.48	54.8	Aug-Sep	breeding females	Kamchatka	Cummins et al. 1971*	
salmon		1375						adult muscle		Sabry 1990	mean
Poecilidae				5823						Cummins et al. 1971	grand mean
Cottidae			4620	5102				whole, mixed sizes & sexes		Cummins et al. 1971	grand mean
Centrarchidae			4677	5130				whole, mixed sizes & sexes		Cummins et al. 1971	grand mean
Gobiidae			3880					whole, mixed sizes & sexes		Cummins et al. 1971	grand mean
Cyprinidae			5761					whole, mixed sizes & sexes		Cummins et al. 1971	grand mean
Labridae		1058	4880					whole, mixed sizes & sexes		Cummins et al. 1971	grand mean
Clupeidea		1927	6360					whole, mixed sizes & sexes		Cummins et al. 1971	grand mean
Salmonidae		1492	3598	3736				breeding females		Cummins et al. 1971	grand mean
Osteichthyes		1493	5086	5296				whole, mixed sizes and sexes		Cummins et al. 1971	grand mean
Fish, Pelagic		1504		5784					NW Atlantic	Steimle et al. 1985	
Fish, Pelagic		1208	4924	5826	16.4	75.3	all		NW Atlantic	Thayer et al. 1973	average values
Fish, Pelagic				5626						Steimle et al. 1985*	
Fish, Pelagic		1459								Steimle et al. 1985*	
Fish, Pelagic		1925								Steimle et al. 1985*	
Grand Means											
Fish			4928	5774						Griffiths 1977	average values 4000-6600 cal/g AFDW
Bristol Bay sockeye prey		1100					Jun-Jul	whole	Bristol Bay	Nishiyama 1977	average value
Zooplankton				6591						Steimle et al. 1985*	
Zooplankton		392		5512						Steimle et al. 1985*	

*data are summarized in this reference, but this is not the original author.