

TROPHIC DYNAMICS IN MARINE NEARSHORE SYSTEMS
OF THE ALASKAN HIGH ARCTIC

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Kenneth Harlow Dunton, B.S., M.S.

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TROPHIC DYNAMICS IN MARINE NEARSHORE SYSTEMS
OF THE ALASKAN HIGH ARCTIC

RECOMMENDED:

DB Hawk
George W. Hupphut
David W. Norton
Ed Brown
William K. Skill
Chairman, Advisory Committee
Henry John A. Sauer
Department Head

APPROVED:

D. J. Sauer
Dean, College of Natural Sciences
DB Hawk
Director of Graduate Programs

AUG 06 1985

Date

ABSTRACT

This dissertation describes two ecological studies in the arctic Alaskan nearshore zone: the productivity and growth strategies of arctic kelp and the use of natural carbon isotope abundances to examine food web structure and energy flow in the marine ecosystem. Linear growth of the kelp, Laminaria solidungula is greatest in winter and early spring when nutrients are available for new tissue growth. Since over 90% of this growth occurs in complete darkness beneath a turbid ice canopy, the plant draws on stored food reserves and is in a carbon deficit during the ice covered period. Annual productivity of L. solidungula under these conditions is about 6 g C m^{-2} compared to about 10 g C m^{-2} if light penetrates the ice canopy.

Carbon isotope abundances were used to assess food web structure and energy flow in the Boulder Patch, an isolated kelp bed community, and in the Alaskan Beaufort Sea fauna. Isotopic analyses of the resident fauna of the Boulder Patch revealed that kelp carbon contributes significantly to the diet of many benthic animals, including suspension feeders. Some crustaceans, such as mysids and euphausiids (which are key prey species for fishes, birds and marine mammals), also incorporate large amounts of kelp carbon into their tissues when resident in the Boulder Patch. Across the shelf of the Alaskan Beaufort Sea, a distinct gradient in the isotopic composition of marine zooplankton and benthic fauna

was related to the intrusion of the Bering Sea water and upwelling in the eastern Beaufort Sea near Barter Island. The ^{13}C depletion in fauna of the eastern Beaufort Sea is presumed due to the cycling of ^{13}C depleted inorganic carbon into the euphotic zone.

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CHAPTER 1. INTRODUCTION

Statement of the problem

In a practical sense, a definite knowledge of the structure and function of marine ecosystems is vital -- both to our understanding of the natural world and in our efforts to manipulate the environment without causing a bewildering variety of ecological crises. Central to this ecological theme is the food web concept. It underlies our basic understanding of the relationship of animals to each other and their ultimate plant carbon sources.

Unfortunately, the complex structures of food webs present major hurdles for scientists who attempt to delineate animal trophic interactions. Collecting sufficient data to accomplish this task requires formidable effort. Large numbers of animals must be collected for analysis of their gut contents, which may or may not represent the predominant diet of a particular species or be significantly assimilated by the animal. The problem is not alleviated by laboratory feeding experiments, since the behavior of animals under such artificial conditions may be different from its behavior in nature. Also, the natural variability of individuals in populations make the quantitative assessment of animal diet composition very difficult or impossible to determine in many cases.

A partial solution to this problem came within the last decade when a number of scientists began to employ stable carbon isotope ratios as natural tracers of carbon in ecological systems. The use of this technique is based on the observation that plant species possess distinctive $^{13}\text{C}:^{12}\text{C}$ ratios (Craig, 1953; Smith and Epstein, 1971) due to differences in the biochemical pathways used during photosynthetic fixation of either CO_2 (terrestrial plants) or HCO_3^- (marine algae) (Park and Epstein, 1960). This isotopic signature is largely preserved as it is transferred through the food chain, reflecting both the animals' diet and its ultimate plant carbon sources (DeNiro and Epstein, 1978). However, the success of this technique is inversely proportional to the complexity of the system under examination. As a result, despite its promise in theory, the technique has met with limited success.

Many food web studies to date using stable carbon isotope ratios have been conducted on highly productive temperate nearshore systems. These have typically included seagrass meadows and salt marshes, but not kelp beds. Kelp beds are among the most productive and widespread communities in the world, and have received considerable attention in both the popular and scientific literature. The productivity and growth of the various species of kelp have been major foci for scientists working from several continents, but very little research has focused on arctic species.

In this light, the recent discovery of an isolated kelp bed community on Alaska's north arctic coast is noteworthy. The

presence of this community, commonly referred to as the Boulder Patch, presented a unique opportunity to examine the productivity and growth strategies of kelp in a light-limited environment and to determine the importance of kelp carbon to the Boulder Patch food web. The isolation of this community and its relative simplicity in terms of its carbon inputs made it an ideal system in which to use $^{13}\text{C}:^{12}\text{C}$ ratios as natural tracers of carbon flow.

Thus, the major objectives of my research were to address the productivity and strategies of growth in arctic kelp and to trace the path of carbon on both a community level (within the Boulder Patch) and on an ecosystem level (the Beaufort Sea) using natural variations of stable carbon isotopes. I accomplished these objectives in a step-wise fashion and present my results in the following six chapters. Two of these chapters (2 and 3) have been published. In the second chapter, I present my initial work on the biology of the Boulder Patch, as well as some background on its discovery and unique geologic features. This chapter also includes my preliminary findings on rapid growth in Laminaria solidungula during nine-month periods of complete darkness.

In Chapter 3, I construct an annual carbon budget for the Boulder Patch. This work is a necessary precursor of the later isotope study since it identifies the magnitude of the various carbon sources available to consumers. In Chapter 4, I address the strategy of growth employed by Laminaria solidungula to complete nearly 90% of its annual linear growth in complete darkness during

the ice covered period. My finding that the plant experiences a large carbon deficit during this period of rapid linear growth is an interesting paradox never before described in kelp. In Chapter 5, I contrast the growth strategy of L. solidungula with that of L. saccharina, another less abundant kelp species in the Boulder Patch. The pattern of growth in the two species differs markedly, possibly indicative of genotypic restrictions in L. saccharina.

The importance of kelp carbon to consumers in the Boulder Patch is the subject of Chapter 6. Using stable carbon isotopes as tracers I conclude that kelp carbon is not only an important food source for macroalgal herbivores (like chitons and some gastropods) but is assimilated by many benthic species that includes sponges, polychaete worms, molluscs and ascidians. I also find that some kelp carbon reaches the pelagic food chain and is incorporated into many crustaceans and an important crustacean predator, the arctic cod. In Chapter 7, I present the results of isotopic analyses of zooplankton across the Beaufort Sea shelf, from Pt. Barrow on the west to the Canadian Border on the east. I find that the zooplankton show a distinct gradient in their isotopic composition, and relate this change to the intrusion of Bering Sea water on the Beaufort Sea shelf and an upwelling in the eastern Beaufort Sea near Barter Island. The upwelling at Barter Island also contributes to with the highest phytoplankton productivity rates on the Alaskan Beaufort Sea shelf and an important bowhead whale feeding area.

As with any study of this size, my research has opened more cans of worms than it has consumed. Several intriguing questions remain especially in respect to the Boulder Patch. These include the origin of the flora and fauna, not the least of which is the paradox that the fauna is decidedly Pacific in origin, while the flora is definitely Atlantic. The problem is a good one for biogeographers. The lack of other herbivores in this community (e.g., sea urchins) is another mystery. The source and mode of transport of the cobbles and boulders are still unresolved as is the presence of a nondepositional environment (the Boulder Patch) at the mouth of a large arctic river. As oil development of the region proceeds, impacts on the Boulder Patch will require careful consideration by knowledgeable marine scientists. The Boulder Patch has already yielded at least two species of animals new to science -- several more undoubtedly remain to be discovered. It is also apparent that the Boulder Patch provides a very unique opportunity to study a complex community in an isolated setting and can provide valuable insights into the structure and function of highly productive macrophyte communities.

CHAPTER 2. AN ARCTIC KELP COMMUNITY IN THE ALASKA BEAUFORT SEA:
LIGHT AND NUTRIENT LIMITED GROWTH IN LAMINARIA
SOLIDUNGULA*

SUMMARY

The discovery of the "Boulder Patch," an area of cobbles and boulders with attached kelp and invertebrate life, is reported from Stefansson Sound, near Prudhoe Bay, Alaska. In the Boulder Patch, rocks provide a substratum for a diverse assortment of invertebrates and several species of algae. Recolonization by the biota was minimal on twelve boulders experimentally denuded and then left undisturbed for a three-year period. Sedimentation and grazing activity appear to be the major factors inhibiting recolonization. Linear growth in the kelp, Laminaria solidungula, is greatest in winter and early spring when nutrients are available for new tissue growth. The plant draws on stored food reserves to complete over 90% of its annual linear growth during the nine months of darkness under a turbid ice canopy. These reserves are accumulated by photosynthetic activity during the previous summer. The total carbon contribution made by kelp in Stefansson Sound under these conditions is about $164 \times 10^6 \text{ g yr}^{-1}$ or $7 \text{ g m}^{-2}\text{yr}^{-1}$.

* The main elements of this paper have appeared in a published paper (Dunton et al., 1982).

INTRODUCTION

A distinctive feature of the Alaskan Beaufort Sea shelf biota is the absence of kelp and other species of benthic macroalgae. Pieces of kelp and red algae have been found only as drift on beaches between Pt. Barrow and the United states--Canadian border, and entire plants are seldom observed in significant numbers in driftlines. Collins (1927), in the last major account of benthic algae of the Alaskan Beaufort Sea, indicated that no extensive stands of laminarioids were found between Pt. Barrow and the MacKenzie River, NWT. In contrast, many species of sublittoral benthic algae grow in the Canadian Arctic (Lee, 1973; Wilce, 1964).

The ecological roles of arctic kelp communities have not been studied, mainly due to the large amount of logistic support needed for a diving operation in the Arctic. Therefore, we know little about the energetic contribution made by sublittoral benthic algal communities to the arctic nearshore environment and the fauna associated with large stands of macroalgae. Lee (1973) postulated that colonization of submerged rocks in the Canadian Arctic by fast-growing ephemeral plants takes place after they are no longer icebound, but this hypothesis has not been tested. In temperate regions, subtidal field studies have addressed the temporal and spatial aspects of recolonization, the interaction among organisms, the importance of physical parameters, and the productivity of the

algae in respect to its carbon or energetic input (Foster, 1975; Hatcher et al., 1977; Vadas, 1977).

Mohr et al. (1957) first reported the existence of a kelp bed in Arctic Alaskan waters. Using a dredge, they collected seaweeds, fishes and invertebrates at 13 meters depth about 80 km southwest of Pt. Barrow in the Chukchi Sea. Collection of algae elsewhere in the Alaskan Arctic has been limited to drift material picked up by various Canadian and American arctic expeditions during the late 19th and early 20th centuries (for complete review, see Mohr et al., 1957).

In August 1971, Erk Reimnitz of the United State Geological Survey discovered abundant kelp and a diverse invertebrate fauna attached to cobbles and boulders near Prudhoe Bay in Stefansson Sound, Alaska, in an area now designated the "Boulder Patch" by the U.S. Board of Geographic Names. The Boulder Patch has been the subject of cooperative geological and biological studies since 1978. These studies resulted from the need to provide adequate protection to this community during exploration of oil reserves in the immediate area that would involve the construction of gravel islands and causeways. The Boulder Patch straddles promising offshore oil structures, as evidenced by some tracts in this area receiving the highest bids in the joint State-Federal Beaufort Sea lease sale in December 1979 (Wilson, 1979).

The Boulder Patch is a rare, perhaps unique feature of the Alaskan Beaufort Sea shelf, which is blanketed predominantly by

silty sands and mud (Barnes and Reimnitz, 1974). Most macroalgae depend on hard rock substrates for attachment, since they require a stable base for successful colonization, growth and reproduction. This fundamental need for a hard substratum was recognized by Kjellman (1883), in his treatise on arctic algae.

This paper combines marine biological and physical studies to; (1) document seasonal variations in the physical environment that affect the development of the biotic community, and (2) describe the composition of the community and determine the productivity of the kelp. Repeated monitoring of a study site allowed detailed description of ecological and biological processes in light of seasonal variations in the environment. Such information is essential in evaluating the importance of kelp communities and their probability of occurrence on arctic nearshore shelves. The locations of other known and suspected occurrences of algal beds in the Alaskan Beaufort Sea are presented.

