

The Gulf of Alaska

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ABSTRACT

This chapter reviews the distribution, seasonal abundance, species composition, and production of zooplankton in the Gulf of Alaska. Emphasis is placed on research conducted since 1970.

Approximately 30 species account for the majority of the biomass and numerical abundance, with copepods being the most common taxa collected when using plankton nets and trawls with mesh sizes ranging between 0.200 and 0.500 millimeters.

Zooplankton standing stock (wet weight) varies seasonally. Summer and fall highs range from 1,600 g/m² for the deep inside waters (Prince William Sound; 700 m) to 30 g/m² in the upper 150 m at Ocean Station P. Winter values decline to 1.5 g/m² in the open ocean, with higher biomass occurring over the shelf and in the inside waters; 40 g/m² in the Strait of Georgia, British Columbia, and 1,320 g/m² in Prince William Sound.

Oceanic zooplankton populations may produce up to 30 g C/m²y (upper 150 m) assuming that all the phytoplankton production is grazed, and that 30% of what is ingested appears as growth. The annual growth of populations over the shelf and in the inside waters is probably higher, with production estimates ranging from 27 to 50 g C/m²y. Since the annual primary production over the shelf (where measured) does not exceed 300 g C/m²y, the zooplankton growth is not likely to be greater than 20% of this value, 60 g C/m²y.

The Alaska Coastal Current (ACC) and the Alaska Current/Alaskan Stream provide physical mechanisms that mix oceanic and shelf populations, and then distribute this assemblage around the periphery of the Gulf. The result is a homogeneous subarctic community occurring over 2,200 km of coastline from northern British Columbia to the tip of the Alaska Peninsula. The abundance of several oceanic zooplankters in shelf and coastal collections demonstrates the influence that the bordering ocean has on shallower-water processes such as synthesis and transfer of organic matter. However, this influence has yet to be fully evaluated.

Introduction

Oceanographic studies in the North Pacific Ocean date from observations made during the *Challenger* Expedition (1872–1876), from three cruises of the American vessel, *Albatross* (1888–1905), and from a portion of the Carnegie Expedition (1929). As early as 1889, the Harriman Alaska Expedition crossed the northern Gulf of Alaska and examined some of the physical and geological features of the coastal zone between Yakutat Bay and Kodiak Island, including much of interior Prince William Sound. This latter effort was furthered by studies conducted during the Canadian Arctic Expedition (1913–1924). These early ven-

tures were, in part, responsible for collecting and describing the common flora and fauna of the open ocean and coastal regions of Alaska.

The International Pacific Halibut Commission (formerly the International Fisheries Commission) collected plankton samples in the northern Gulf of Alaska from 1926 to 1934 in order to support studies of the distribution and abundance of fish eggs and larvae (Thompson and Van Cleve 1936). Samples from the *Northern Holiday* expedition and the International Fisheries Commission also form a basis for descriptions of euphausiid distributions in the North Pacific (Brinton 1962). In 1955, Japan, Canada, and the United States began an international study of the North Pacific Ocean

titled NORPAC. Nineteen research vessels and 14 institutions studied the physics, biology, and fisheries of this region. The most ambitious zooplankton research for multi-year time series at Ocean Station 'P' (OSP) and from broader reaches of the northeastern Pacific was reported by LeBrasseur (1965a, 1965b) and Fulton and LeBrasseur (1985). Seasonal and annual variability for copepods, euphausiids, amphipods, decapods, chaetognaths, pteropods, and small cephalopods was described from a collection of ~5,000 vertical tows (taken with a NORPAC net with 0.3-mm mesh size). Only a small percentage of the 5,000 samples was obtained from shelf and coastal regions. In addition, several Soviet investigators described the ecological importance of the large upper-layer oceanic copepods in seasonal studies of the North Pacific Ocean (Vinogradov 1968; Heinrich 1968; Vinogradov and Arashkevich 1969).

The purpose of this chapter is to review both the published manuscripts and the unpublished reports that describe the distribution, abundance, and species composition of zooplankton communities occurring in the oceanic and shelf/coastal regions of the Gulf of Alaska. Particular attention is given to investigations sponsored by BLM/NOAA under the Alaska Outer Continental Shelf (OCS) studies (1974–1979). The intent is to summarize and discuss the present knowledge of zooplankton in this northern temperate ocean and to identify areas where future research needs to be done. Although the study area has been defined as that portion of the northeastern Pacific Ocean north of 52°N and extending west to 176°W, it is necessary to draw on information (mostly Canadian) published for a few more southerly locations to supplement the available information.

The Database

This review is limited to information that describes the distribution, abundance, and standing stock of zooplankters that were collected using nets and trawls with mesh sizes ranging between 0.200 and 0.500 millimeters. Consequently, crustacean microzooplankton and marine protozoans are excluded from this chapter.

In a number of the OCS-sponsored studies, the standing stock of net-caught zooplankton is reported as settled volume. In the interest of consistency within this chapter, settled volumes in ml/m³ or ml/m² were converted to g/m³ or g/m² after Weibe, Boyd, and Cox (1975). This conversion assumes that 70% of the settled volume in milliliters is equivalent to the wet weight in grams. Since at least two different mesh sizes (0.333 or 0.211 mm) and several nets (1-m, 0.5-m, neuston, 60-cm bongo, and 2-m Tucker trawl) were used, strict comparisons between standing stocks reported by various investigators are probably not appropriate in view of errors associated with active avoidance or losses through the mesh. Also, it is likely that nets fished with 0.211-mm mesh contained higher amounts of phytoplankton than did 0.333-mm nets. However, there is neither a way to tell if this is true, nor a method to remove this bias from settled volume measurements.

In those few cases where formalin dry-weight values were reported, wet weights were estimated by first using a 15% conversion factor (Ikeda and Motoda 1978) and then doubling the resultant values to account for preservation losses (Paffenhofer 1980). Zooplankton carbon was considered to be 45% of the reported or estimated dry weight since the samples were dominated primarily by copepods (euphausiids were probably not well sampled in most studies). These problems with the database are acknowledged so the reader may be aware of the limitations inherent in the underlying observations and their subsequent interpretation.

Community Composition

In all, 284 species and six generic composites have been reported for zooplankton and micronekton collected from the oceanic, shelf, and coastal waters of the northern Gulf of Alaska (Fig. 10-1; Appendix I, II). Four taxa constitute the most diverse groups: Cnidaria, Copepoda, Amphipoda, and Osteichthys (Table 10-1). In general, the Gulf of Alaska community reflects a similarity with the zooplankton and micronekton communities reported previously for the Bering Sea (Cooney 1981) and (though not shown) for British Columbia (Arai and Brinckmann-Voss 1980; Gardner and Szabo 1982). The Copepoda and Amphipoda are apparently much less diverse in the northern Gulf than in the Bering Sea (Cooney 1981). Since the collection techniques have generally been similar in these two regions (vertical tows, mostly upper 150–200 m), and the database roughly the same size, it seems possible that the Bering Sea may host a mixture of both subarctic and arctic species. This mixture may account for the difference in Copepoda and Amphipoda diversity. (Motoda and Minoda 1974).

Table 10-1.
Numbers of species and generic composites reported for the Gulf of Alaska and southern Bering Sea.

TAXON	GULF OF ALASKA ^a	BERING SEA ^b
Cnidaria	42	41
Ctenophora	3	1
Polychaeta	9	17
Mollusca	9	8
Cladocera	5	2
Ostracoda	4	7
Copepoda	76	111
Cumacea	3	8
Mysidacea	10	20
Isopoda	3	
Amphipoda	29	67
Euphausiacea	8	7
Decapoda	14	13
Chaetognatha	5	6
Larvacea	4	2
Thaliacea	2	0
Osteichthys	64	27
Total	290	337