STUDY AREA

Description of Stefansson Sound

Stefansson Sound extends from the Midway Islands in the west to Tigvariak Island in the east, and is enclosed by the protecting barrier island chain that consists of Narwhal Island, Cross Island and the Midway Islands (Fig. 1). Water depths in Stefansson Sound

do not exceed 10 meters, and range from three to nine meters within the Boulder Patch. Waves have a short period because of shallow depth and limited fetch. Even during storms, wave amplitudes rarely exceed 1.5 meters. Currents are predominantly wind driven during the open-water period, when easterly winds dominate. Therefore, the net drift is westward during the summer (Barnes et al., 1977; Matthews, 1981a). The rivers discharging into the sound supply only sand-size and finer materials. Peak discharge occurs in June following the river breakup, but very little sediment accumulates within the sound (Reimnitz and Ross, 1979). Currents are very weak to undetectable during the period of total ice cover (from mid-October through June). Bottom water temperatures in the vicinity of the Boulder Patch range from a nearly constant -1.8°C under the sea ice to 7°C during the open-water period. Salinity varies from 14 to $35\text{ }^{\circ}/\text{oo}$ (Barnes et al., 1977). With the exception of the Boulder Patch, the bottom is characterized by silty sands and mud, and an infaunal assemblage dominated by polychaete worms, small molluscs and crustaceans (Feder and Schamel, 1976; Broad et al., 1973).

Freezeup is usually complete by mid-October, and breakup begins in late June or early July. The benthic environment is largely protected from gouging by deep-draft ice keels by the offshore islands and shoals which intercept them. The winter ice field within Stefansson Sound is shorefast (i.e., attached to the shore), with minimal movement from early November through June.

Ice thickness reaches a maximum of 2 m in early May before melting of the ice canopy begins.

The distribution of areas of cobbles and boulders is shown in Figure 1. This map is a compilation of all available data from the trackline geophysical surveys, supported by benthic samples and diving traverses completed by Reimnitz and Ross (1979). The rocks are not distributed uniformly but in patches of various sizes. Figure 1 shows clearly identifiable areas of dense rock bottom, and transition areas where finer sediments dominate, or where the data are uncertain. Subsequent geophysical studies in portions of Stefansson Sound (Toimil, 1980) generally agree with this distribution.

The origin and modern physical processes of the Boulder Patch

Deposits of gravel, cobbles and boulders similar to those found in the Boulder Patch of Stefansson Sound are being formed today in a number of places during the erosion of coastal bluffs containing coarse materials. Such stones are found in parts of the Quaternary Gubik Formation, which blankets much of the coastal plain (Black, 1964). Leffingwell (1919) first drew attention to the boulders occurring in large numbers along the beaches of Flaxman Island, and called them the Flaxman Formation. The Flaxman boulders have since been studied in other areas by MacCarthy (1958), Rodeick (1975), and Hopkins (1979). According to these

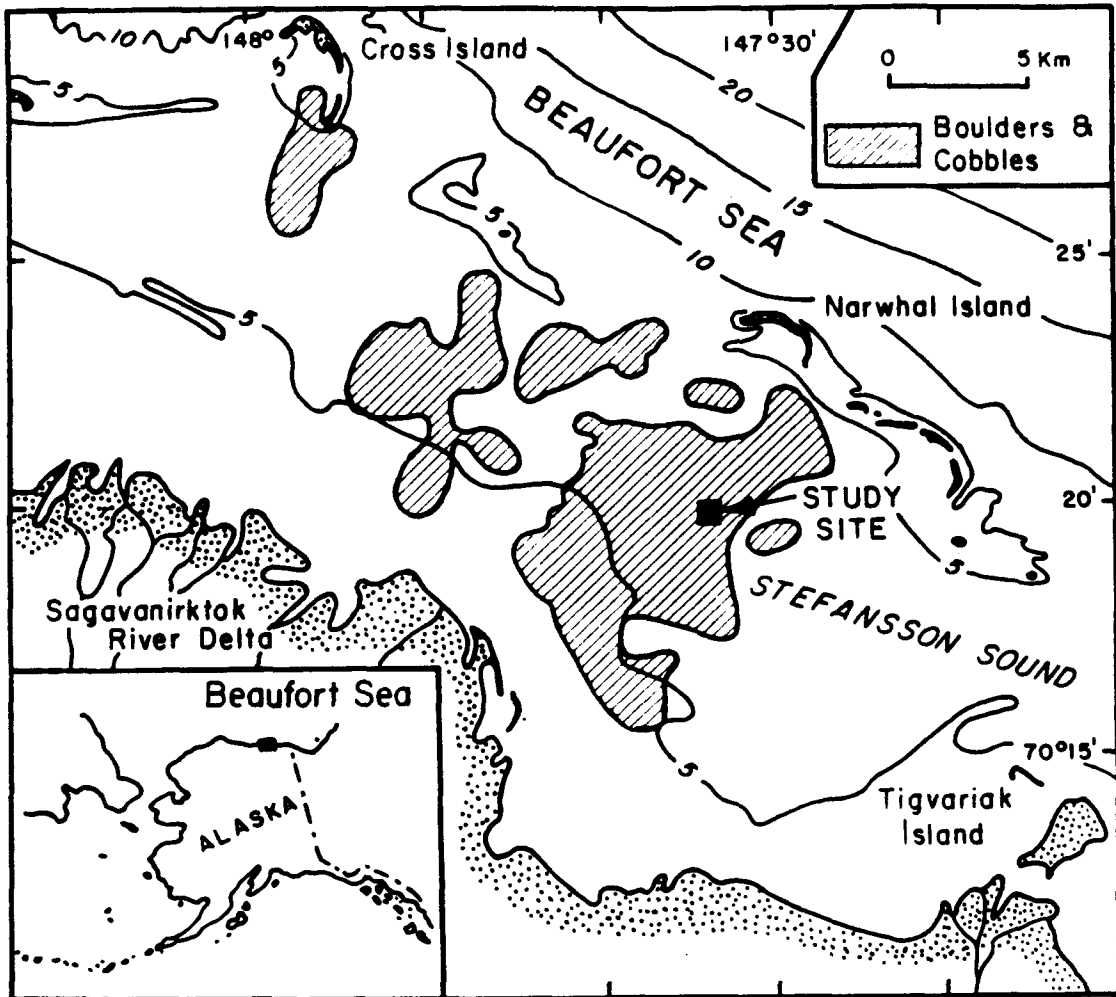


Figure 1. The location of the study site, Dive Site 11 (DS-11) in Stefansson Sound and the configuration of the Boulder Patch.

studies, the rocks include many types clearly extrinsic to northern Alaska. Among them are red granite, granulite-facies metamorphic rocks, pyroxenite, diabase, pink quartzite, and dolomite. The origin, mode of transport and emplacement of these erratics is under debate. One theory proposes that the rocks were rafted by ice to northern Alaska during times of relatively higher sea level (Hopkins, 1979). A second theory suggests that the boulders and cobbles were transported via a continental ice sheet (A. S. Naidu, personal communication). The source of rocks whose mineralogy match those in the Boulder Patch are northern Greenland for ice-rafted erratics, or the Canadian shield for rocks transported via a continental ice sheet.

Studies of sections of the Gubik Formation exposed on land, and of offshore borings (including several from Stefansson Sound, Harding-Lawson Associates, 1979), identify the layer containing cobbles and boulders as a thin sheet of glaciomarine stony sandy silt (Hopkins, 1979). The layer overlies marine clays deposited during the last major interglacial transgression, and -- according to Hopkins -- it may mark a local transgression resulting from the weight of ice over arctic Canada during early Wisconsinan Age. This Flaxman Formation is older than 42,800 years (Hopkins, 1979).

Bluffs along the Beaufort Sea shores usually retreat 1 to 3 m per year (Owens et al., 1980). Wherever the eroded materials contain glacial dropstones from the Flaxman Formation, the fine materials are winnowed out by waves and currents, and the cobbles

and boulders are left behind. The cobbles and boulders left behind on the beach are known as lag deposits. In many nearshore areas, these lag deposits rest on consolidated mud and are common on the beaches of Stefansson Sound (Fig. 1). During continuing coastal retreat, the cobbles and boulders are left behind and may be buried eventually by shallow marine sediments, as pointed out by Reimnitz and Ross (1979). Coastal bluffs west of Stefansson Sound rarely contain boulders.

All evidence suggests that the modern littoral boulder lag deposits are separated from the Boulder Patch by a wide belt of surficial shallow marine deposits as shown in Figure 2. Since the boulders in many areas of the Boulder Patch are resting directly on consolidated mud (similar to numerous places on shore) one is tempted to connect the coastal boulder lag deposits with the Boulder Patch, but there is no evidence to support this connection (Reimnitz and Ross, 1979). Thus the Boulder Patch appears to be an isolated area.

The seismic reflection records in many regions of the Boulder Patch show "windows" in the Holocene marine sediment cover where boulders are found on the sea floor. These windows are considered an erosional surface. Diving observations indicate that the cobbles and boulders generally rest loosely on top of a firm mud substratum, and are not enclosed by the substratum. Thus the Boulder Patch is a lag deposit presently resting on older marine mud, while the formerly overlying Flaxman Formation has been eroded

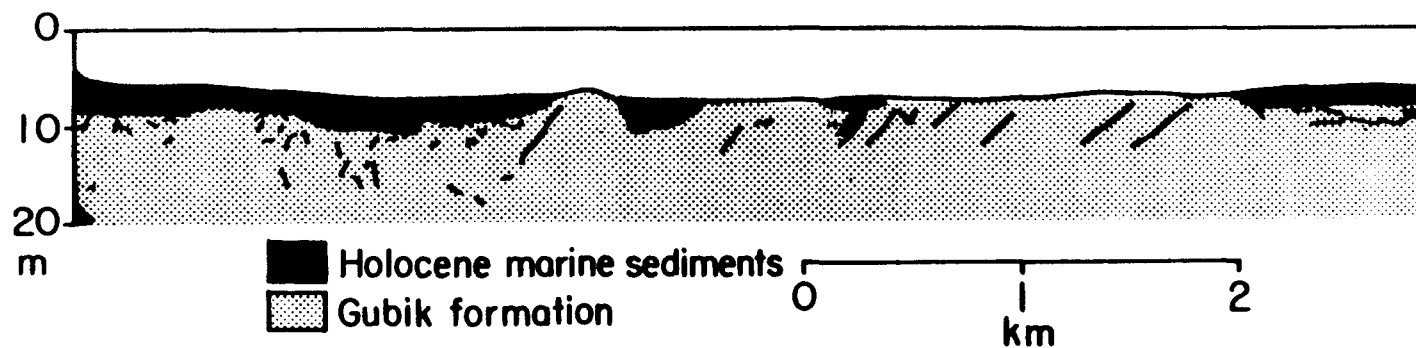


Figure 2. Line drawing of a 7 kHz seismic subbottom record across part of the Boulder Patch, showing the underlying Gubik exposed and truncated by the sea floor. Vertical exaggeration is 1:45 (adapted from Reimnitz and Ross, 1979).

away. This erosion may have occurred during lower sea level stands of the Holocene transgression (Reimnitz and Ross, 1979). Recent observations provide evidence that the erosion is an ongoing process (Toimil and England, 1982).

MATERIALS AND METHODS

Field logistics

During the open-water period, we sampled from a 6-m Boston Whaler (the R.V. Arctic Char; National Oceanic and Atmospheric Administration). In the winter, we did most of the diving at an acoustically marked study site, Dive Site 11 (DS-11; 70°19.25'N, 147°35.1'W; Fig. 1). During ice covered periods divers entered the water through holes cut in the ice using augers and ice chisels. Ice blocks were removed by helicopter or multiterrain vehicle (Rolligon). A heated insulated hut (Parcoll, Panebec Ltd., Montreal) placed over the dive hole functioned as a dive shelter and laboratory. Each diver wore a dry suit, a primary and backup breathing system, and headphones for wireless underwater communication with the surface (UDI-SUBCOM, Aberdeen, Scotland). Liquid silicone injected into the barrel of the first stage of the regulator prevented freezeups in the breathing system, especially when we dove without a shelter. Divers were tethered by rope to the surface and were usually limited to a 25-m radius of the hole,

although we occasionally ventured up to 50 m distant for short periods under special circumstances.

The physical and chemical environment

At DS-11, divers observed the accumulation of sediments over a two-year period. Here sediment settled upon biota and boulders, and on large plastic trays anchored in place. Measurements of the sediment cover were made with a ruler to the nearest 0.5 mm when the accumulation was greater than 0.5 mm. Sediments were collected for analysis in a large plastic cylinder, approximately 150 cm in diameter and 50 cm high, suspended 1 m above the seafloor. This sediment collector was deployed for a period of 4 months, from late May to late August 1981. Textural analysis of the trapped sediment was accomplished using the methods of Folk (1974). Percent organic composition was calculated by loss on ignition at 550°C for two hours.

Inorganic nitrogen (nitrate and nitrite) was measured in water samples collected 1 to 3 m off the bottom near DS-11. Nitrate and nitrite were determined according to Strickland and Parsons (1972).

Photon flux density was measured with a LI-185 quantum radiometer/photometer with a LI-192S underwater quantum sensor (LI-COR, Inc., Lincoln, Nebraska)

The biological community

Biological sampling and in situ experiments were conducted by a team of divers at approximately three-month intervals between July 1978, and November 1981, at DS-11 (Fig. 1). During the open water period, samples were collected at DS-11 and at several of the locations in the Boulder Patch. Fauna were preserved in formalin and bottled in the field. Macroalgae were mounted on herbarium paper or preserved in formalin.

Species composition and biomass of epilithic organisms were determined by scraping and airlifting all biota within 50 replicate 0.05 m^2 areas on rock surfaces. Samples were taken haphazardly but rocks with attached brown algae were avoided due to the difficulty of sucking these large plants into the airlift without breaking them into many pieces. This also allowed efficient collection of the epilithic biota without clogging the airlift intake with large pieces of Laminaria. The material from each scrape was sorted, identified, enumerated and weighed in the laboratory. Biomass and density of the biota are expressed per m^2 of rock substrata, not per m^2 of seabed (rock cover at DS-11 is estimated at 42%).

Brown algal standing crop was estimated by collecting all attached plants within 25 areas each measuring 0.25 m^2 along 50-m transect lines. Ten transects were examined in areas where rock cover exceeded 25%, and 10 were examined in areas where rock cover

ranged between 10 and 25%. These areas were defined by recent industry-sponsored geophysical surveys of the Boulder Patch (Toimil, 1980).

Recolonization

Recolonization of 0.05 m^2 plots denuded with paint scrapers and wire brushes was observed and photographed during each visit to DS-11. Two to four plots were denuded at approximately three-month intervals beginning in August 1978 and ending in May 1979, for a total of 14 plots. Composition, density and percent cover of the colonizing organisms were determined from both photographs and in situ analysis of the plots. Only the central 100 cm^2 area was analyzed to reduce edge effects. All plots were located on level surfaces on boulders.

Primary production

Linear growth of Laminaria solidungula, the predominant kelp, was followed by punching holes in the base of the blade, above the meristematic region (Chapman and Craigie, 1977).

Production-to-biomass ratios were calculated to determine the total carbon input made by the brown algae to the marine environment. Since L. solidungula constitutes over 90% of the brown algal biomass, I focused on the productivity of this plant.

The blade of L. solidungula is divided into distinct ovate segments of different sizes by constrictions that form annually. The growth of a new basal blade segment starts in November and continues until the following November. Since attrition occurs at the distal portion of the blade, the biomass (wet weight) of the basal segment is an accurate measurement of the plant's annual production. Seventeen plants weighing between 1.5 and 33 grams, were carefully detached from their substratum in November 1979, and banded to a large plastic Vexar cage anchored to the seafloor for one year. Following retrieval of the cage in November 1980, the new basal segments of the plants were individually removed and weighed. These wet weights represented the annual production of the plant. The average annual production-to-biomass (P:B) ratio was obtained by dividing the biomass of the first blade segment by the initial biomass of the entire frond. The percentage of dry weight to wet weight was determined by drying algal tissue in an oven at 30°C for 48 hours. The plants used for wet weight to dry weight determinations were collected randomly by divers at DS-11.

RESULTS

Fauna and flora of the Boulder Patch

The Stefansson Sound Boulder Patch supports a well-established kelp community characterized by several species of red and brown

algae, and by a diverse assortment of invertebrates representing every major taxonomic phylum. With the exception of rocks clearly upheaved and overturned recently, algae and epilithic invertebrates cover nearly all exposed substrata. Table 1 lists the predominant fauna and flora of the Boulder Patch, and provides data on density, biomass, and frequency of the various species. Many of these organisms were previously unreported from the Alaskan Beaufort Sea and are currently only known from the Boulder Patch. The animal species listed in Table 1 constitute about 86% of the faunal biomass based on the results of fifty 0.05 m^2 scrapes. Polychaete worms and representatives of other phyla (e.g., Foraminifera, Nemertea, Echinodermata) constitute the remaining 14%. I saw no obvious changes in the biomass or density of the flora or fauna over the three-year period of sampling.

The most conspicuous member of the community was the brown alga, Laminaria solidungula, whose distribution is primarily limited to arctic regions although it does occur as far south as Nova Scotia (A.R.O. Chapman, personal communication). Two other less common kelp species -- Laminaria saccharina, and Alaria esculenta -- were also present; they and L. solidungula formed a brown algal overstory. Beneath the kelp blades and in areas where kelp cover was sparse or absent, another floral assemblage dominates. This community is typified by several species of foliose and terete forms of red algae. These species, in descending order of their relative biomass, include Phycodrys

TABLE 1. Density ($N\ m^{-2}$), biomass ($g\ m^{-2}$) and frequency of occurrence (F, %) of the predominant benthic biota on rock substrata of the Boulder Patch.

Species	$N\ m^{-2}$	$g\ m^{-2}$	F(%)
PORIFERA			
<u>Choanites lutkenii</u>		3.6	4
<u>Halichondria panicea</u>		3.0	32
<u>Haliclona rufescens</u>		2.5	44
<u>Leucandra</u> sp.		0.2	26
<u>Phakettia cribrosa</u>		11.8	34
CNIDARIA			
HYDROZOA			
<u>Abietinaria</u> sp.		0.2	2
<u>Calicella syringa</u>		0.1	30
<u>Corymorpha</u> sp.		0.1	2
<u>Eudendrium</u> sp.		0.1	8
<u>Lafoeina maxima</u>		0.3	28
<u>Obelia</u> sp.		0.1	12
<u>Rathkea</u> sp.		0.1	2
<u>Sertularia cupressoides</u>		8.5	86
<u>Sertularia</u> sp. cf. <u>albimaris</u>		0.4	6
ANTHOZOA			
<u>Gersemia rubiformis</u>		3.0	14
MOLLUSCA			
GASTROPODA			
<u>Amauropsis purpurea</u>	0.4	0.1	2
<u>Lacuna</u> sp.	0.4	0.1	2
<u>Margarites</u> sp.	2.4	0.1	10

TABLE 1 (Continued)

Species	N m ⁻²	g m ⁻²	F(%)
<u>Margarites costalis</u>	1.6	0.1	2
<u>Oenopota</u> sp.	1.6	0.1	6
<u>Plicifusus</u> sp.	1.2	0.1	2
<u>Polinices</u> sp.	0.8	0.1	2
<u>Retusa obtusa</u>	1.2	0.1	2
<u>Solariella</u> sp.	2.0	0.1	6
<u>Solariella varicosa</u>	0.8	0.1	4
POLYPLACOPHORA			
<u>Amicula vestita</u>	16.0	11.0	38
<u>Ischnochiton albus</u>	1.2	0.1	2
BIVALVIA			
<u>Astarte</u> sp.	1.6	0.1	6
<u>Boreacola vadosa</u>	0.8	0.1	4
<u>Musculus</u> sp.	239.6	0.1	82
<u>Musculus discors</u>	69.2	2.1	8
<u>Macoma calcarea</u>	0.4	0.1	2
<u>Portlandia arctica</u>	0.4	0.1	2
BRYOZOA			
<u>Alcyonidium</u> sp.		1.0	44
<u>Callopora lineata</u>		2.6	90
<u>Carbasea carbasea</u>		0.1	2
<u>Crisia</u> sp.		0.1	10
<u>Cyclostomata</u>		0.2	20
<u>Dendrobeania</u> sp.		0.1	2
<u>Eucratea loricata</u>		3.8	66
<u>Flustra</u> sp.		0.1	2

TABLE 1 (Continued)

Species	N m ⁻²	g m ⁻²	F(%)
<u>Flustrella</u> sp.		0.1	2
<u>Hippothoa</u> <u>hyalina</u>		5.1	90
CHORDATA			
ASCIDEACEA			
<u>Chelyosoma</u> <u>macleayanum</u>	2.0	0.1	8
<u>Mogula</u> sp. cf. <u>siphonalis</u>	0.4	0.4	2
<u>Mogula</u> <u>griffithsii</u>	1.2	0.3	8
<u>Styela</u> <u>rustica</u>	0.4	0.1	2
OSTEICTHYES			
<u>Liparis</u> <u>herschelinus</u>	0.4	0.1	2
<u>Myoxocephalus</u> <u>quadricornis</u>	0.4	2.9	2
PHAEOPHYTA			
Laminariales (10-25% rock cover) ¹		66.7	20
Laminariales (25% rock cover) ¹		262.1	54
RHODOPHYTA			
Crustose corallines		0.5	20
<u>Neodilsea</u> <u>integra</u>		30.9	26
<u>Odonthalis</u> <u>dentata</u>		4.2	40
<u>Phycodryis</u> <u>rubens</u>		45.3	88
<u>Phyllophora</u> <u>truncata</u>		33.4	80
<u>Rhodomela</u> <u>confervoides</u>		5.3	58

¹ Includes Laminaria solidungula, L. saccharina and Alaria esculenta.

rubens, Phyllophora truncata, Neodilsea integra, Rhodomela confervoides and Odonthalia dentata. Ahnfeltia plicata (a filiform red alga) was not collected in the scrapes, but it was present in the Boulder Patch. These red algal species and crustose corallines such as Lithothamnium were used by many invertebrates as a substratum for attachment.

This algal assemblage appears similar in species composition to algal assemblages found in the north Atlantic Ocean. Of the nine species of macroalgae, two are restricted to the Arctic Ocean, three are common to the Atlantic Ocean, and four are found in both the Atlantic and Pacific oceans. None has a distribution that is strictly Pacific. Lee (1973) noted in his review of Canadian macroalgae that the Canadian Arctic marine flora is distinctly temperate Atlantic in composition.

Sponges and cnidarians are the most conspicuous invertebrates. This is due to the large size of some species, their abundance, and their striking shapes and colors. Two sponges -- Choanites lutkenii and Phakettia cribrosa -- and the delicate pink soft coral Gersemia rubiformis are widespread. All three species are represented by individuals of all size classes. At least four sea anemones (Order Actinaria) are present, but their species identities remain uncertain at this time. Other conspicuous invertebrates include several species of Tubularia, a stalked hydrozoan. Smaller less-conspicuous epilithic animals (such as hydroids and encrusting sponges) form a turf-like covering

on rocks. They are associated with Rhodomela confervoides (a terete-branched red alga) and stringy masses of the red alga, Phycodrys rubens.

Molluscs, bryozoans, and members of the urochordate group are common on rocks and attached to other biota, but are less conspicuous than the cnidarians and sponges. The chiton Amicula vestita constitutes the greatest percentage of molluscan biomass, and juvenile mussels of the genus Musculus has the greatest density. Amicula is an active herbivore; it feeds primarily on the blade and stipes of Laminaria solidungula. Erect and encrusting colonies of bryozoans are common on rocks and red algae. Colonies are often associated with hydroids and the translucent ascidian, Mogula griffithsii. The inconspicuous sea spider, Nymphon grossipes (not listed), is usually found among these dense mats of algae and attached invertebrates.

Several species of bottom-dwelling fishes are present in the Boulder Patch. Only two -- the clingfish Liparis herschelinus and the four-horned sculpin Myoxocephalus quadricornis -- were collected in scrapes. The other species include the eelpout Gymnelis viridis and juvenile Liparis sp. In March of 1979 and 1980, thousands of small eggs were found attached to kelp stipes, wire flags, and anchor lines. Large numbers of tiny liparid-like fishes were also observed, suggesting that these eggs were laid by adult Liparis females in the preceding months.

A majority of the species collected, but not listed in Table 1, are those found in the annelid, arthropod, and echinoderm groups. Over 100 species of annelids and arthropods were found in the Boulder Patch, and many of them are found throughout the Arctic. Those annelids and arthropods uncommon on soft bottoms but common in the Boulder Patch include the tubicolous polychaetes Spirorbis spp., the fanworm Potamilla neglecta, and the barnacle Balanus sp. Spirorbis forms small (1 to 4 mm) spiraled tubes attached to rocks, algae, hydroids and snail shells. Potamilla, a much larger polychaete, was found attached to rocks and algae, and had membranous tubes 8 cm or longer. The small barnacle Balanus was also observed frequently but was never seen in clusters of more than three individuals.

The largest motile invertebrate was the crustacean Hyas coarctatus alutaceus. I frequently found this animal and the hermit crab Pagurus trigonocheirus in thick kelp, but they were rare where kelp cover was sparse. Small motile crustaceans common to the Boulder Patch were mysids, amphipods, and (to a lesser extent) isopods. Other motile invertebrates included five-rayed and six-rayed seastars, Leptasterias spp. and the 10-rayed sunstar, Crossaster papposus. These seastars are usually found on rocks, Laminaria blades or the seafloor.