^aAppendix I

^bCooney 1981

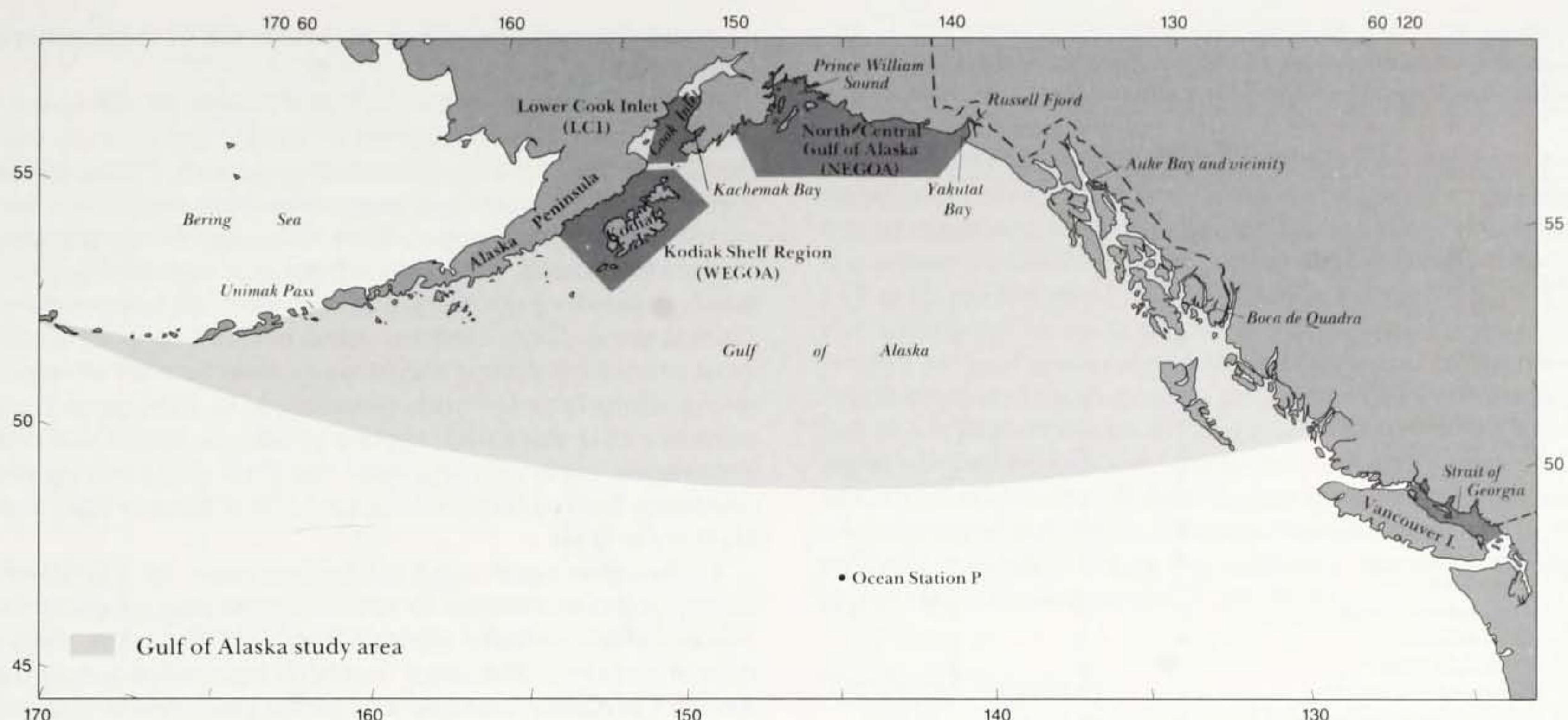


Figure 10-1 Locations of data sets used to describe the distribution, abundance, and production of zooplankton covered in this chapter. Large study areas are depicted by dark shading.

Zooplankton communities in the Gulf of Alaska are numerically dominated by relatively few species; approximately 30 species constitute the numerically common taxa, with copepods being the most numerous (Table 10-2). Cooney (1975) reports 14 species and 2 generic composites as common in the northern Gulf of Alaska (NEGOA). All but one of these categories appear on the list of common species from OSP and the western Gulf of Alaska (WEGOA). Fourteen of 25 taxa from OSP are common to both the other locations, while 18 taxa are common to at least one of the other locations. There are no taxa (common or otherwise) listed for OSP that do not occur at the other locations. Damkaer (1977) reports 19 species and four generic composites from lower Cook Inlet (LCI) (including Kachemak Bay). Nine taxonomic categories listed for this inshore area are also commonly found at OSP.

These listings demonstrate a continuity in the subarctic oceanic zooplankton community that spans roughly a thousand nautical miles—from OSP to Kodiak Island. Unlike the southeastern Bering Sea (Cooney 1981), a mixed assemblage of oceanic and neritic species inhabits the entire shelf and coastal zone including sounds, fjords, and protected inside waters.

Life History Considerations

Scientists have long recognized that the oceanic production cycle in the subarctic Pacific differs from the cycle in most other temperate latitude oceans. In spite of sufficient year-round nutrients and illumination in the surface waters, subarctic Pacific waters lack a well-defined spring phytoplankton bloom. This lack is attributed to the evolution of a specialized grazing community. Heinrich (1957,

1962) and Beklemishev (1957) suggested that seasonally non-varying stocks of oceanic phytoplankton in the northern North Pacific Ocean result from intense grazing by herbivorous copepods.

Unlike *Calanus finmarchicus* in the North Atlantic, the large calanoid copepods in the Pacific subarctic, *Neocalanus cristatus* and *N. plumchrus*, reproduce at depth in late winter when primary production is still light-limited. This places their annual broods in the photic zone ahead of the seasonal phytoplankton growth period. The energy for their egg production comes from lipid reserves stored at the sea surface during the previous year's phytoplankton production cycle. This ability to anticipate and reproduce before seasonal phytoplankton growth, rather than in response to it, assures an extremely close coupling between plant and animal stocks. This coupling eliminates the classic lag period observed in other high-latitude oceans. Because of the intensity of the grazing afforded by this reproductive strategy, the seasonal biomass increase at OSP occurs at the secondary (zooplankton) rather than primary (phytoplankton) level (Parsons 1965; Fulton 1983).

A third large calanoid, *Eucalanus bungii*, augments oceanic grazing by producing surface broods later in the spring and summer when much of the *Neocalanus* biomass is descending to its overwintering and reproductive depths far below the surface. Together, these three copepods contribute as much as 75% to the net zooplankton biomass (>0.333-mm mesh) in the upper 2,000 m of the open ocean (Miller, Frost, Batchelder, Clemons, and Conway 1984). The medium-sized copepod, *Metridia pacifica*, is also an important contributor to the oceanic biomass, particularly in the surface waters after the interzonal species have migrated to depth. Cooney (1975) reports a species of similar size, *Calanus pacificus*, as the most abundant near-surface oceanic

Table 10-2.
Numerically common zooplankton and micronekton from oceanic
and shelf regions of the Gulf of Alaska.

TAXON	LOCATION			
	OSP ^a	NEGOA ^b	WEGOA ^c	LCI ^d
Cnidaria				
Hydrozoa				
<i>Aglantha digitale</i>	x	x		
Chaetognatha				
<i>Sagitta elegans</i>	x	x	x	x
<i>Eukrohnia hamata</i>	x	x	x	
Arthropoda				
Copepoda				
<i>Aetideus</i> sp.	x			
<i>Acartia clausi</i>	x	x		
<i>A. longiremis</i>	x	x	x	x
<i>A. tumida</i>	x	x		
<i>Calanus marshallae</i>	x	x		
<i>C. pacificus</i>	x	x	x	x
<i>C. glacialis</i>	x			
<i>Neocalanus cristatus</i>	x	x	x	x
<i>N. plumchrus</i>	x	x	x	
<i>Eucalanus bungii</i>	x	x	x	
<i>Centropages arcuicornis</i>	x			
<i>Clausocalanus abdominalis</i>	x	x		
<i>Epilabidocera longipedata</i>	x			
<i>Mesocalanus tenuicornis</i>	x			
<i>Microcalanus</i> spp.	x	x		
<i>Metridia pacifica</i> (= <i>M. lucens</i>)	x	x	x	x
<i>Eurytemora</i> spp.	x			
<i>Oithona similis</i>	x	x	x	x
<i>O. spinirostris</i>	x			
<i>Pseudocalanus</i> spp.	x	x	x	x
<i>Scolecithricella minor</i>	x			
<i>Tortanus discaudatus</i>	x	x		
<i>Cyclopina</i> sp.	x			
<i>Oncaeaa borealis</i>	x			
<i>Tegastes</i> sp.	x			
<i>Tisbe gracilis</i>	x			
Amphipoda				
<i>Parathemisto libellula</i>	x			
<i>P. pacifica</i>	x	x	x	
<i>Cyphocaris challengerii</i>	x			
<i>Hyperoche medusarum</i>	x			
<i>Hyperia</i> sp.	x			
<i>Euprimno</i> sp.	x			
Ostracoda				
<i>Conchoecia</i> spp.	x	x		
Cladocera				
<i>Podon</i> spp.	x	x		
<i>Evadne</i> spp.	x			
Euphausiacea				
<i>Euphausia pacifica</i>	x	x	x	
<i>Thysanoessa inermis</i>	x			
<i>T. longipes</i>	x	x	x	x
<i>T. spinifera</i>	x	x		
<i>T. raschii</i>	x			
Annelida				
Polychaeta				
<i>Tomopteris</i> spp.	x			
Mollusca				
Pteropoda				
<i>Limacina helicina</i>	x	x		
<i>Clione limacina</i>	x			
Cephalopoda				
<i>Gonatus</i> spp.	x			
Chordata				
Larvacea				
<i>Oikopleura</i> spp.	x	x	x	x
<i>Fritillaria borealis</i>	x			
Total	25	16	33	23

^aOcean Weather Station P (LeBrasseur 1965b).

^bNortheastern Gulf of Alaska (Cooney 1975).

^cWestern Gulf of Alaska (Kendall, Dunn, Wolotira, Bowerman, Day, Matarese, and Munk 1980; Vogel and McMurray 1986).

^dLower Cook Inlet (Damkaer 1977).

calanoid during late summer and early fall in the northern Gulf of Alaska.

The life histories of the shelf and coastal neritic species exhibit a more classic response to the annual primary production cycle. The abundant small copepods, *Pseudocalanus* spp., *Acartia* spp., and *Centropages abdominalis*, build their late spring and summer populations following the spring phytoplankton bloom. All produce from one to several generations, depending upon food availability and temperature. *Calanus marshallae*, a medium-sized neritic copepod, is also most numerous during the summer months after overwintering adults have fed and reproduced. To date, there is no evidence that this latter species produces more than one generation each year in either the Gulf of Alaska or the southern Bering Sea (Smith and Vidal 1984; Vogel and McMurray 1982).

Ctenophores and small cnidarians make up a relatively unimportant portion of the seasonally varying zooplankton stocks in the northern and western Gulf of Alaska, unlike their numbers in the more southerly waters bordering the British Columbia coastline and in the protected straits and sounds (Cooney 1975; Vogel and McMurray 1982). However, midsummer blooms of larvaceans are not uncommon, as is also the case in waters further south (Harrison, Fulton, Taylor, and Parsons 1983).

Seasonality in Abundance and Biomass

The Oceanic/Slope Community

Kendall, Dunn, Wolotira, Bowerman, Dey, Matarese, and Munk (1980) report seasonal variations in total zooplankton biomass as mean settled volumes for nearshore, shelf, and slope locations in the western Gulf of Alaska near Kodiak Island (Fig. 10-2). The seasonal variations for a 150-m water column in the slope regime range from a low of 9.5 g/m² in the winter to a high of 65.1 g/m² in the summer. Cooney (unpubl. NEGOA data) measured a seasonal high of 19.9 g/m² in May, falling to 3.3 g/m² in late winter for the northern portion of the Gulf of Alaska (Table 10-3). Further to the west, Larrance (1971) reported a summer high volume of 29.4 g/m², and a winter low of 7.4 g/m². This seasonality compares with a high of 30.2 g/m² and low of 1.5 g/m² based on observations at OSP (McAllister 1969; LeBrasseur 1965b). Thus, over broad areas of the open Gulf of Alaska, seasonal variations in standing stock of near-surface zooplankton are roughly comparable, with the largest seasonal variability occurring at OSP, and the smallest variability occurring at locations to the north and west.