Several species of marine organisms appear to be associated with the presence of the turbid ice canopy (Table 2). Gravid amphipods and polychaete worms were commonly observed between ice

TABLE 2. Organisms found in the turbid ice canopy and their reproductive condition.

Organism	Reproductive State
<hr/>	
INVERTEBRATA	
POLYCHAETA	
<u>Antinoella sarsi</u>	gravid
AMPHIPODS	
<u>Gammaracanthus loricatus</u>	gravid
<u>Gammarus setosus</u>	
<u>Melita formosa</u>	gravid
<u>Onisimus litoralis</u>	
<u>Weyprechtia pinguis</u>	
VERTEBRATA	
OSTEICHTHYES	
<u>Boreogadus saida</u>	

platelets or clinging to large crystals. Arctic cod were seen swimming along the ice formations. I collected several types of benthic biota from this ice canopy, including red algae, Laminaria, bryozoans, bivalves, and hydroids. These benthic organisms eventually disappear as they become incorporated into the ice canopy but the motile organisms are present throughout the winter.

Recolonization

The results of the recolonization experiment are presented in Table 3. Recolonization of the denuded plots was a slow process and was still incomplete after three years. At least 50% of the substratum remained bare on all plots; on most plots, over 75% of the substratum was uncolonized. Of the 14 denuded plots, 11 showed the establishment of some type of animal or plant assemblage, one remained bare, and two (numbers 10 and 12) were dropped from the experiment due to inadequate photographic documentation of the recolonization process. Recolonization by algae and hydroid colonies was quantified by estimating percent cover, and density was used to document the establishment of Spirorbis worms and one unidentified animal. The recolonization of the 11 plots was characterized by the appearance of either crustose coralline algae, Neodilsea integra, hydroids, Spirorbis, or by a red circular encrusting organism that I designated Unknown Species A. This

TABLE 3. The density (no. of animals) and percent cover of organisms observed on plots in November 1981, on plots denuded in 1978 and 1979.

RECOLONIZING SPECIES							
Plot Number	Date Denuded	Crustose Corallines % cover		<u>Neodilsea</u> % cover	Hydroids % cover	<u>Spirorbis</u> density	Unknown Species A density
		Start	Final				
1	8/78	12	25	2			
2	8/78	25	35		2		
3	8/78	5	10	5		4	
4	11/78	1	3				
5	11/78	8	10	30	1	1	
6	11/78	5	8				
7	11/78	8	10		3		
8	3/79					5	3
9	3/79					2	3
11	3/79	Colonization not sufficient to quantify					
13	5/79			1		2	
14	5/79					10	

species is very small, 1 to 2 mm in diameter, and is impossible to identify from photographs.

My photographs showed the encrusting coralline algae were seldom entirely removed from the rock substratum, regardless of our scraping efforts. Therefore, in Table 3, I present data on the recovery of crustose corallines in plots where they existed previously. In no case were encrusting coralline algae observed to colonize a completely bare substratum. Spirorbis colonized the most plots. Hydroids and Neodilsea were found on only three plots

by November 1981. In some cases, the hydroid cover appeared to decrease between successive field seasons. The time of denuding did not appear to have any effect on the appearance of the plots after a three-year period. I did note that Spirorbis settlement took place between March and May and Unknown Species A settled between February and August. But these two species did not colonize the rock surfaces within the first 12 months following denuding.

Most plots contained an assemblage of biota within nine months of denuding. Many of the colonizing organisms first appeared in the early winter months. This may be due to the lack of sediment covering the plots at that time. The sediment cover is substantial in the summer and fall, and small organisms -- if they exist -- cannot be observed. Motile invertebrates (primarily chitons, snails, seastars and polychaetes) were frequently observed on the plots. These animals were observed in more than 15% of the plot photographs taken over the study period. But I found it impossible to determine whether these animals were actively feeding or merely traversing the substratum in search of food. Many of the seastars I observed on the plots were in a pinwheel configuration, brooding eggs, and obviously not feeding.

Sedimentation

Figure 3 shows the pattern of sedimentation at DS-11 between August 1978 and November 1981. Sedimentation was greatest in the late summer and fall when 1 to 5 mm of sediment accumulated on the seafloor and biota. Storms in August and September created wave turbulence and wind-driven currents that suspended large amounts of sediment in the water column. These sediments remained suspended for long periods and settled slowly following freezeup in October. Intense storms were common just prior to or during freezeup. Sedimentation decreased through the winter; less than 1.25 mm accumulated on the seafloor between mid-November and late February. Little or no sedimentation was documented between February and May, when I observed maximum water visibility (greater than 20 m). One to two mm of sediment accumulated on the seafloor between May and late July. Water visibility in July and August ranged between 1 and 3 m, and continued to decrease through the summer and fall, until it reached a low of 0.5 in early November.

Despite the periodic accumulation of sediments on the seafloor, observations made since 1971 indicate that the Boulder Patch is a nondepositional environment. My observations over three years showed that sediments did not steadily accumulate on biota and boulders. I also have not noted the burial of hard substrata at other locations in the Boulder Patch.

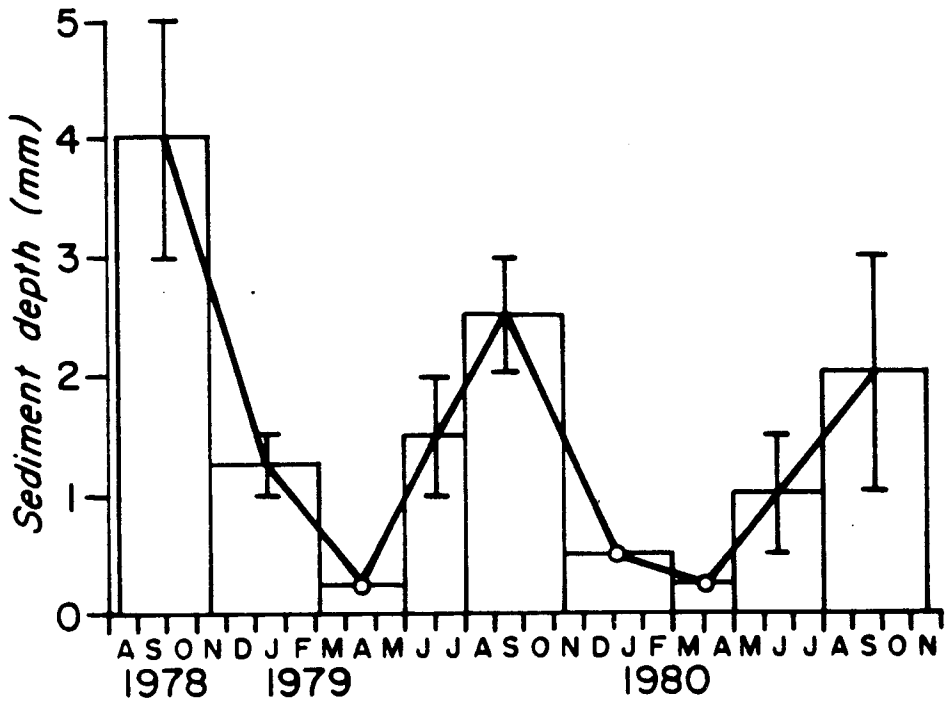


Figure 3. The pattern of sedimentation at DS-11, as measured seasonally on biota and anchored trays. Vertical bars represent ranges in sediment thickness. Open circles denote values below the limits of precise measurement (< 0.5 mm).

Silt constituted the highest percentage (58.5%) of the material retrieved from the sediment collector between May and August, 1981. Clay (38.3%) and sand (3.2%) constituted the remaining fractions. The percentage of organic matter of the sediment was 8.4%

Existence of other macrophyte beds in the Alaskan Beaufort Sea

Recently, other macrophyte beds have been located or are presumed present based on biological and geological evidence. The location of these beds in the Alaskan Beaufort Sea is shown in Figure 4. In two cases, algae were present in the absence of significant concentrations of rock substrata. However, none of the algal beds were large, not all contained kelp, and none possessed the diverse epilithic fauna that characterizes the Boulder Patch in Stefansson Sound.

Boulders and cobbles with attached kelp exist in a small area southeast of Belvedere Island in the Stockton Island chain, and northwest of Kangigvik Point in western Camden Bay (Barnes, 1981). Boulders and cobbles with attached kelp occur in a small area seaward of Flaxman Island at 10 m depth. In Nuvagapak Lagoon, kelp are absent but several species of red algae exist on a sandy-mud seafloor. Large Laminaria saccharina plants (1 to 3 m long) lay on a mud seafloor in Demarcation Bay. Their holdfasts are attached to clods of peat, clumps of tangled red algae, and detritus. Further

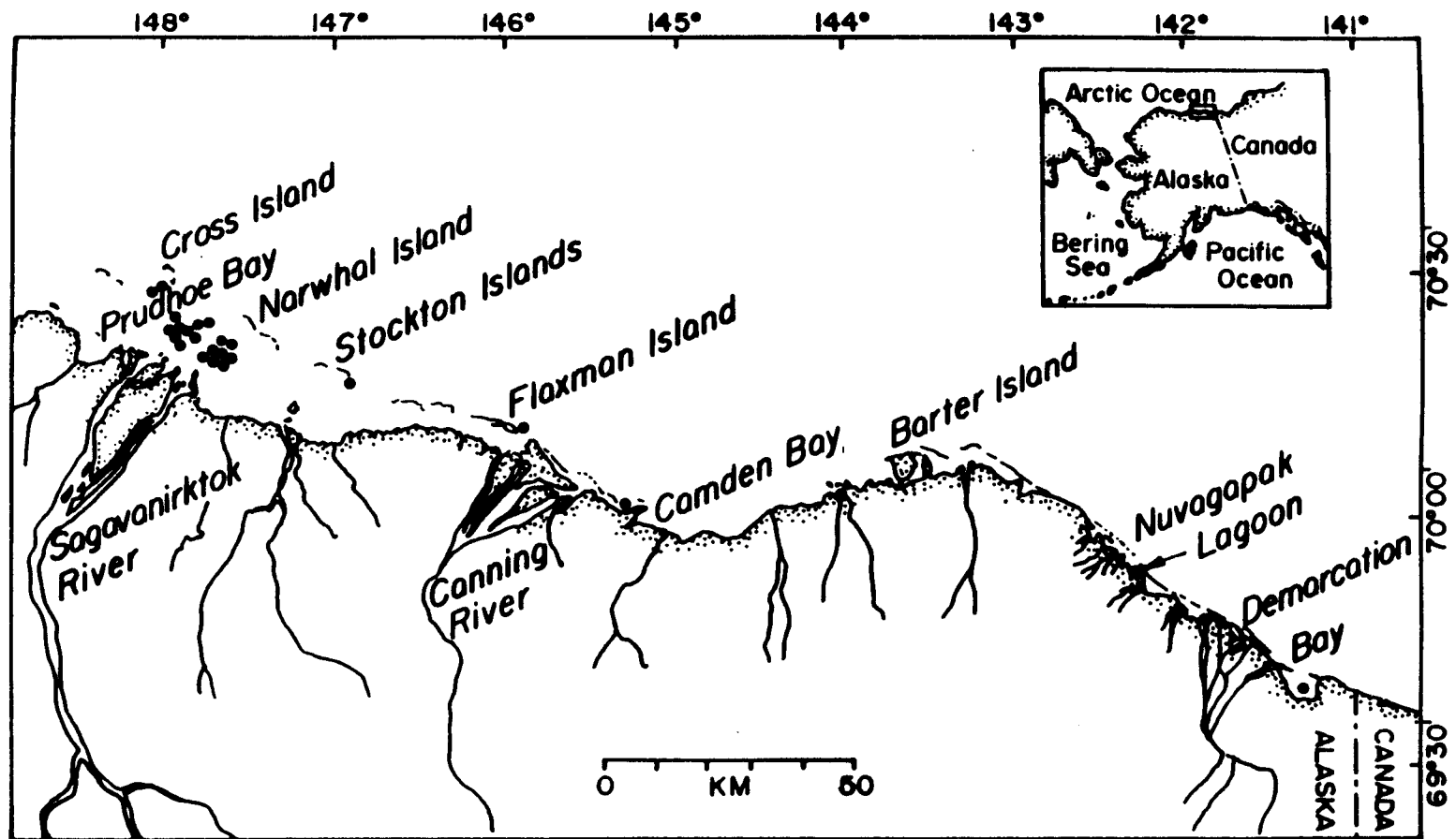


Figure 4. The eastern Alaskan Beaufort Sea shelf. Solid circles denote the location or suspected location of macroalgal beds based on biological or geological evidence.

offshore in the area north of Cross and Narwhal islands, cobbles and small boulders are numerous on the seabed at depths of 13-15 m. The establishment of macroalgae on these rocks is prevented by intensive ice gouging. However, the presence of kelp and red algae as drift on barrier islands and beaches along the entire Alaskan eastern Beaufort Sea coast suggests that at least scattered populations of benthic macroalgae exist on the nearshore shelf.