A considerable portion of the seasonal biomass variation that occurs in the slope and oceanic regions probably reflects the life histories of three interzonal copepods: *Neocalanus cristatus*, *N. plumchrus*, and *Eucalanus bungii*. These large species are present at some stage of development in the upper 150 m for at least 10 months of each year (Miller *et al.* 1984). Unlike populations that occur in the deeper inside waters of British Columbia (Fulton 1973) and Alaska (Cooney, Urquhart, and Barnard 1981), the oceanic species demonstrate far less synchrony in their reproduction. Therefore, a variety of copepodid stages occur together, both at depth and in the surface waters.

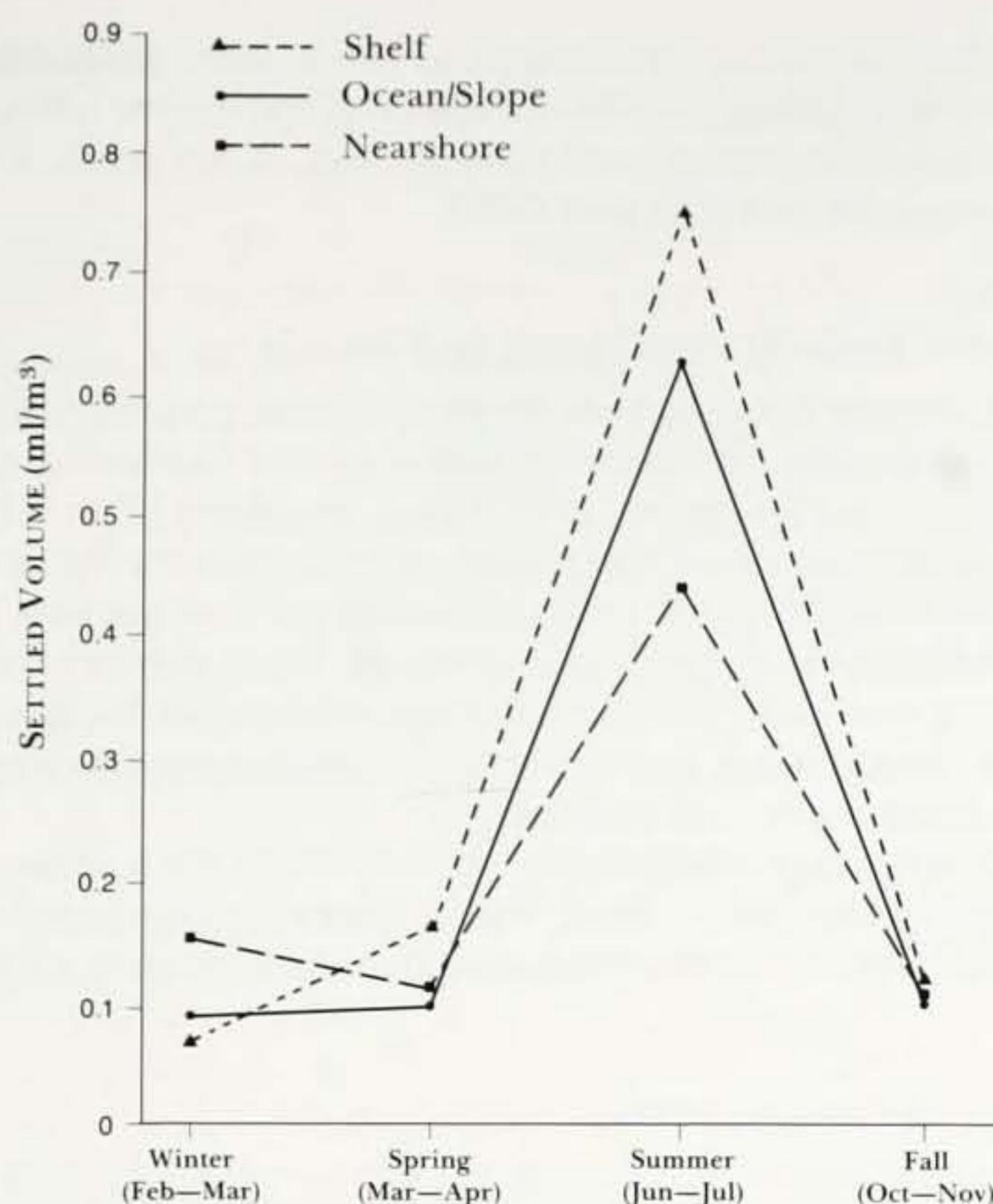


Figure 10-2 Seasonal variability in zooplankton biomass near Kodiak Island, Alaska, based on samples collected with 60-cm bongo nets with 0.333-mm mesh. (Modified from Kendall *et al.* 1980.)

Although the oceanic biomass of net zooplankton is dominated by the large interzonal copepods, several other taxa contribute to the seasonality. The smaller copepods, *Calanus pacificus* and *Metridia pacifica*, occur abundantly and at different times of the year. *C. pacificus* exhibits a strong seasonal signal with its highest amplitude occurring in the fall. *M. pacifica* populations are less variable with time, but have been reported as being the most numerous in late winter and spring (LeBrasseur 1965b). The even-smaller species, *Pseudocalanus* spp., *Scolecithricella ovata*, *Pseudocalanus parvus*, and *Oithona* spp., are all most apparent during times when

the larger species are less abundant in the near-surface waters. The chaetognath, *Sagitta elegans*, is most common in the summer and fall months, as are the pteropods, *Limacina helicina* and *Clione limacina*.

Kendall *et al.* (1980) report chaetognaths occurring in densities of about 6 organisms/m³ in the summer, fall, and winter months in slope waters near Kodiak Island. Likewise, the ostracods, *Conchoecia* spp., are present in concentrations of 1 to 2 organisms/m³ with the highest values occurring in the summer. The most common amphipod, *Parathemisto pacifica*, is most numerous in the summer and fall months. Adult euphausiids, *Euphausia pacifica* and *Thysanoessa longipes*, reach peak densities in the winter. *Oikopleura* spp. occur most abundantly in the open ocean in the summer. In oceanic surface waters bordering the shelf, the zooplankton community composition reflects a distinct neritic cast in the summer and early fall as the shallower water assemblage grows and spreads seaward (Table 10-4).

The Shelf Community

Cooney (unpubl. data) measured 30.6 g/m² in July and 6.2 g/m² in February (150-m water column) for the northeastern portion of the Gulf. This compares with summer values of 78.8 g/m² and winter values of 6.3 g/m² measured by Kendall *et al.* (1980) further to the west over the shelf near Kodiak Island. Since these studies were conducted in different years and with different nets, there is no way to determine whether the summer differences represent interannual, location, or merely sampling variability.

Table 10-4.

Seasonal variations in abundance by rank order for WEGOA offshore locations (Vogel and McMurray 1986).

Table 10-3.
Zooplankton standing stocks (in mg/m³) for the Gulf of Alaska.

LOCATION	WINTER	SPRING	SUMMER	FALL
OSP ^a	10.0	88.0	190.0	80.0
NEGOA ^b				
1. Shelf	41.2	140.8	168.1	70.2
2. Oceanic	22.8	132.8	33.3	25.6
WEGOA ^c				
1. Shelf	42.0	112.0	525.0	77.0
2. Oceanic	63.0	70.0	434.0	70.0
LCI ^d	-	5,010.0	1,440.0	-
Prince William Sound ^d	-	1,890.0	2,060.0	2,290.0
Russell Fjord ^e	-	110.0	470.0	250.0
Strait of Georgia ^f	-	100.0	-	800.0

^aOcean Weather Station PaPa (Fulton 1983).

^bNortheastern Gulf of Alaska (R.T. Cooney, University of Alaska, unpubl. data).

^cWestern Gulf of Alaska (Kendall *et al.* 1980) (settled volumes converted).

^dLower Cook Inlet (Damkaer 1977) (settled volumes converted).

^eReeburgh, Muench, and Cooney 1976.

^fHarrison *et al.* 1983.

RANK ORDER	MONTH	MARCH 1978	JUNE 1978
		OCTOBER 1978	FEBRUARY 1979
1	<i>Neocalanus plumchrus</i>	<i>Pseudocalanus</i> spp.	
2	<i>Pseudocalanus</i> spp.	<i>Metridia</i> spp.	
3	<i>Metridia</i> spp.	<i>Neocalanus plumchrus</i>	
4	<i>Neocalanus cristatus</i>	<i>Acartia longiremis</i>	
5	<i>Limacina helicina</i>	<i>Eucalanus bungii</i>	
6	<i>Scolecithricella minor</i>	<i>Acartia tumida</i>	
7	<i>Oikopleura</i> spp.	<i>Centropages abdominalis</i>	
8	<i>Sagitta</i> spp.	<i>Calanus marshallae</i>	
9	<i>Oithona</i> spp.	<i>Oikopleura</i> spp.	
10	Cnidarians (unidentified)	<i>Parathemisto pacifica</i>	

Zooplankton and micronekton communities on the shelf are composed of a mixture of oceanic and neritic species (Table 10-5). Expressed in the rank order of their abundance, the copepods *Pseudocalanus* spp., *Metridia* spp., *Acartia longiremis*, *A. tumida*, *Calanus marshallae*, *Neocalanus plumchrus*, *N. cristatus*, *Eucalanus bungii*, *Scolecithricella minor*, *Oithona* spp., and *Centropages abdominalis* all occur in the top ten rankings at least once each season. Unidentified cnidarians, medusae, and euphausiids, the cladocerans *Podon* spp. and *Evadne* spp., the chaetognaths *Sagitta* spp., the pteropod *Limacina helicina*, and larvaceans *Oikopleura* spp. complete the list of dominant zooplankton and micronekton found on the shelf.