Linear growth and productivity of *Laminaria solidungula*

Laminaria solidungula is attached to the substratum with a discoidal holdfast that gives rise to a stipe of variable length and a blade that is divided by constrictions into one-to-four ovate segments of different sizes. My initial studies found that the constrictions formed in late November, followed by the appearance of a new ovate segment by the following February. I observed this pattern of growth for over three consecutive years and have confirmed that the length of each ovate segment corresponds to one year's linear growth of the plant.

Figure 5 shows the results of growth measurements taken from August 1978 to November 1980. The lowest rate of linear growth occurred during the ice-free periods (from July to November), and the growth averaged 0.16 to 0.25 mm per day. The growth rates increased in fall and reached an average maximum of 1.14 to 1.41 mm per day in late winter or early spring. I may not have measured

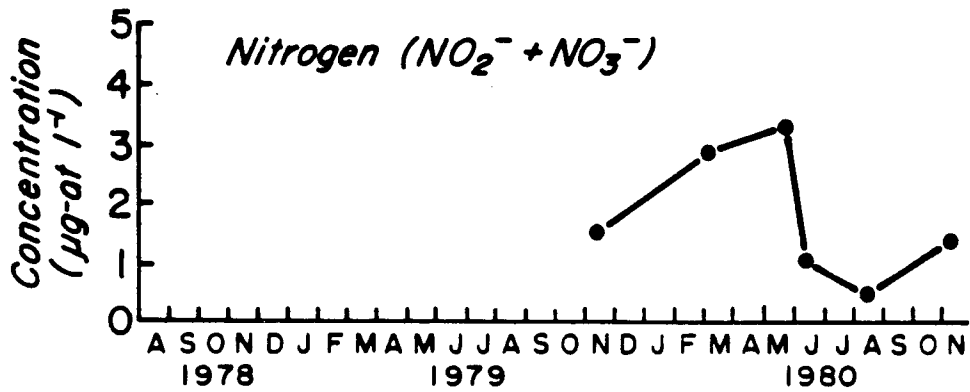
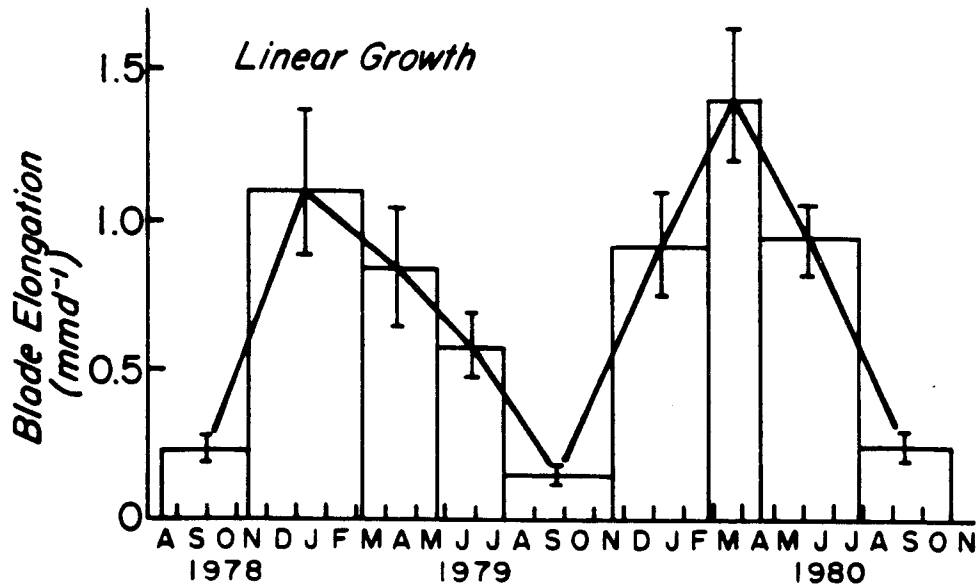


Figure 5. The pattern of blade growth (means \pm 95% confidence limits) in Laminaria solidungula in relation to seasonal variation in inorganic nitrogen concentrations.

peak growth during the 1978-1979 winter season because of the timing of the visits to the study site. Growth rates decreased during spring and early summer. Since the turbid ice canopy in Stefansson Sound prevented penetration of light between October and early July, these plants completed almost all of their annual linear growth in absolute darkness.

Levels of inorganic nitrogen in the form of NO_2^- and NO_3^- in the seawater are shown beneath the growth curves in Figure 5. The concentrations of inorganic nitrogen follow an annual cycle typical of Arctic (Chapman and Lindley, 1980) and temperate waters (Chapman and Craigie, 1977; Wheeler and North, 1981). In November 1979, the level of inorganic-N was $1.5 \text{ microgram-atoms liter}^{-1}$ ($\mu\text{g-at l}^{-1}$) and it increased to $3.3 \mu\text{g-at l}^{-1}$ in late May before decreasing to less than 0.1 in August. By November 1980, the concentration had increased to a level similar to that of the previous November ($1.2 \mu\text{g-at l}^{-1}$). The winter growth of L. solidungula occurs during higher concentrations of inorganic nitrogen. A similar pattern between growth and nitrogen availability were also observed for L. solidungula in the Canadian high Arctic by Chapman and Lindley (1980).

Figure 6 shows the annual net increase in biomass of 17 plants as a function of their initial weight. The average annual production-to-biomass ratio (P:B) was 0.95 ± 0.14 (mean \pm 95% confidence limit), and the annual mean growth was $0.0022 \text{ g g}^{-1} \text{ day}^{-1}$ (grams of wet weight added per gram of plant per day). The

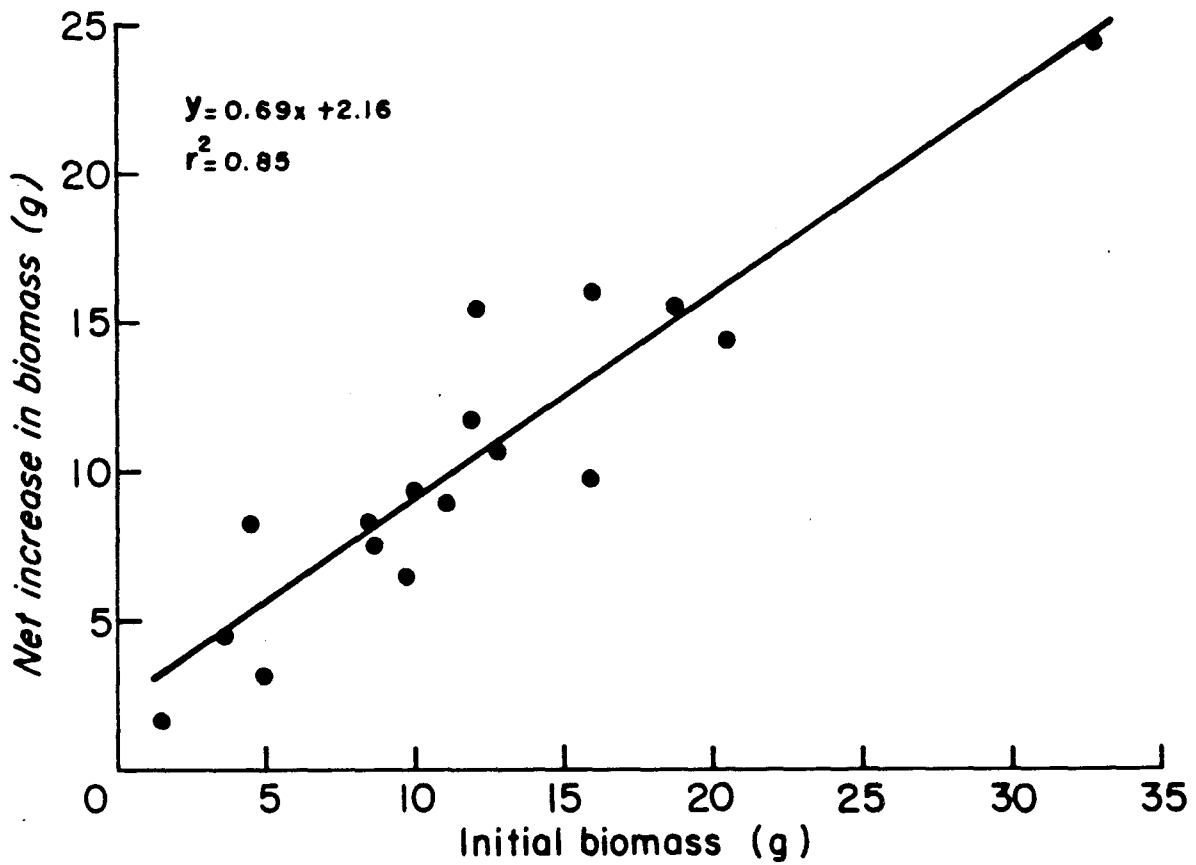


Figure 6. Annual net increase in biomass as a function of initial biomass in *L. solidungula* plants living under a turbid ice canopy; correlation coefficient, 0.92.

standing crop of all three species of kelp (of which L. solidungula constituted over 95%) ranged from 67 g m^{-2} in areas of 10 to 25% rock cover to 262 g m^{-2} where rock cover exceeds 25%. Using the results of the geophysical surveys conducted by Toimil (1980), the area of 10 to 25% rock cover is about $13 \times 10^6 \text{ m}^2$, and the areas with cover greater than 25% is $7.3 \times 10^6 \text{ m}^2$. Integrated over these areas, the standing crop of the kelp is estimated to be $2.8 \times 10^9 \text{ g}$.

The changes in percentage dry weight to wet weight of several plants ($N = 15$ to 25) and their blades are shown in Figure 7. The highest percentage dry weight of the entire blade occurred in November, decreased between November and May, and increased from May to previous November levels. The percentage dry weight of the second segment (the growth increment of the previous season) and the developing first (basal) blade segment varied inversely to each other. Between November and February, the percentage dry weight of the second segment dropped from 24 to 17%, which coincided with the formation of a new basal segment. The percentage dry weight of the new basal segment increased steadily from 10% in late February to 24% by November, when a new basal segment again began to develop. The second segment did not retain its original dry weight percentage, but dropped to 15% by early November. The percentage dry weight of blade segments distal to the second segment and the stipe (data not shown) varied little throughout the year. Percentage dry weight of the segments distal to the second blade

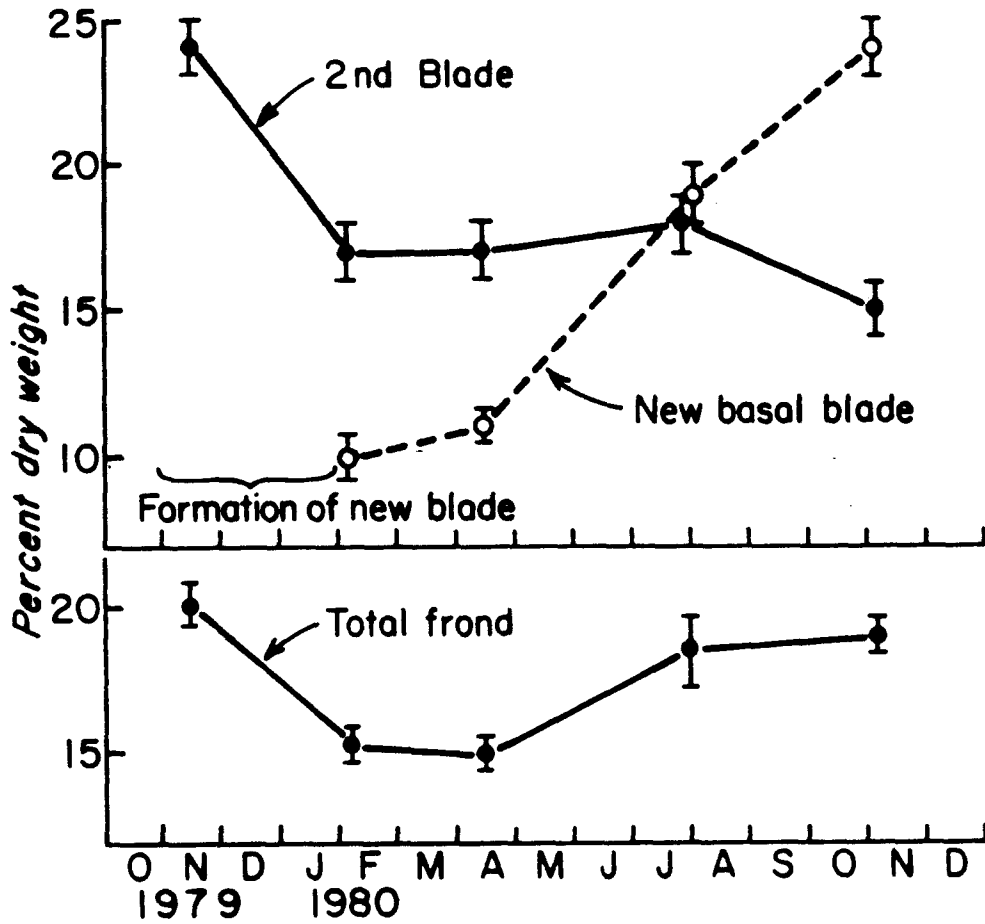


Figure 7. Seasonal variation in percent dry weight of wet weight in the entire blade (or frond), and in the basal and second blade segments of *L. solidungula* plants. All means \pm 95% confidence limits.