Seasonally, the zooplankton community shifts from its oceanic domination in late winter through early spring, to a greater neritic influence in mid- to late-summer and fall. *Neocalanus* spp. drop out of the ten most abundant taxa in July and August, being replaced by the cladocerans, *Podon* spp. and *Evadne* spp. *Centropages abdominalis* and *Acartia long-*

iremis become more prominent as the season progresses from winter through summer. *Sagitta* spp. are most numerous in the fall, winter, and early spring, as are adult *Thysanoessa inermis* (Kendall *et al.* 1980).

Protected Inside Waters, Fjords, and Sounds

Few studies have focused on zooplankton and micronekton populations in protected inside waters bordering the Gulf of Alaska (Damkaer 1977; Wing and Reid 1972; VTN 1983). A description of the pelagic ecosystem in the Strait of Georgia (Harrison *et al.* 1983) is considered first because of its thoroughness and seasonal coverage. Three distinct communities were described in this deep (<400 m) basin: an epipelagic community, a mid-water community, and a deep-water community (Table 10-6).

The epipelagic community extends from the surface to the base of the mixed layer, and is generally composed of small copepods. These organisms are supplemented in the

Table 10-5.

Seasonal variations in abundance by rank order for WEGOA inshore locations (Vogel and McMurray 1986).

RANK ORDER	MARCH 1978	APRIL 1978	MAY 1978
1	<i>Calanus</i> ^a copepodites I-III	<i>Pseudocalanus</i> spp.	<i>Pseudocalanus</i> spp.
2	<i>Pseudocalanus</i> spp.	<i>Calanus</i> copepodites I-III	<i>Acartia longiremis</i>
3	<i>Metridia</i> spp.	<i>Neocalanus plumchrus</i>	<i>Calanus marshallae</i>
4	<i>Acartia longiremis</i>	<i>Acartia tumida</i>	<i>Acartia tumida</i>
5	<i>Acartia tumida</i>	<i>Metridia</i> spp.	<i>Metridia</i> spp.
6	<i>Oikopleura</i> spp.	<i>Neocalanus cristatus</i>	<i>Centropages abdominalis</i>
7	<i>Neocalanus plumchrus</i>	<i>Oikopleura</i> spp.	<i>Calanus</i> copepodites I-III
8	<i>Neocalanus cristatus</i>	<i>Scolecithricella minor</i>	<i>Oithona</i> spp.
9	Cnidarians (unidentified)	<i>Acartia longiremis</i>	<i>Limacina helicina</i>
10	<i>Scolecithricella minor</i>	<i>Limacina helicina</i>	Medusae (unidentified)
<u>JUNE 1978</u>			
1	<i>Pseudocalanus</i> spp.	<i>Pseudocalanus</i> spp.	<i>Acartia longiremis</i>
2	<i>Acartia tumida</i>	<i>Acartia longiremis</i>	<i>Pseudocalanus</i> spp.
3	<i>Acartia longiremis</i>	<i>Calanus marshallae</i>	<i>Podon</i> spp.
4	<i>Calanus marshallae</i>	<i>Centropages abdominalis</i>	<i>Centropages abdominalis</i>
5	<i>Metridia</i> spp.	<i>Metridia</i> spp.	<i>Oikopleura</i> spp.
6	<i>Neocalanus plumchrus</i>	<i>Podon</i> spp.	<i>Calanus marshallae</i>
7	Cnidarians (unidentified)	<i>Oikopleura</i> spp.	<i>Oithona</i> spp.
8	<i>Centropages abdominalis</i>	<i>Parathemisto pacifica</i>	<i>Metridia</i> spp.
9	<i>Eucalanus bungii</i>	<i>Eucalanus bungii</i>	<i>Limacina helicina</i>
10	<i>Scolecithricella minor</i>	<i>Oithona</i> spp.	<i>Parathemisto pacifica</i>
<u>NOVEMBER 1978</u>			
1	<i>Acartia longiremis</i>		
2	<i>Metridia</i> spp.		
3	<i>Pseudocalanus</i> spp.		
4	<i>Oithona</i> spp.		
5	<i>Calanus marshallae</i>		
6	<i>Sagitta</i> spp.		
7	<i>Parathemisto pacifica</i>		
8	<i>Limacina helicina</i>		
9	<i>Calanus pacificus</i>		
10	<i>Eucalanus bungii</i>		

^aIncludes *Neocalanus* spp. copepodites.

Table 10-6.

Zooplankton communities in the Strait of Georgia, B.C. (Harrison *et al.* 1983).

DEPTH ZONE	WINTER	SPRING	SEASON	
			SUMMER	FALL
Epipelagic (0–100 m)	<i>Pseudocalanus</i> spp. <i>Paracalanus parvus</i> <i>Oithona helgolandica</i> <i>Corycaeus</i> sp.	<i>Neocalanus plumchrus</i> <i>Calanus marshallae</i> <i>C. pacificus</i> <i>Metridia pacifica</i> <i>Sagitta elegans</i>		
Midwater (100–250 m)	<i>Euphausia pacifica</i> ^a <i>Pasiphaea pacifica</i> ^a <i>Cyphocaris challengerii</i> ^a <i>Tomopteris septentrionalis</i>	<i>Aglantha digitale</i> ^a <i>Aegina citrea</i>	<i>Pleurobrachia</i> spp. <i>Phialidium</i> sp. <i>Oikopleura</i> sp.	
Deepwater (> 250 m)			<i>Neocalanus plumchrus</i> <i>Calanus marshallae</i> <i>C. pacificus</i> <i>Pseudocalanus</i> spp.	

^aDiel migration into the epipelagic zone at night.

spring by large numbers of the early stage copepodids of *Neocalanus plumchrus* that are recruited to the surface waters along with adult *Calanus marshallae* and *C. pacificus*. Both small and large species respond to the spring phytoplankton bloom by rapidly increasing their population biomass. By mid spring, *N. plumchrus* reaches its biomass high at 30 g/m² (upper 20 m), during which time *Pseudocalanus* spp. show a high of 4 g/m². *Calanus marshallae* follows with highs of 10 g/m² in the late spring. *Euphausia pacifica* reaches its seasonal peak of 14 g/m² as a diel migrator into the surface waters in late fall and winter. Spring is also the time when the cnidarian *Phialidium* sp. and the ctenophore *Pleurobrachia* sp. begin a rapid increase in number and biomass.

The jelly-like zooplankton, including *Oikopleura* sp., reach seasonal highs in the summer and fall months, along with *Sagitta* sp. and amphipods. Later in the fall, small blooms of *C. marshallae*, *C. pacificus*, *Metridia pacifica*, and *Pseudocalanus* spp. occur in response to renewed phytoplankton growth. During the late fall and winter, the epipelagic community is composed mainly of the small copepods *Pseudocalanus* spp., *Paracalanus parvus*, *Oithona helgolandica*, and *Corycaeus* sp., supplemented by *Euphausia pacifica* during the hours of darkness. At this time, the overwintering populations of *N. plumchrus* have migrated below 250 m in the Strait.

The midwater community between 100 and 250 m is dominated primarily by the euphausiid *Euphausia pacifica* (during the day), the glass shrimp *Pasiphaea pacifica*, the amphipod *Cyphocaris challengerii*, the polychaete *Tomopteris septentrionalis*, and hydromedusae that include *Aglantha digitale* and *Aegina citrea*. Most of these species also migrate into the epipelagic zone during darkness.

The deep-water or mesopelagic community below 250 m is dominated by the overwintering herbivorous copepods, *Neocalanus plumchrus*, *Calanus marshallae*, *C. pacificus*, and

Pseudocalanus spp. *N. plumchrus* enters a diapause in late fall in the copepodid stage V (CV), and later molts to become an adult. Spawning occurs at depth from January through April. The other species migrate to the surface either as CV or adult stages. Once at the surface, they first feed and then reproduce. Zooplankton tows made from 400 m to the surface yielded 0.8 g/m³, or 320 g/m² in October and November. Most of this biomass is made up of the deep overwintering copepods. Seasonal lows from zooplankton tows (also 400 m to the surface) occur in April and May when the biomass is reduced to 40 g/m². These lows occur mostly in the surface waters.

Considerably less is known about the zooplankton and micronekton communities of Alaska's inside waters. Wing and Reid (1972) reported zooplankton data for samples collected between 1962 and 1964 in surface waters of Auke Bay and vicinity. Unfortunately, this report provides no synthesis of seasonal patterns or any interpretation of results. Damkaer (1977) reports settled volumes for Prince William Sound and for a series of locations in lower Cook Inlet. Samples taken in the fall in Prince William Sound had settled volumes of ~ 770 g/m² for a water column 730 m deep. Much of this biomass was associated with *Neocalanus plumchrus* that was overwintering at depths below 300 meters. A diel migration of copepods, amphipods, euphausiids, and pteropods contributed to an increase in the night biomass in the upper 100 meters.

Cooney, Urquhart, Nevé, Hilsinger, Clasby, and Barnard (1978) and Cooney *et al.* (1981) describe the zooplankton community in the upper 25 m during the spring and early summer months in Prince William Sound. The mixture of neritic and oceanic species that was numerically dominated by copepods suggests that this large enclosed basin is influenced by circulation processes originating outside the Sound. *Pseudocalanus* spp., *Acartia longiremis*, and *Oithona similis* were consistently the most numerous zooplankters. The

only seasonal observations in Prince William Sound demonstrate a succession in numerical dominance for large zooplankton beginning with *N. plumchrus*, *Calanus marshallae*, and *Sagitta elegans* in late spring, shifting to *C. marshallae*, *Metridia okhotensis* and *M. pacifica*, and *Thysanoessa raschii* in mid-summer, followed by *Sagitta elegans* and *M. pacifica* in the fall and winter (Cooney, Redburn, and Shiels 1973).

In lower Cook Inlet, including Kachemak Bay, zooplankton populations vary seasonally, with the biomass in the upper 25 m reaching lows of 1.8 to 10.5 g/m² in the early spring and highs of 267.8 to 542.2 g/m² in the late spring and summer months (Damkaer 1977). These spring and summer stock estimates seem somewhat high for a shallow environment, and may be influenced by measurable amounts of phytoplankton (mesh size, 0.211 mm). Similarly, an upper 150-m summer measurement of 242.2 g/m² (reported for a location in the oceanic Gulf of Alaska upstream from Kodiak Island), is roughly four times the oceanic seasonal high measured in a nearby area by Kendall *et al.* (1980). Reducing the spring and summer standing stock estimates in lower Cook Inlet by this difference provides what appears to be more reasonable estimates of between 67 and 135.6 g/m² for seasonal highs. Conversely, the higher values reported by Damkaer (1977) may include large quantities of small zooplankton and meroplankton missed by the larger-mesh nets.

The zooplankton community in Kachemak Bay and lower Cook Inlet is also composed of a mixture of oceanic and neritic species. During the months of April through August, barnacle nauplii and crab zoea contribute large numbers to the meroplankton. During the spring and summer months, the small copepods, *Pseudocalanus* spp., *Acartia longiremis*, and *Oithona similis*, numerically dominate the community (Damkaer 1977).

Annual Production

Few attempts have been made to measure secondary productivity in any of the major hydrographic regions of the Gulf of Alaska. McAllister (1969) estimated the annual secondary production at 13 g C/m²y for OSP based on the rate at which phytoplankton was grazed by oceanic herbivores and assuming that sinking losses were negligible. If it can be assumed that, as a first approximation, zooplankters (including microzooplankton) ingest all of the annual production (as hypothesized by Heinrich 1957, 1962; Beklemishev 1957), and further that 30% of this material is used for growth (Copping and Lorenzen 1980), then some additional estimates of secondary production can be calculated from other measures of oceanic annual primary production. Koblents-Mishke (1965), in a summary of data from the Pacific Ocean, estimated the annual primary production for the mid-subarctic region to be between 55 and 91 g C/m²y, with between 35 and 55 g C/m²y occurring in the transition zone. Although these estimates were admittedly subject to error because of the methodology, they nonetheless generally agree with those estimates reported by other investigators (Larrance 1971; Anderson 1964; and McAllister 1969). Under the assumption that the annual contribution is

Table 10-7.

Zooplankton annual production estimates for the oceanic Gulf of Alaska and Strait of Georgia.

AUTHOR	METHOD	ANNUAL PRODUCTION g C/m ²
McAllister 1969	Phytoplankton grazing losses	13.0
Parsons <i>et al.</i> 1969	<i>Neocalanus plumchrus</i> growth; 81 mg C/m ² d	9.72 ^a
This paper; using Koblents-Mishke 1965	30% phytoplankton production	10.5-27.3 ^b
Larrance 1971	30% phytoplankton production	24-30 ^b

^aCalculated for a 120-d growth period

^bAssumes all the primary production is grazed and 30% of what is ingested appears as growth

entirely grazed by zooplankton, estimates of secondary production range from a low of 10.5 g C/m²y to a high of 30 g C/m²y (Table 10-7).

Measures of zooplankton production for shelf and inside-water environments are practically non-existent. Parsons, LeBrasseur, Fulton, and Kennedy (1969) report production of 81 mg C/m²d for *Neocalanus plumchrus* in the Fraser River plume. If this rate were sustained for the four months that *N. plumchrus* is in the surface waters, then production on the order of 9.72 g C/m² would be realized. However, since the measured annual increase in zooplankton standing stock was 18.9 g C/m²y (not including losses to mortality) for the deeper portion of the Strait of Georgia, the *N. plumchrus* contribution represents a substantial, but unknown fraction of the total annual secondary production.

Cooney and Coyle (1982) report zooplankton grazing rates of 76 mg C/g dry weight of grazers per day in the middle-shelf domain of the southeastern Bering Sea (comparable community, and similar temperatures in April and May). If this value is applied to spring, summer, and fall zooplankton stocks occurring over the shelf near Kodiak Island, and if 30% of the material ingested can be assumed to go to growth, then the annual zooplankton production would be ~32 g C/m²y (Table 10-8). This value is somewhat less than

Table 10-8.

Seasonal zooplankton production rates for shelf populations in the WEGOA area (Kendall *et al.* 1980).

SEASON	STANDING STOCK ^a mg/m ²	INGESTION ^b mg C/m ² d	PRODUCTION ^c mg C/m ² 90d
Spring			
Mar-May	2,520	192	5,171
Summer			
Jun-Aug	11,813	898	24,239
Fall			
Sep-Nov	1,733	132	3,555
			Total 33.0 g C/m ² y

^aDry wt calculated as 15% wet wt (150 m water column).

^bUsing Cooney and Coyle (1982); 76 mg C/g dry wt 'grazer'/d.

^cUsing 30% gross growth efficiency and a period of 90 days.

Table 10-9.
Seasonal zooplankton production rates for Russell Fjord, Alaska
(Reeburgh *et al.* 1976).

SEASON	STANDING STOCK ^a mg/m ²	INGESTION ^b mg C/m ² d	PRODUCTION ^c mg C/m ² 90d
Spring			
Mar-May	3,380	257	6,939
Summer			
Jun-Aug	14,040	1,067	28,809
Fall			
Sep-Nov	7,460	467	15,309
		Total	51.1 g C/m ² y

^aMeasured dry wt; zooplankters > 0.571 mm.

^bUsing Cooney and Coyle (1982); 76 mg C/g dry wt 'grazer'/d.

the 51.1 g C/m²y that was obtained by using the same method on standing stock data reported by Reeburgh, Muench, and Cooney (1976) for Russell Fjord, Alaska (Table 10-9).

Finally, since most of the estimates of primary production for the fjords and inside waters range between 100 and 300 g C/m²y, it seems unlikely that the annual secondary production will exceed 10 to 20% of these values. Thus, the zooplankton production, though largely unknown, is probably greater than 10 g C/m²y and less than 60 g C/m²y in these protected coastal environments.

Oceanographic/Ecological Significance

Practically nothing is known about broad-scale abundance distributions of zooplankton in the open Gulf of Alaska. Parsons, Giovando, and LeBrasseur (1966) report generally higher copepod stocks around the northern, eastern, and southern periphery of the oceanic gyre. They made this determination using averages for areas composed of 2° latitude and 10° longitude, and based on collections made during 1962 and 1963. This places the highest surface concentrations of copepods in portions of the subarctic and Alaska Current systems.

Wickett (1967) concluded that, given this general pattern of distribution, concentrations of zooplankton along the California coast and in the eastern Bering Sea could be correlated with interannual variations in Ekman transport computed at seven locations in the northeast Pacific and Gulf of Alaska. In years following an above-average southerly component of surface flow, zooplankton volumes were higher than average off California. Conversely, under these same conditions, Bering Sea zooplankton populations were diminished. Wickett suggested that during those years when the southerly component of Ekman transport was strongly developed, more oceanic zooplankters were deflected southward into the California Current and fewer were deflected into the Alaska Current/Alaskan Stream. Since the transit time to these adjacent areas is roughly one year, the effects of transport variations in the Gulf lagged by this amount of time.

Frost (1983) found that there was considerable interannual variation in the standing stock at OSP. These differences showed a weak positive correlation with surface

salinities measured at the same location, as had previously been noted by Wickett (1967). However, since plant growth is apparently not limited by nutrients, it seems unlikely that zooplankton production is enhanced either by increased upwelling or by wind mixing as suggested by the relationship with salinity.

While the large-scale distributions of oceanic zooplankters are only vaguely known, both seasonal and vertical variations in abundance and biomass of oceanic species have been described in detail for OSP and other locations in the subarctic Pacific (Fulton 1978, 1983; Heinrich 1968; LeBrasseur 1965b; Marlowe and Miller 1974; Miller *et al.* 1984; Sekiguchi 1975; and Vinogradov and Arashkevich 1969). The most obvious feature is the approximately twenty-fold increase in surface layer biomass (upper 150 m) associated with the annual growth of the net plankton community. This community is dominated by the interzonal copepods, *Neocalanus cristatus*, *N. plumchrus*, and *Eucalanus bungii*. The rise in biomass to a spring peak in June tapers off during the fall and closely tracks the seasonal variation in light. This phenomenon, coupled with the fact that the oceanic phytoplankton standing stock remains relatively constant throughout the year (most values < 0.4 mg Chl a/m³), suggests that zooplankton grazing must play a significant role in balancing the primary productivity.

That hypothesis has recently been critically examined at OSP (Frost, Landry, and Hassett 1983; Miller *et al.* 1984). It is now known that the reproductive strategies of the major grazers are much more complex than originally thought, and that *N. plumchrus* and *N. cristatus* exhibit behavioral and morphological adaptations that allow them to very efficiently exploit the phytoplankton stocks. Most recently, Miller (C. Miller, Oregon State University, pers. comm., 1985) has demonstrated that two distinct forms of *N. plumchrus* are present at OSP. These forms differ in color, size, and breeding cycle—one is reddish, smaller than 4 mm as adults, and reproduces in mid-summer, while the other (the typical *Neocalanus plumchrus*) is orange, larger than 4 mm, and reproduces in the fall. It is unknown how this discovery will affect the present understanding of how the zooplankton community functions in the open northeast Pacific Ocean.