were highest in the summer, and ranged annually between 14 and 18%. The percentage dry weight of the stipe ranged between 23 and 25%

DISCUSSION

Physical processes and the occurrence of macroalgae

Reimnitz et al. (1979) discussed the enigma of the apparent lack of arctic delta accretion, and the existence of the Boulder Patch instead of deltaic deposits of the Sagavanirktok River. Midsummer measurements at DS-11 (made shortly after peak discharge of the nearby Sagavanirktok River) showed only small amounts of suspended sediment accretion, while the largest inputs of suspended sediment were collected in fall, when river discharge is low. By February, sediment cover on plants and rocks was reduced to a barely measurable film of ooze. Matthews (1981b) recorded under-ice currents decreasing from 1.4 to 0.7 cm s⁻¹ during the period between November and December at DS-11. Peak velocities during this time barely exceeded 9 cm s⁻¹. By late January, maximum velocities were less than the threshold of the instrument (about 2 cm s⁻¹). The fact that the major seasonal sediment accumulations at DS-11 were being swept away by currents of less than 10 cm s⁻¹ suggests that the sediments had been deposited after, not during, the major fall storms when currents are strong.

The major fall events, during which the large volumes of resuspended bottom sediments are entrained into a thick turbid ice layer (Reimnitz and Dunton, 1979; Barnes et al, 1982), were not recorded by my sedimentation measurements. The turbid ice above DS-11 contained coarse shell fragments and pebbles up to 2 cm in diameter. These particles could be rafted several tens of kilometers during ice breakup. Summer sediments settling from suspension into the trap at DS-11 contain 97% silt and clay-size materials, and 3% sand. Barnes et al. (1977) recorded summer currents in Stefansson Sound "strong enough to erode and transport medium to fine sand." Thus there is not only suspended sediment transport, but also bedload transport, mainly westward through the Boulder Patch. Observations on stakes driven into consolidated mud, and repeated photography of a cobble with an attached kelp in Stefansson Sound also demonstrated erosion within a period of several months (Toimil and England, 1982).

A hard rock substratum is one requirements for the growth of macroalgae, and is provided by the presence of boulders, cobbles, and pebbles on the floor of Stefansson Sound. Another requirement is that this substratum be cleaned periodically of fine sediments that accumulate seasonally, since these sediments would eventually smother the community. Waves and currents provide such cleaning. Cleaning may also result from the erosive action of frazil ice formed during fall storms, and from the subsequent ice rafting of entrained sediment. Still another requirement is protection from

deep draft multiyear ice which has the potential to physically disrupt and overturn bottom materials at frequent intervals (Reimnitz et al., 1977; Barnes et al., 1978). This requirement is satisfied by a chain of protecting barrier islands that greatly reduce the flux of pack ice and allow the establishment of a floating fast-ice canopy in winter. Understanding these requirements will aid in the search for other kelp beds in the Beaufort Sea.

The scattered occurrences of kelp beds found in my reconnaissance surveys of the Beaufort Sea largely reflect the above requirements. All but the Demarcation Bay occurrence are found in association with boulders and cobbles of the Flaxman Formation, and all are in areas of minimum sedimentation. The occurrences lie either in partial protection of islands, or in the protection of grounded ice which plays the role of offshore islands in the stamukhi zone (Reimnitz et al., 1978). However, off the major coastal promontories (where westward moving pack ice interacts with the continent), frequent ice-bottom interaction precludes the establishment of kelp on cobbles. The stamukhi zone closely skirts Narwhal and Cross islands, where pebbles and cobbles are abundant on the sea floor, but bare of growth.

The number of boulders and cobbles increases eastward of Stefansson Sound toward the Canadian border, and so does the amount of surficial gravel, as seen in recent reconnaissance surveys east of Barter Island. But to date, I suspect no other major

occurrences of kelp on the Alaskan Beaufort Sea shelf. A semielliptical region of sandy gravels, sands and consolidated pebbly mud exists on the shelf east of the Canadian border. Yorath et al. (1970) tentatively identified these as relict glacial deposits and ice pressed tills. The shallowest portions of this area are free of modern sediment and relatively protected by Herschel Island against the westward-moving pack. These shallows seem to be suitable for the growth of macroalgae. This region may be the source for much of the algal remains washed up on the beaches east of Camden Bay.

Physical processes and community development

The results of my recolonization studies show that development of an epilithic assemblage of organisms is a slow process in the Arctic compared to temperate latitudes. This is in part due to the total absence of ephemeral species. Recolonization experiments in temperate kelp beds show that a diverse and dense assemblage of biota is established within one year (Foster, 1975). Only a sparsely established assemblage was seen after three years in Stefansson Sound. The factors influencing establishment of an epilithic community on the boulders denuded in the Boulder Patch include the stability of the substratum, temporal variability in the composition and abundance of larvae and spores, biological interactions such as predation, herbivory, and competition, and the

growth rates of the species that settle. These factors have been identified as important in the establishment and development of communities in temperate regions by Dayton (1971), Foster (1975), Dunton (1977), and Osman (1977).

A completely different pattern of establishment and development compared to that on natural substratum was noted on polystyrene floats used to mark the different experimental plots. These small square floats (100 cm^2) were suspended one meter above the seafloor at different seasons. They were not examined quantitatively since they were never intended as experimental substrates. However, they provided interesting comparative data on the process of recolonization in the Boulder Patch. The floats were smaller than the experimental plots and remained relatively free of sediments. Furthermore, the floats were not subject to grazing or predation pressures by benthic animals.

The floats were first examined about 12 months after initial deployment. At that time, all were covered with hydroids, bryozoans, red algae and polychaete worm tubes. The early establishments of these colonizers on the suspended floats suggest that the absence of spores and larvae in the water column is not a factor responsible for the limited colonization of denuded boulders. Growth of species identical or similar to those on suspended floats also appear to be slower on the denuded plots. Although larvae and spores may be exhibiting a substratum preference for polystyrene, it is not likely that all epilithic

species would possess a common selectivity for an artificial substratum. Instead, I believe other factors must be involved; i.e., colonization is either being prevented by sedimentation or an efficient predator or grazer is removing the organisms from the rock substratum.

Periodic sedimentation and the existence of active grazers and predators may act together in inhibiting settlement and in regulating development of opportunistic species. Competition is probably not important due to the abundance of free space on the plots after three years and the limited contact among colonizing species. This is in contrast to the total utilization of rock space in the mature community. My observations indicate that sedimentation is a periodic physical disturbance that inhibits successful settlement by larvae and spores. In addition, potential grazing and predation pressures may interfere substantially with subsequent growth and development of the species that become established.

The periodic inundation by sediment in the Boulder Patch may adversely affect the process of recolonization by effectively blocking larvae or spores from reaching the rock surface, or by smothering epilithic biota having a stature of less than 1 or 2 mm. The availability of primary substratum for recolonization is thus substantially limited during periods of sedimentation. Provision of primary substratum in the Boulder Patch is dependent on physical processes to remove sediment and disturb the cobbles and boulders.

New primary rock surfaces are exposed by water currents and ice gouging. Biological interactions do not appear to prevent the monopolization of space in the Boulder Patch by a benthic organism (such as by crustose corallines) as has been shown in intertidal communities (Dayton, 1971; Menge, 1976; Grant, 1977). Ice gouging, although infrequent, is the only mechanism by which large cobbles and boulders are displaced. The factors that determine the frequency by which small cobbles are overturned are drag resistance caused by large epilithic organisms (kelp, soft corals, and sponges) attached to the rock, and the size of the rock. The existence of white calcified deposits of crustose corallines covering the underside of many small cobbles in the Boulder Patch suggest that this process is a common event. I have documented the overturn of rocks with attached biota by strong currents. The displacement of rocks by currents appears to be one of the most effective mechanisms supplying substrata free of crustose corallines for recolonization.

Growth and productivity of *Laminaria solidungula* and its importance to the community

The pattern of growth in *Laminaria solidungula* corresponds closely to that of perennial kelps examined in other north temperate and arctic regions. The results of these studies demonstrate that seasonal growth is strongly correlated with the

availability of inorganic-N in both L. longicruris off Nova Scotia (Chapman and Craigie, 1977) and L. solidungula in the Canadian High Arctic (Chapman and Lindley, 1980). The ability of these plants to store carbohydrate reserves in the form of laminarin or mannitol has also been shown, but the utilization of these reserves is probably limited to short periods when photosynthesis does not entirely support the carbon demand of blade elongation (Hatcher et al., 1977; Chapman and Lindley, 1980). In contrast, my findings show complete dependence by L. solidungula on stored carbohydrate reserves to complete nearly all of its annual linear growth over long periods of total darkness.

In L. solidungula, as in other Laminaria species, variation in percentage dry weight follows laminarin variation closely (Black, 1950; Chapman and Lindley, 1980), reflecting the amount of carbohydrate stored in the blade. Carbon fixed during the previous summer (and stored in what becomes the second distal blade segment) provided the carbon needed for the basal segment, as evidenced by a 7% drop in tissue density in the second segment between November and February. Growth of the new basal segment may also be supplemented to a small degree by carbon translocation from portions of the plant distal to the second segment. The ability to translocate photosynthetic products is characteristic of the kelp order Laminariales (Schmitz and Lobban, 1976) and appears to be characteristic of L. solidungula. The dependence of L. solidungula on stored food reserves reflects the functional significance of

carbohydrate storage in these plants. A similar function has been documented in Laminaria hyperborea, which grows on the west coast of Europe. Luning (1971) found that L. hyperborea relied heavily on stored reserves for growth between October and March, when irradiance was below the compensation point. In another study he found that plants can produce a small new blade during their first half year in complete darkness (Luning, 1969). In contrast to both L. solidungula and L. hyperborea, the carbohydrate reserve in L. longicruris is exhausted before the onset of winter growth (Chapman and Craigie, 1978). The ability to store the products of photosynthesis thus appears best developed in plants periodically exposed to prolonged periods of low light.

Growth in L. solidungula in the Boulder Patch appears both energy- and nitrogen-limited, since neither resource is available in sufficient quantities simultaneously. During the summer open-water period when light is available, the plants must fix all the carbon necessary for their annual growth, reproduction, and metabolism. Little growth occurs during this period due to insufficient concentrations of ambient inorganic-N needed for the synthesis of new tissue. Instead, the products of photosynthesis are stored and used during the winter when inorganic-N is available for the production of a new blade. Inorganic-N is depleted as a result of the annual spring bloom of microalgae and is slowly replenished during winter months through regeneration and exchange with ocean water. My in situ growth studies of L. solidungula show

that these plants can produce 95% of their original biomass as new plant tissue annually. Based on this, the net carbon contribution made by these plants to the ecosystem can be calculated from data on standing crop and carbon content.

The standing crop of kelp in Stefansson Sound is 0.48×10^9 g dry weight assuming that the standing crop of 2.8×10^9 g is about 17% dry matter (Fig. 7). Over 90% of the standing crop is L. solidungula. The carbon content of the dry matter in L. solidungula is approximately 31% (Chapman and Lindley, 1981) and varies little seasonally. On this basis, the annual energetic contribution made by the kelp in Stefansson Sound is 146×10^6 g C or about 7.2 g C m^{-2} based on a P:B ratio of 0.95. This estimate does not take into account any patchiness in the turbid ice canopy or its complete absence in some years.