In addition to Miller's discovery, it is now also known that the large herbivorous copepods are partitioned vertically in the water column during their upper-layer development. Both forms of *Neocalanus plumchrus* occur above the seasonal thermocline (upper 30 m), whereas *N. cristatus* and *Eucalanus bungii* are generally restricted to depths below the thermocline.

Cooney (1986) demonstrates the seasonal presence of the oceanic inter-zonal copepods over the shelf of the northern Gulf of Alaska. This presence is associated both with the time these species reside in the wind-influenced surface layer of the bordering ocean and with the duration of the shelf convergence season that lasts from October to April each year (Royer 1981). These and other oceanic zooplankters are dominant members of the shelf and coastal communities, a fact that adds support to the notion that the bordering ocean may be the source for substantial amounts of organic matter that is advected shoreward in the seasonally persistent onshore Ekman flow (Cooney 1984). The Gulf

of Alaska shelf is unlike the middle shelf domain of the southeastern Bering Sea, which is isolated from oceanic influence by a strong mid-shelf frontal system. The considerably narrower shelf of the Gulf of Alaska has a much more advective environment due to influences by both the Alaska Current over and along the shelf break, and by the Alaska Coastal Current (ACC) that occupies the first 40 km from the beach seaward. The ACC originates in northern British Columbia, and continues north and west around the periphery of coastal Alaska as far as Unimak Pass on the Alaska Peninsula (Royer 1983). Interaction between these two currents (where the shelf is < 50 km wide) presumably provides a mechanism to mix and transport the coastal and oceanic faunas over and along the shelf. This mechanism, combined with the wind-induced onshore Ekman flow, assures that near-surface (upper 200 m) zooplankters of oceanic origin become a seasonal part of the shelf/coastal zooplankton communities.

The degree to which the shelf is enriched by oceanic biomass can be estimated by measuring both the standing stocks and the rate of onshore surface flow. Cooney (1984) proposes that over an eight-month period from March to November of each year, $\sim 10 \times 10^6$ mt of zooplankton biomass are advected shoreward from the upper 50 m of the bordering ocean. This biomass then moves into the outer edge of the ACC along 1,000 km of coastline in the northern Gulf of Alaska. This advected zooplankton biomass compares to the $\sim 2 \times 10^6$ mt estimated as the production yielded by zooplankters resident in the ACC. If this calculated contribution is at all accurate, the bordering ocean supplies an immense and significant amount of biomass to both shelf and coastal food webs each year.

Mesoscale processes such as fronts and eddies concentrate forage species for higher trophic levels, and may also be extremely important in the process of organic matter transfer. Cooney (1984) suggests one such mechanism that may be associated with vertical circulation patterns in the outer margin of the ACC. Interactions between either upwelling or downwelling in the front separating the ACC from the shelf waters, coupled with the distributions of oceanically derived zooplankters, point to periods when forage biomass is concentrated in the frontal region of the ACC. This theoretical concentration may partially explain the apparent obligate use of the ACC by millions of out-migrating juvenile salmon each year (Rogers, Ch. 15, this volume).

The continuous counterclockwise flow of both the ACC and the Alaska Current/Alaskan Stream around the Gulf of Alaska implies a constant relationship between the upstream source regions and the downstream distributions for both oceanic and shelf/coastal zooplankton populations. Using a conservative estimate of 20 km/d for flow in the ACC (Royer 1981), and given the standing stock information for NEGOA shelf zooplankton (Table 10-3), it is possible to estimate the biomass of the zooplankton that is transported downstream each year. Under these conditions, approximately 1.5×10^6 mt of zooplankton are moved past fixed locations annually in a current 20 km wide and 100 m deep. In this context it is not surprising that the community composition of populations in the northern and western por-

tions of the Gulf of Alaska is similar to the fauna occurring at OSP. The system is at least partially closed as a gyre, and the cross-shelf Ekman flow and meander in the Alaska Current/Alaskan Stream both provide further means for mixing the oceanic and coastal communities. Even the zooplankton assemblages in Alaska's protected inside waters reflect an oceanic influence. The non-reversing nature of the flow further suggests that while population fluctuations that originate in British Columbian and southeastern Alaska waters may retain their continuity until they are observed off Kodiak, the converse of that is not likely—except for populations that retain their continuity while being circulated completely around the gyre.

Zooplankton in the Gulf of Alaska serve as forage for higher trophic levels including fishes, marine birds, and mammals (Vogel and McMurray 1986; Appendix III). In addition to these consumers, larval fishes may depend on the early life-history stages of zooplankton, particularly the Copepoda, for their first feeding (Dagg, Clarke, Nishiyama, and Smith 1984). It has long been assumed, but rarely observed in nature, that most fish larvae enter a critical phase at the time when their yolk sac is nearly absorbed and they must begin external feeding (May 1974). At this time, the presence of sufficient quantities of appropriate kinds of food is thought to be extremely important. Copepod nauplii have been described as one of these critical food items (Kamba 1977; Clarke 1978; Nishiyama and Hirano 1983; Laurence 1974; and Paul 1983). In this regard, *Pseudocalanus* is probably one of the most ecologically important genera affecting fish production in the Gulf of Alaska, particularly in the shelf and coastal zones. *Pseudocalanus* spp. continuously produce nauplii while food is available and conditions are favorable (McLaren 1978), thus providing food for first-feeding larvae from April through November of each year. The tiny cyclopoids, *Oithona* spp., may also be important in the diets of first-feeding larvae, both because of their small size (even as late stage copepodids) and their great abundance (Miller *et al.* 1984).

Kendall *et al.* (1980) found that the greatest abundance of fish larvae occurred in both offshore and inshore regions near Kodiak during the summer when zooplankton stocks were also at their seasonal highs. Calanoid copepods, harpacticoid copepods, euphausiids, decapod larvae, fish larvae, mysids, and pelagic amphipods are all known as food sources for a variety of species, ranging from both juvenile and adult pelagic and demersal fishes to sea birds and several whale species.

Vogel and McMurray (1986) discuss relationships between fish, bird, and mammal consumer populations and the forage stocks in the WEGOA region. In the Kodiak area, the distribution of juvenile and adult walleye pollock was related to the distribution of both copepods and the euphausiids, *Euphausia pacifica* and *Thysanoessa spinifera*. These two species are also forage for juvenile pollock (Rogers, Rabin, Rogers, Garrison, and Wangerin 1979). A similar relationship was found for the larval Atka mackerel along the slope regime in this same area. In contrast, the distribution of herring in the inshore waters, including bays and channels, was most strongly related to the abundance of copepods and cladocerans. The most abundant pelagic fish

collected over the shelf near Kodiak, the capelin (Harris and Hartt 1977; Kendall *et al.* 1980), was distributed spatially according to zooplankton abundance, but was seasonally out of phase with the zooplankton biomass. Distributions of Pacific sand lance were weakly related to both copepod distribution and seasonal abundance.

The occurrence and distributions of some marine birds were positively related to the distribution of their food. Shearwaters frequented areas of high euphausiid, copepod, and capelin densities. Since the capelin feed on copepods and euphausiids, and the birds on euphausiids and capelin, the concomitance is expected. Distribution of tufted puffins and black-legged kittiwakes was strongly correlated to areas with larval capelin, but their distribution was weakly correlated to distributions of euphausiids and copepods (Rogers *et al.* 1979).

Five species of filter-feeding whales are found in the Kodiak area: minke, humpback, sei, fin, and blue whales (Science Applications, Inc. 1980; Calkins, Ch. 17, this volume). Humpbacks occur most abundantly over the shelf in the vicinity of the major bathymetric trenches where oceanic copepod and euphausiid populations are high. Both humpback and sei whales forage on copepods, euphausiids, and planktivorous fishes such as capelin and herring (Nemoto 1957, 1970; Nishiwaki 1972).

Conclusions

1. The composition of zooplankton communities in the Gulf of Alaska displays a homogeneity of species across oceanic, shelf, and coastal and inside waters. This composition reflects both the influence of the open ocean on the shallower, protected environments and the highly advective nature of the overall system. The Gulf of Alaska appears closed, and coastal and shelf-break currents distribute populations over ~2,200 km of coastline from northern British Columbia to Unimak Pass, Alaska.

2. Copepods are the dominant taxa reported in samples taken from all marine environments in the Gulf of Alaska. In the oceanic domain, more than 70% of the biomass (nets of 0.333 mm mesh and larger) is associated with three species, *Neocalanus cristatus*, *N. plumchrus*, and *Eucalanus bungii*. A complex life history pattern, including ontogenetic migrations and reproduction at depth, places a mixture of these large copepods in the upper 150 m for at least 10 months of each year.

3. Recent studies tend to confirm the hypothesis that grazing by oceanic herbivores controls both the stock and the production of phytoplankton in the open ocean. Oceanic zooplankton standing stocks vary seasonally by as much as a factor of 20 (between 1.5 and 30.0 g/m²; upper 150 m), with somewhat higher winter values occurring along the northern and western continental margin. It is unlikely that the annual production of oceanic zooplankton exceeds the 30.0 g C/m²y figure.

4. Shelf and coastal zooplankton stocks vary in abundance and species composition according to the season. Winter and early spring populations are augmented by oceanic species that are moved into the shallower waters by

the seasonally persistent onshore Ekman transport. The numerical importance of the open ocean community is diminished during the summer and fall months when the shelf and coastal communities are dominated by a more neritic assemblage. At this time, the copepods *Pseudocalanus* spp., *Acartia longiremis*, *A. tumida*, *Calanus marshallae*, *Metridia* spp., and *Centropages abdominalis* are common. The marine cladocerans, *Podon* and *Evadne*, and the larvaceans, *Oikopleura* spp., are also evident during the summer.

5. Shelf and coastal zooplankton stocks exhibit growth cycles that respond to phytoplankton production. Winter and early spring stocks are lowest (3–10 g/m²), followed by substantial increases (30–78 g/m²) in the summer and fall. In the deeper inshore waters of the Strait of Georgia, seasonal variations in a 400-m water column range from a low of 40 g/m² in the spring to a high of 320 g/m² in the fall. Annual zooplankton production probably does not exceed 30 to 60 g C/m²y in shelf and coastal areas.

6. Zooplankton serve as forage for fishes, shellfishes, marine birds, and mammals. Copepod nauplii are critical in the diets of most larval fishes. In this respect, the prolific small copepods, *Pseudocalanus* spp. and *Oithona* spp., are probably extremely important in the life cycles of most pelagic and demersal fishes. The larger copepods and euphausiids represent critical food items, particularly for marine birds, whales, and juvenile and adult pelagic fishes.

7. Our present understanding of both the zooplankton community structure and its function is flawed by our inadequate understanding of the production of key species in both shelf and inside water environments. General seasonal cycles have been described for biomass, but very few attempts have been made to determine those factors that enhance or constrain population growth rates and how those factors might vary interannually. Sizable annual variations in the returns of pink salmon (a species that feeds almost entirely on zooplankton and microneuston as juveniles) suggest that the coastal, shelf, and oceanic environments are all 'noisier' than our data sets portray. In addition, although the availability of food may not be the only factor affecting survival, it is probably extremely important. In this regard, information on mesoscale patchiness (1–10 km) is also lacking, although there is little doubt about its primary importance.

Future Studies

The zooplankton community plays a unique role in controlling the production cycle in the open portion of the Gulf of Alaska. Further, zooplankton are of significant trophic importance. Considering these facts, it seems appropriate to expand the more site-specific studies of zooplankton distribution and abundance into broader, hydrographically defined domains such as currents, convergences, and divergences. Studies at this level of complexity will certainly benefit from a close working tie with physical oceanographers who use a variety of techniques, including mass balance, satellite-tracked surface buoys, and multiple current meter deployments, to describe the Gulf's responses to seasonal wind and freshwater forcing patterns.

Recent advances in high-frequency quantitative acoustic sampling let investigators make hundreds of thousands of biomass measurements as routinely as they now take temperature and salinity readings both along cruise tracks that cross the currents and in upwelling regions which define the gyre in the northeast Pacific Ocean. While it is true that surveys of this kind still rely on net tows for identification of the zooplankton, the actual amount of direct sampling can be reduced to manageable limits. Euphausiids, which are likely to be as important in trophic exchange processes as copepods, are poorly sampled by conventional means. These organisms are particularly suited for acoustic censusing, and knowledge of their mesoscale distribution and abundance will benefit from the use of quantitative sonic methods.

Vast manpower and monetary resources have been expended on studies to determine how the oceanography of the northeast Pacific Ocean affects the production of commercially important fish and shellfish. These studies have generally lacked interdisciplinary coordination, and because of this, have been unfocused in terms of ecosystem function. Completion of the OCSEAP-sponsored research and its synthesis in this book will provide one of the first attempts—in a single volume—to assemble what is understood about the Gulf of Alaska. It is essential that this compilation not represent an end in itself, but rather become a point of departure for more focused oceanographic studies of the interrelationships between the living and non-living components of this system. In the spirit of the new initiatives to describe ocean productivity that are stated by the Division of Ocean Sciences, NSF, this is surely one area ripe for both continued and expanded research.

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It is my desire to dedicate this review of zooplankton in the Gulf of Alaska to my dear friend and mentor, the late Dr. T. Saunders English, Professor of Oceanography, University of Washington, Seattle, Washington. His dedication to oceanography, his inspiration as a colleague, and his boundless enthusiasm for life infected all who were privileged to know him. It seems fitting that many of his friends and associates were in some way involved in the preparation of this monograph on the Gulf of Alaska. Tom would have liked that.

Appendix I.

Zooplankton and ichthyoplankton, reported in samples taken from the northern Gulf of Alaska (LeBrasseur 1965b; Cooney *et al.* 1973; Cooney 1975; Damkaer 1977; Kendall *et al.* 1980; Cooney *et al.* 1981; Vogel and McMurray 1986; VTN 1983; Wing and Reid 1972).

Cnidaria

Rathkea octopunctata

Bougainvilla superciliaris (= *B. multotentaculata*)

Euphysa japonica

Hybocodon prolifer

Calycopsis sp.

Sarsia tubulosa

S. princeps

S. rosaria

Leuckartiara octona

L. nobilis

L. breviconis (= *Neoturris breviconis*)

Perigonimus vesicarius

Halimedusa typus

Stomotoca atra

Polyorchis penicillatus

Obelia borealis

Phialidium gregarium

Aequorea aequorea (= *A. victoria*)

Melicertum octostatum

Halistaura cellularia

Tiaropsisidium sp.

Stauropora mertensi

Eutonina indicans

Gonianemus vertens

Proboscidactyla flavidirrata

Aglantha digitale

Pantachogon haackeli

Aegina citrea

Cunina globosa

Lensia conoidea

Muggiacea atlantica

Dimophyes arctica

Vogtia serrata

Agalma elegans

Chuniphyes multidentata

Nanomia sp.

Periphylla periphylla

Nectopyramis diomedae

Aurelia aurita

Cyanea capillata

Praya reticulata

Crysaora melanaster

Ctenophora

Bolinopsidae infundibulum

Beroe sp.

Pleurobrachia pileus

Polychaeta

Pelagobia longicirrata

Tomopteris septentrionalis

T. pacifica

<i>T. planktonis</i>	<i>Undinella</i> sp.	<i>Holmesiella anomala</i>
<i>T. renata</i>	<i>Metridia curticauda</i>	<i>Neomysis rayii</i>
<i>Plotohelmis tenius</i>	<i>M. okhotensis</i>	<i>N. kadiakensis</i>
<i>Autolytus</i> sp.	<i>M. pacifica</i> (= <i>M. lucens</i>)	<i>N. nakazawai</i>
<i>Typhloscolex mulleri</i>	<i>M. princeps</i>	<i>Pseudomma truncatum</i>
<i>Poeobius meseres</i>	<i>Pleuromamma scutullata</i>	<i>Meterythrops robusta</i>
Mollusca	<i>P. robusta</i>	<i>Gnathophausia gigas</i>
<i>Limacina helicina</i> (= <i>Spiratella pacifica</i>)	<i>Centropages abdominalis</i>	<i>Mysis oculata</i>
<i>Euclio pyramidata</i>	<i>Paracalanus parvus</i>	
<i>Clione limacina</i>	<i>Limnocalanus macrurus</i>	Amphipoda
<i>Gasteropteron pacificum</i>	<i>Diaptomus</i> sp.	<i>Andaniexis subabyssi</i>
<i>Rossia pacifica</i>	<i>Eurytemora americana</i>	<i>Calliopioides laeviuscula</i>
<i>Eledone</i> sp.	<i>E. pacifica</i> (= <i>E. herdmani</i>)	<i>C. behringi</i>
<i>Chiroteuthis veranyi</i>	<i>Lucicutia flavigornis</i>	<i>Cyphocaris challengerii</i>
<i>Galiteuthis armata</i>	<i>L. ovalis</i>	<i>C. anonyx</i>
<i>Octopus</i> sp.	<i>Dissita scopularis</i>	<i>Eusiriella multicalceola</i>
Cladocera	<i>Heterorhabdus tanneri</i>	<i>Koroga megalops</i>
<i>Daphnia schodleri</i>	<i>H. compactus</i>	<i>Hyperia medusarum hystrix</i>
<i>Evadne nordmanni</i>	<i>H. robustoides</i>	<i>Hyperoche medusarum</i>
<i>E. tergestina</i>	<i>Heterostylites major</i>	<i>Monoculodes zernovi</i>
<i>Podon leuckarti</i>	<i>Haloptilus pseudooxycephalus</i>	<i>Orchomene</i> sp.
<i>P. polyphemoides</i>	<i>Candacia columbiae</i>	<i>Parathemisto gracilipes</i>
Ostracoda	<i>Pachyptilis pacificus</i>	<i>P. pacifica</i>
<i>Philomedes</i> sp.	<i>Epilabidocera longipedata</i>	<i>P. libellula</i>
<i>P. trituberculatus</i>	<i>Acartia clausi</i>	<i>Phronima sedentaria</i>
<i>Conchoecia alata minor</i>	<i>A. longiremis</i>	<i>Primno macropa</i>
<i>C. elegans</i>	<i>A. tumida</i>	<i>Proscina birsteini</i>
Copepoda	<i>Tortanus discaudatus</i>	<i>Scina stebbingi</i>
<i>Neocalanus cristatus</i> (= <i>Calanus cristatus</i>)	<i>Microsetella rosea</i>	<i>S. borealis</i>
<i>N. plumchrus</i> (= <i>C. plumchrus</i>)	<i>Harpacticus</i> sp.	<i>S. rattrayi</i>
<i>Calanus marshallae</i>	<i>Tegastes</i> sp.	<i>Streetsia</i> sp.
<i>C. pacificus</i>	<i>Tisbe</i> sp.	<i>Tryphaena malmii</i>
<i>Mesocalanus tenuicornis</i> (= <i>Calanus tenuicornis</i>)	<i>Lubbockia wilsonae</i>	<i>Lanceola pacifica</i>
<i>Eucalanus bungii</i>	<i>Pseudolubbockia dilatata</i>	<i>Westwoodilla rectangulata</i>
<i>Clausocalanus arcuicornis</i>	<i>Oncea conifera</i>	<i>Vibila australis</i>
<i>Microcalanus</i> spp.	<i>O. borealis</i>	<i>Paraphronima crassipes</i>
<i>Pseudocalanus</i> spp.	<i>O. parila</i>	<i>Caprella</i> sp.
<i>Spinocalanus brevicaudatus</i>	<i>O. notopus</i>	<i>Paracallisoma alberti</i>
<i>Aetideus divergens</i>	<i>O. prolata</i>	<i>Rhachotropis natator</i>
<i>A. pacificus</i>	<i>Corycaeus anglicus</i>	
<i>Chiridius gracilis</i>	<i>Oithona helgolandica</i> (= <i>O. similis</i>)	Euphausiacea
<i>C. poppei</i>	<i>O. spinirostris</i>	<i>Euphausia pacifica</i>
<i>Bradyidius saanichi</i>	<i>Monstrilla helgolandica</i>	<i>Thysanoessa inermis</i>
<i>Gaetanus intermedius</i>	<i>M. longiremis</i>	<i>T. inspinata</i>
<i>Gaidius tenuispinus</i>	<i>M. wandlii</i>	<i>T. longipes</i>
<i>G. simplex</i>	<i>M. canadiensis</i>	<i>T. raschii</i>
<i>G. variabilis</i>	<i>Cymbasoma rigidum</i>	<i>T. spinifera</i>
<i>Pseudochirella</i> sp.		<i>Tessarabrachion oculata</i>
<i>Pareuchaeta elongata</i>		<i>Stylocheiron</i> sp.
<i>P. sarsi</i>	Isopoda	
<i>Lophothrix frontalis</i>	<i>Gnorimosphaeroma oregonensis</i>	
<i>Amallothrix inornata</i>	<i>Idothea wosnesenskii</i>	
<i>Racovitzanus antarcticus</i>	<i>Neosphaeroma oregonensis</i>	
<i>Scaphocalanus magnus</i>		Cumacea
<i>S. brevicornis</i>		<i>Cumella</i> sp.
<i>Scolecithricella minor</i>		<i>Diastylis dawsoni</i>
<i>S. ovata</i>		<i>Vaunthompsonia</i> sp.
	Mysidacea	
	<i>Acanthomysis nephrophthalma</i>	
	<i>A. pseudomacropsis</i>	