Using similar techniques at the same latitude in the Canadian High Arctic, Chapman and Lindley (1980, 1981) calculated the productivity of L. solidungula to be about $20 \text{ g C m}^{-1} \text{ yr}^{-1}$. Linear growth was nearly 60% greater than in the Alaskan plants. The apparent lower productivity of the Boulder Patch community compared to the Canadian kelp bed is due to two factors: the absence of winter and spring photosynthesis in Alaskan plants and a lower standing crop. Beneath patches of clean, transparent ice near DS-11, annual linear growth of kelp increases by 35% (Chapter 3). I attribute this growth to under ice photosynthesis. In the Canadian kelp bed, the mean standing crop was ca. 870 g m^{-2}

(Chapman and Lindley, 1981), whereas the standing crop in the Boulder Patch ranged from ca. 70 to 260 g m⁻². The difference in standing crop alone could account for the higher productivity recorded in the Canadian High Arctic.

My estimate of carbon production does not include the carbon released as dissolved organic matter. This may occur during the summer, when there is an assimilatory surplus, or in early winter when meiospores are released. The release of dissolved organics by kelp may be 25 to 40% of gross production based on recent studies (Khailov and Burlakova, 1969; Hatcher et al., 1977; Newell et al., 1982). The carbon contribution by kelp in the Stefansson Sound Boulder Patch appears to be roughly equivalent to the contribution made by phytoplankton, which ranges from 5 to 20 g m⁻² yr⁻¹ at this latitude (Apollonio, 1980; Schell et al., 1982). However, it is much lower than kelp production at more temperate latitudes (e.g., a L. longicruris community in Nova Scotia ranged between 143 and 428 g C m⁻² yr⁻¹; Hatcher et al., 1977).

The role of kelp as a carbon source in the marine environment is not well understood. My observations show that few organisms feed directly on kelp in the Boulder Patch. Herbivores include chitons and snails. I suspect, however, that other organisms derive nutrition from this abundant and ever-present carbon source. Over 90% of the carbon produced by macroalgae is thought to enter detritus food chains either in dissolved or particulate form (Mann, 1975). But tracking the path of kelp carbon through a detrital

food chain is difficult using conventional biological methods. In Chapter 7 I will address the importance of kelp as a source of carbon for the biota of the Boulder Patch using natural carbon isotope ratios. But the success of this technique requires a knowledge of the carbon sources available to consumer organisms and their magnitudes. In the following chapter I will construct such a carbon budget for the Boulder Patch.

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CHAPTER 3. AN ANNUAL CARBON BUDGET FOR AN ARCTIC KELP COMMUNITY*

SUMMARY

The sources of carbon available to invertebrate consumers in an arctic kelp community were examined under different winter ice conditions. In years characterized by the presence of a turbid ice canopy, kelp and phytoplankton contribute equivalent amounts of carbon to account for over 98% of the total carbon input to this community. Under clean ice, annual linear growth of the dominant kelp Laminaria solidungula increases by 55% and kelp production balances the combined energetic input derived from phytoplankton, ice algae and benthic microalgae. One active herbivore, the chiton Amicula vestita, consumes between 8 and 12% of annual kelp primary productivity. Based on the previous years' annual linear growth in L. solidungula (recorded in the frond) at two different sites, turbid ice appears to be a widespread and frequent occurrence in this area.

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INTRODUCTION

Most of what we know concerning the growth of seaweeds and their productivity in coastal systems is the result of studies in temperate climates. These studies have documented that marine algae make substantial contributions of carbon to coastal systems (Clendenning, 1971; Mann, 1972; Johnston et al., 1977; Dieckmann, 1980). In some cases, the productivity of the seaweeds matches or exceeds the highest estimated productivity of the phytoplankton. For example, in St. Margaret's Bay, Nova Scotia, the annual carbon input of the seaweeds averaged over the entire bay was 603 g m^{-2} , three times greater than phytoplankton production (Mann, 1972).

In arctic regions, the productivity of benthic macroalgae has been largely ignored and considered insignificant. This is due both to the limited exploration of the arctic shelf for benthic macroalgae and the nature of the physical environment, which in general is not favorable for the attachment and growth of macroalgae. But the recent discovery of a large area of kelp associated with a diverse and abundant invertebrate population off the north arctic coast of Alaska (Dunton et al., 1982), and the work of Chapman and Lindley (1981) on the productivity of Laminaria solidungula in a kelp bed in the Canadian High Arctic, indicate that this carbon source may be more important than previously thought.

To date, a complete annual carbon budget for an arctic kelp community has not been achieved. Although measurements of growth and productivity have been reported for the predominant alga, L. solidungula, the effect of herbivores on standing crop have not been considered, and with the exception of phytoplankton production, the presence of other carbon inputs has not been ascertained. In temperate regions, these factors have been addressed by several investigators who have assessed the role of kelp carbon in the environment (Miller et al., 1971; Vadas, 1977; Carter, 1982; Newell et al., 1982).

In the Canadian High Arctic, Chapman and Lindley (1981) found that the annual productivity of an arctic kelp bed dominated by L. solidungula was about 20 g C m^{-2} , roughly equivalent to phytoplankton production on an area basis in open water. Growth was greatest in the late winter and early spring, and was correlated with the concentration of inorganic nitrogen, as in most perennial kelps (Chapman and Lindley, 1980). Dunton et al. (1982) also studied the growth of L. solidungula during the same period and latitude as Chapman and Lindley (1980, 1981) but in the Alaskan Beaufort Sea. In an area known as the Boulder Patch in Stefansson Sound, Dunton et al. estimated annual productivity at 7 g C m^{-2} , but under substantially different light regimes. In the Boulder Patch, L. solidungula is subject to nine-month periods of complete darkness caused by the presence of a turbid ice canopy. The kelp

relies on stored food materials to complete over 90% of its annual linear growth (Dunton et al., 1982).

The patchy occurrence of turbid ice in the Stefansson Sound Boulder Patch, however, exposes areas of seafloor to light throughout the fall and spring, resulting in changes in the growth and productivity of L. solidungula. The annual consumption of kelp by herbivores in the Boulder Patch had also not been estimated quantitatively. In temperate kelp communities, about 10% of the annual productivity is utilized directly by herbivores (Miller et al., 1971; Newell et al., 1982). The remaining 90% is released in dissolved or particulate form, and is a potential food source for filter-feeding animals by conversion into bacterial biomass (Lucas et al., 1981; Stuart et al., 1981).

In this chapter, I summarize the sources of carbon available to consumers in the Boulder Patch and estimate the fraction of kelp carbon derived from Laminaria solidungula that is consumed by a common herbivore. Quantitative variation in the annual carbon input of L. solidungula -- caused by differences in winter light availability -- are presented and compared quantitatively to the carbon contributions made by benthic microalgae, ice algae, and phytoplankton.

STUDY AREA

The Boulder Patch lies in Stefansson Sound, 20 km northeast of Prudhoe Bay in the Beaufort Sea, Alaska (Fig. 1), and consists of boulders and cobbles that occur in patches of various sizes and densities. Field studies were conducted at an acoustically marked site, dive site 11 (DS-11; 70°19.25'N, 147°35.1'W), on the eastern side of the Boulder Patch (Fig. 1). The rocks provide a substrate for a diverse assortment of invertebrates and several species of algae (Dunton et al., 1982). The predominant brown alga is Laminaria solidungula, which constitutes over 90% of the brown algal biomass. The area covered by the Boulder Patch is approximately $2.03 \times 10^7 \text{ m}^2$. Rock cover at DS-11 is estimated at 42%.

Water depths in the Boulder Patch range from 3 to 9 meters. Freeze-up is usually complete by mid-October, and breakup begins in late June or early July. Ice thickness reaches a maximum of 2 m in early May before deterioration of the ice canopy begins. Bottom water temperatures range from a nearly constant -1.8°C under the sea ice to 7°C during the summer open-water period. Salinity varies from 14 to 35 ‰ (Barnes et al., 1977).

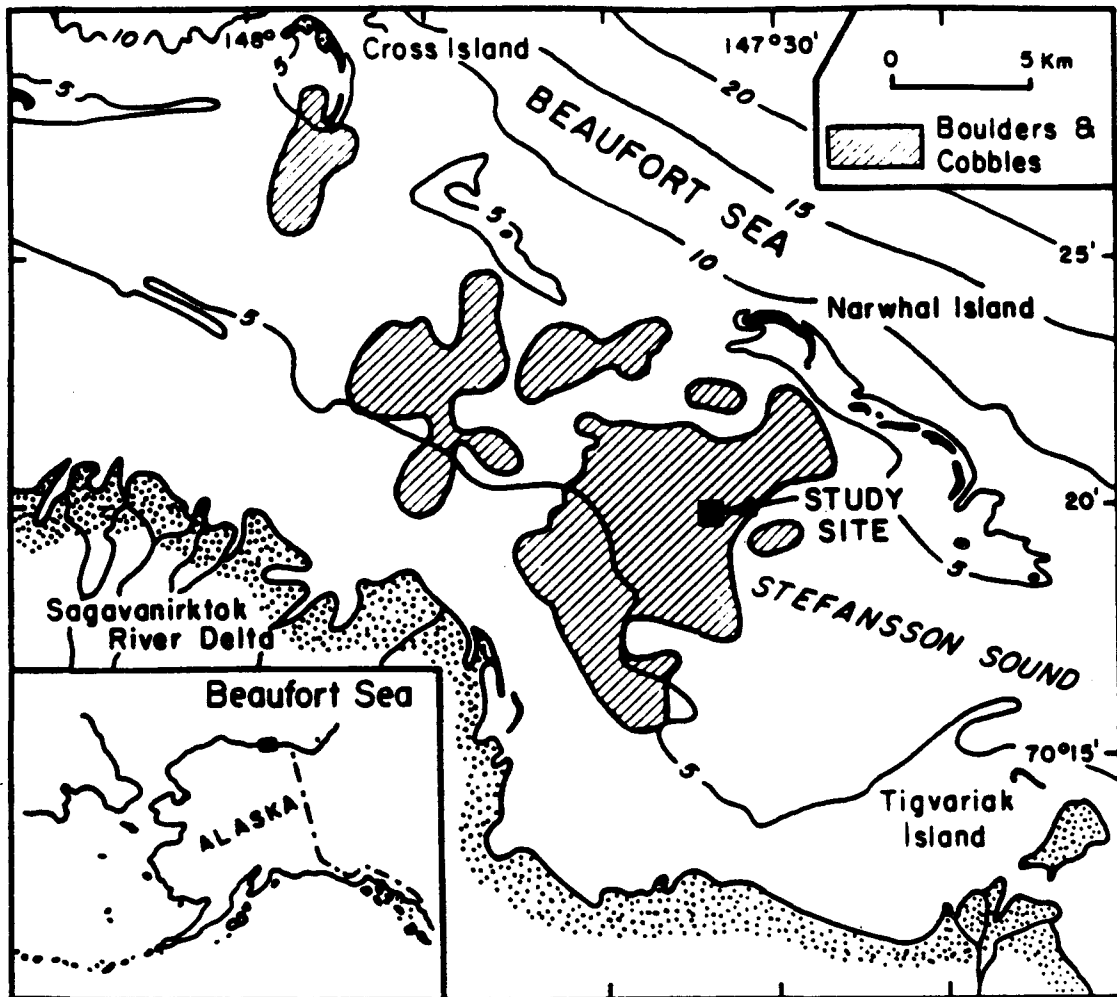


Figure 1. The location of the Boulder Patch and Dive Site 11 (DS-11) in Stefansson Sound. Depth contours are shown in meters.

MATERIALS AND METHODS

During ice-covered periods, divers entered the water through holes cut in the ice using augers and ice chisels. A heated insulated hut (Parcoll, Panebec Ltd., Montreal) placed over the dive hole functioned as a dive shelter and laboratory. Biological sampling and in situ experiments were conducted at approximately three-month intervals by a team of divers between July 1978 and November 1981. All plants and animals used in this study were haphazardly collected or tagged in situ.

Linear growth and productivity of *Laminaria solidungula*

Linear growth in *Laminaria solidungula* was followed by punching holes in the base of the blade, above the meristematic region (Chapman and Craigie, 1977). Since *L. solidungula* constitutes over 90% of the brown algal biomass, I focused on the productivity of this plant. The frond of *L. solidungula* is divided into distinct ovate blades of different sizes by constrictions which form annually. The growth of a new basal blade starts in November and continues until the following November, allowing an accurate measurement of the plant's annual production. Here I define a growth year (gwyr) as the period beginning 15 November one year and ending on 14 November the following year.

The formation of a constriction in November followed by the growth of a new blade segment made it possible to monitor linear growth in untagged plants subjected to different light conditions at another site. The distance from the junction of stipe and frond to the first constriction gave an accurate measurement of total linear growth since the preceding November. Linear growth in previous years was also assessed by measuring the distance between successive constrictions up the frond. In May 1979 two sites (DS-11, located under turbid ice near the tagged plants) and DS-11A (200 m distant under clear ice) were chosen for the comparative study. Over 40 plants were collected at each site for linear measurement in May and again following ice breakup in late July 1979.