<i>Crangon alaskensis</i>	<i>Trichodon trichodon</i>
<i>Sergestes similis</i>	<i>Aptocyclus ventricosus</i>
<i>Chionoecetes spp.</i>	<i>Bathymaster sp.</i>
<i>Paralithodes sp.</i>	<i>Anoplarchus insignis</i>
Chaetognatha	<i>Ronquilus jordani</i>
<i>Eukrohnia hamata</i>	<i>Chiroplophis polyactocephalus</i>
<i>E. fowleri</i>	<i>Lumpenella longirostris</i>
<i>E. bathypelagica</i>	<i>Lumpenus sagitta</i>
<i>Sagitta elegans</i>	<i>L. maculatus</i>
<i>S. scrippsae</i>	<i>Stichaeus punctatus</i>
Larvacea	<i>Lyconectes aleutensis</i>
<i>Oikopleura dioica</i>	<i>Pholis sp.</i>
<i>O. labradoriensis</i>	<i>P. laeta</i>
<i>O. vanhoeffeni</i>	<i>Zaprora silenus</i>
<i>Fritillaria borealis</i>	<i>Ammodytes hexapterus</i>
Thaliacea	<i>Atheresthes stomias</i>
<i>Salpa fusiformis</i>	<i>Glyptocephalus zachirus</i>
<i>S. maxima</i>	<i>Hippoglossoides elassodon</i>
Osteichthyes	<i>Isopsetta isolepis</i>
<i>Clupea harengus pallasii</i>	<i>Lepidopsetta bilineata</i>
<i>Mallotus villosus</i>	<i>Microstomus pacificus</i>
<i>Thaleichthys pacificus</i>	<i>Platichthys stellatus</i>
<i>Bathylagus milleri</i>	<i>Psettichthys melanostictus</i>
<i>B. pacificus</i>	<i>Hippoglossus stenolepis</i>
<i>Lampanyctus regalis</i>	<i>Cyclothona sp.</i>
<i>Leuroglossus schmidti</i>	<i>Chauliodus macouni</i>
<i>Stenobrachius sp.</i>	<i>Lycodapus mandibularis</i>
<i>S. leucopsarus</i>	<i>Gasterosteus aculeatus</i>
<i>S. nannochir</i>	
<i>Protomyctophum crockeri</i>	
<i>P. thompsoni</i>	
<i>Gadus macrocephalus</i>	
<i>Theragra chalcogramma</i>	
<i>Sebastes sp.</i>	
<i>Hexagrammos sp.</i>	
<i>H. decagrammus</i>	
<i>H. lagocephalus</i>	
<i>H. octogrammus</i>	
<i>H. stelleri</i>	
<i>Ophiodon elongatus</i>	
<i>Pleurogrammus monopterygius</i>	
<i>Anoplopoma fimbria</i>	
<i>Artedius spp.</i>	
<i>Clinocottus sp.</i>	
<i>Dasyocottus setiger</i>	
<i>Gymnocanthus sp.</i>	
<i>Hemilepidotus spp.</i>	
<i>H. hemilepidotus</i>	
<i>Icelinus borealis</i>	
<i>Malacocottus zonurus</i>	
<i>Myoxocephalus spp.</i>	
<i>Radulinus asperellus</i>	
<i>Triglops sp.</i>	
<i>Liparis florae</i>	
<i>Lifucensis spp.</i>	
	Appendix II.
	Zooplankton collected in B de Quadra fjord during 1982 (V 1984).
	Cnidaria
	Hydrozoans
	Anthomedusae
	<i>Leuckartiara sp.</i>
	<i>Rathkea octopunctata</i>
	<i>Sarsia rosaria</i>
	<i>Bougainvilla sp.</i>
	Leptomedusae
	<i>Obelia sp.</i>
	<i>Phialidium gregarium</i>
	<i>Aequorea aequorea</i>
	Limnomedusae
	<i>Proboscidactyla flavicirrata</i>
	Trachymedusae
	<i>Aglantha digitale</i>
	Siphonophora
	<i>Nanomia bijuga</i>
	<i>Lensia conoidea</i>
	<i>Muggiacea atlantica</i>
	<i>Dimophyes arctica</i>
	Scyphozoans
	<i>Aurelia aurita</i>
	<i>Cyanea capillata</i>

Appendix II.

Zooplankton collected in Boca de Quadra fjord during 1982 (VTN 1984).

Cnidaria

Hydrozoans

Anthomedusae

- Leuckartiara* sp.
- Rathkea octopunctata*
- Sarsia rosaria*
- Bougainvilla* sp.

Leptomedusae

- Obelia* sp.
- Phialidium gregarium*
- Aequorea aequorea*

Limnomedusae

- Proboscidactyla flavicirrata*

Trachymedusae

- Aglantha digitale*

Siphonophora

- Nanomia bijuga*
- Lensia conoidea*
- Muggiacea atlantica*
- Dimophyes arctica*

Scyphozoans

- Aurelia aurita*
- Cyanea capillata*

Ctenophora

Pleurobrachia pileus

Annelida

Polychaete larvae
Tomopteris septentrionalis
Rhynchonerella angelini

Mollusca

Gastropod larvae
Limacina helicina
Clione sp.
Bivalve larvae
Cephalopod larvae

Cladocera

Evadne nordmanni
Podon leuckarti

Ostracoda

Conchoecia spp.

Copepoda

Calanoida

- Calanus marshallae*
- C. pacificus*
- C. plumchrus*
- C. cristatus*
- Eucalanus bungii*
- Paracalanus parvus*
- Microcalanus pusillus*
- Pseudocalanus minutus*
- Aetideus armatus*
- Gaetanus simplex*
- Pareuchaeta elongata*
- Metridia okhotensis*
- Metridia pacifica*
- Centropages abdominalis*
- Eurytemora* sp.
- E. pacifica*
- E. americana*
- Candacia columbiae*
- Epilabidocera longipedata*
- Acartia clausi*
- A. longiremis*
- Tortanus discaudatus*

Harpacticoida

- Microsetella rosea*
- Harpacticus* sp.

Cyclopoida

- Oncaeа borealis*
- Corycaeus anglicus*
- Oithona helgolandica*
- O. spinirostris*

Cirripeda

Balanus sp. larvae

Mysidacea	Pacific sand lance
Unidentified mysid	juvenile whitespotted greenling
Isopoda	juvenile masked greenling
<i>Gnorimosphaeroma oregonensis</i>	juvenile pollock
Amphipoda	Pacific cod
<i>Cyphocaris challengerii</i>	
<i>Orchomene</i> sp.	
<i>Parathemisto pacifica</i>	Mysids
<i>Primno macropa</i>	sand sole
<i>Scina borealis</i>	pollock
Euphausiacea	
Euphausiid larvae	Pelagic Amphipods
<i>Euphausia pacifica</i>	juvenile chum salmon
<i>Thysanoessa raschii</i>	herring
<i>T. longipes</i>	
<i>T. inermis</i>	Euphausiids
<i>T. spinifera</i>	pollock
Chaetognatha	Pacific Ocean perch
<i>Sagitta elegans</i>	yellow Irish lord
Tunicata	yellowfin sole
<i>Oikopleura</i> spp.	rex sole
<i>Fritillaria borealis</i>	flathead sole
Ascidian larvae	juvenile arrowtooth flounder
	short-tailed shearwater
	tufted puffin
	black-legged kittiwake
	minke whale
	fin whale
	blue whale
	humpback whale

Appendix III.

Planktivorous organisms off Kodiak Island classified by known food sources (Vogel and McMurray 1986).

Calanoid Copepods

juvenile salmonids
capelin
herring
Pacific sand lance
juvenile whitespotted greenling
juvenile pollock
juvenile rock sole
juvenile yellowfin sole
gray whale
sei whale
fin whale
right whale

Fish Larvae

juvenile salmonids
Pacific sand lance
juvenile whitespotted greenling

Harpacticoid Copepods

juvenile salmonids capelin

Decapod Larvae

Pacific Ocean perch
herring
smelt
juvenile pink salmon
pandalid shrimp

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