To establish the relationship between basal (new) blade segment length and tissue biomass, about 20 plants were randomly collected in late April and again in early August 1980. In addition, length-to-biomass relationships were established for entire blades from a total of 87 plants collected in November 1979, 1980, and 1981. Production-to-biomass (P:B) ratios were obtained from plants collected in July at both sites and November 1979 at DS-11. The weight of the first blade segment (annual production) in each plant was divided by the weight of the remaining blades (initial biomass). This fractional value was used to compute annual productivity for the growth year 1979 (gwyr 1979).

Net kelp carbon production ($\text{g m}^{-2} \text{ yr}^{-1}$) was calculated by multiplying the P:B ratio by a mean standing crop of 137 g m^{-2} , the percent dry weight of wet weight (17%), and percent carbon of dry weight (31%). The standing crop of the kelp and the conversion factors are from Dunton et al. (1982). Production of new stipe tissue was not taken into account in this study because stipe growth rarely exceeds 0.5 cm yr^{-1} and is, therefore, negligible in comparison to annual blade production.

Biomass and productivity of microalgae

Quantitative sampling of the biota by scraping and airlifting all organisms in 0.05 m^2 areas on rock surfaces resulted in the unexpected but frequent collection of chained diatoms. In situ observations confirmed that these diatoms were attached to epilithic organisms and thus easy to collect without significant loss using an airlift. Water flow in the airlift is created in a 1-m tube by the expansion of compressed air introduced at the bottom of the tube.

In the laboratory, filamentous diatoms were sorted and removed from other material, blotted to remove excess water and weighed to the nearest 0.001 g. Biomass of the benthic microalgae is expressed per m^2 of rock substrate and is based on 50 replicate samples collected randomly over a three-year period. Carbon

content of the microalgae was determined using a Leco TC-12 automatic carbon determinator.

Biomass and productivity data for ice algae and phytoplankton were obtained from Schell et al. (1984), from their site BP in Stefansson Sound, which is close to DS-11 (within one mile).

Macroalgal consumption by herbivores

The chiton Amicula vestita is an active herbivore in the Boulder Patch, and grazes almost exclusively on L. solidungula. The animal leaves distinct grazing scars on blade and stipe tissues of the plant. Examination of over 100 plants collected in 1980 showed 42% with recent grazing scars on stipes or blades. Biomass and density of A. vestita in the Boulder Patch have been reported by Dunton et al. (1982). Since animals smaller than about 1 g in wet weight have been observed to feed primarily on detritus, not kelp, the raw data were reanalyzed to determine the biomass of chitons greater than 1 g in wet weight per m². The mean biomass of all animals heavier than 1 g wet weight was also calculated.

Feeding experiments were conducted in the laboratory to determine the amount of tissue consumed by A. vestita. Chitons, weighing 1.7, 3.3 and 5.2 g, were placed in separate small mesh cages, 17 x 12 x 12 cm, and given preweighed fresh blades from L. solidungula. The cages were placed in a 200 liter Instant Ocean Aquarium kept in darkness at a constant temperature of 1°C ± 1.5.

Three feeding experiments were conducted lasting periods of 67, 51, and 58 days. At the end of each experiment, the biomass of the kelp consumed by each chiton was determined by weighing the remaining blade tissue. Decreases in the wet weight of the blade tissue (due to respiratory loss of carbon) was small, accounting for less than 10% of the mean daily uptake of kelp tissue by the chitons.

Light energy

Photon flux density was measured with a LI-185 quantum radiometer/photometer with a LI-192S underwater quantum sensor (LI-COR, Inc., Lincoln, Nebraska).

RESULTS

Linear growth in *L. solidungula* beneath turbid and clean ice

The light available for photosynthesis between October and July is dependent on the conditions of ice formation, so the effective day length varies from year to year. In Stefansson Sound, a considerable amount of sediments are entrapped in the ice canopy during its formation in October, resulting in what is referred to as "turbid ice" (Reimnitz and Dunton, 1979; Dunton et al., 1982). Turbid ice blocks light transmission completely, even

during periods of 24 hour daylight. For example, photon flux density on the bottom at DS-11 in May 1979 under turbid ice was below the detection limits of the LI-COR instrument (less than ca $0.05 \mu\text{E s}^{-1}\text{m}^{-2}$).

Despite the widespread distribution of turbid ice in Stefansson Sound, "windows" of clean ice occurred that allowed light to penetrate to the bottom. Photon flux density in May 1979 at one such location about 200 m from DS-11 (DS-11A) ranged from 1.8 to $3.5 \mu\text{E s}^{-1}\text{m}^{-2}$. Photon flux density under a similar ice canopy in April was $2.4 \mu\text{E s}^{-1}\text{m}^{-2}$ which represented 0.57% of the total incident illumination at the upper surface of the ice (D. M. Schell, personal communication).

The growth of L. solidungula over the past three years at two locations, DS-11 and DS-11A, with differing ice cover during the 1978-79 winter, is shown in Figure 2. With the exception of the latest growth cycle at DS-11A, where plants were exposed to light under the ice canopy in the spring of 1979, linear growth between years and between sites is not significantly different (analysis of variance [ANOVA] completely randomized design, Student-Newman-Keuls-test [SNK], $p > 0.05$). This similarity in growth suggests that turbid ice was present at both locations in the winter seasons of 1976-1977 and 1977-1978. The greater growth of plants under clean ice in 1979 is significant (SNK, $p < 0.05$) and suggests that these plants are actively photosynthesizing under the ice canopy. The mean length of the basal blades in plants that had

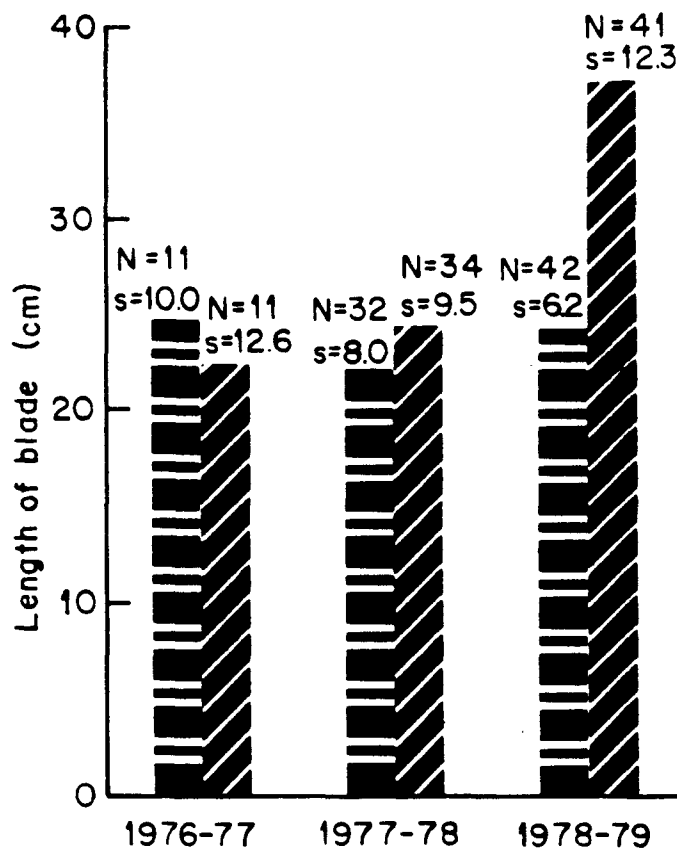


Figure 2. Annual linear growth in L. solidungula at two adjacent sites since 1976-1977. The number of plants sampled (N) and the standard deviation (s) are listed above the bars. The difference in linear growth between the two sites in 1978-1979 is significant (ANOVA, $p < 0.05$). DS-11 is indicated by the left bar, DS-11A by the right bar.

grown under clean ice at DS-11A was 37.7 cm compared to 24.1 cm under turbid ice at DS-11.

Productivity in *L. solidungula* exposed to light under the ice canopy

The productivities of *L. solidungula* exposed to winter light at DS-11A and winter darkness at DS-11 in 1979 were determined by correlating blade lengths with biomass. Figure 3 shows the relationship between basal blade segment length and biomass in plants collected in late April and early August 1980. Measured first blade segments at DS-11 and DS-11A in 1979 were transformed to biomass using this correlation. Figure 4 shows the relationship between total blade length (X-axis) and biomass (Y-axis) in plants collected in November 1979, 1980 and 1981. Another relationship, $Y = 0.03x^{1.67}$, was obtained by Chapman (1981; personal communication) for *L. solidungula* in the Canadian arctic. The two equations (one linear, the other a power function) are different because of the much higher productivity of the Canadian plants in an environment not limited by light. Using a regression equation derived from Figure 4, the initial blade biomasses of plants collected at DS-11A and DS-11 in 1979 were calculated from measured lengths. From these data, I obtained an average production (basal blade segment biomass)-to-biomass (initial blade weight of entire plant) ratio (P:B) for each plant.

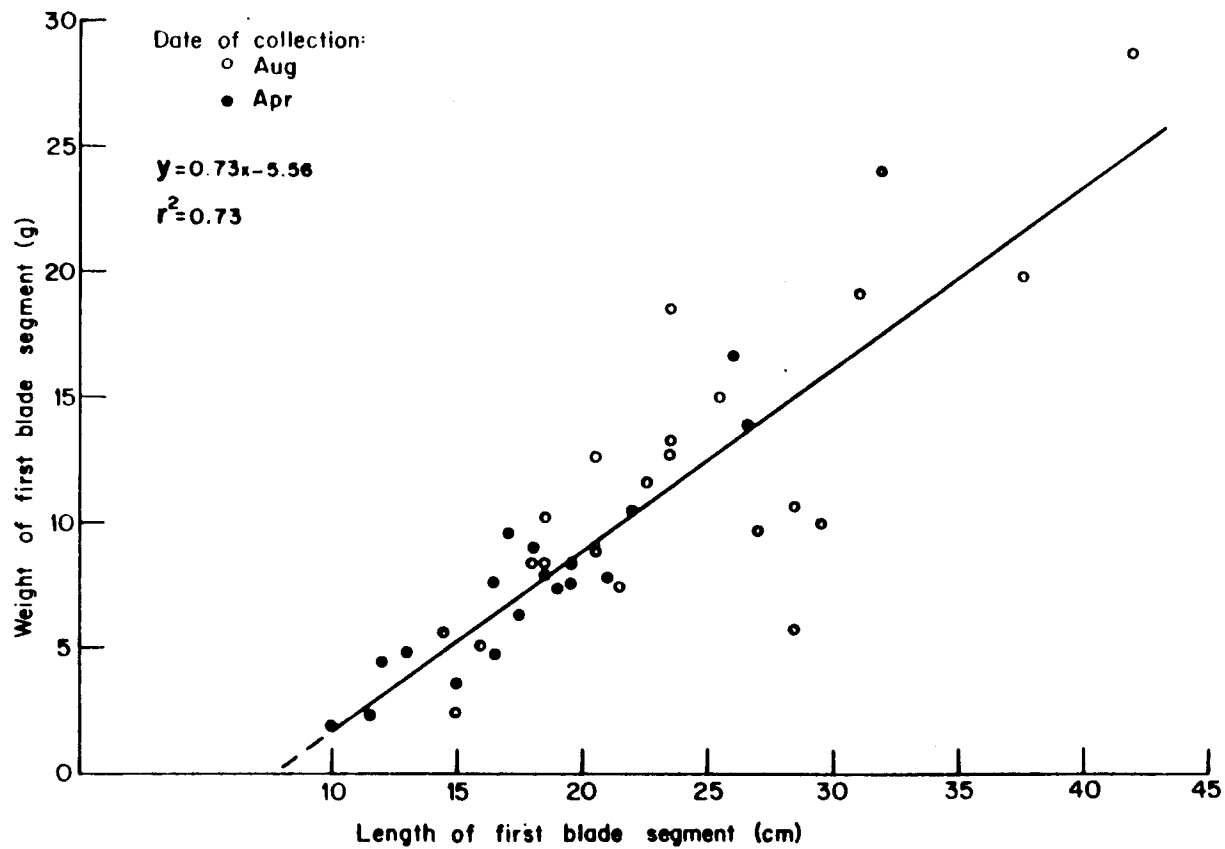


Figure 3. The relationship of basal blade segment length and biomass in L. solidungula plants randomly collected in late April (open circles) and early August (solid circles) at DS-11 in 1980; correlation coefficient, 0.85.

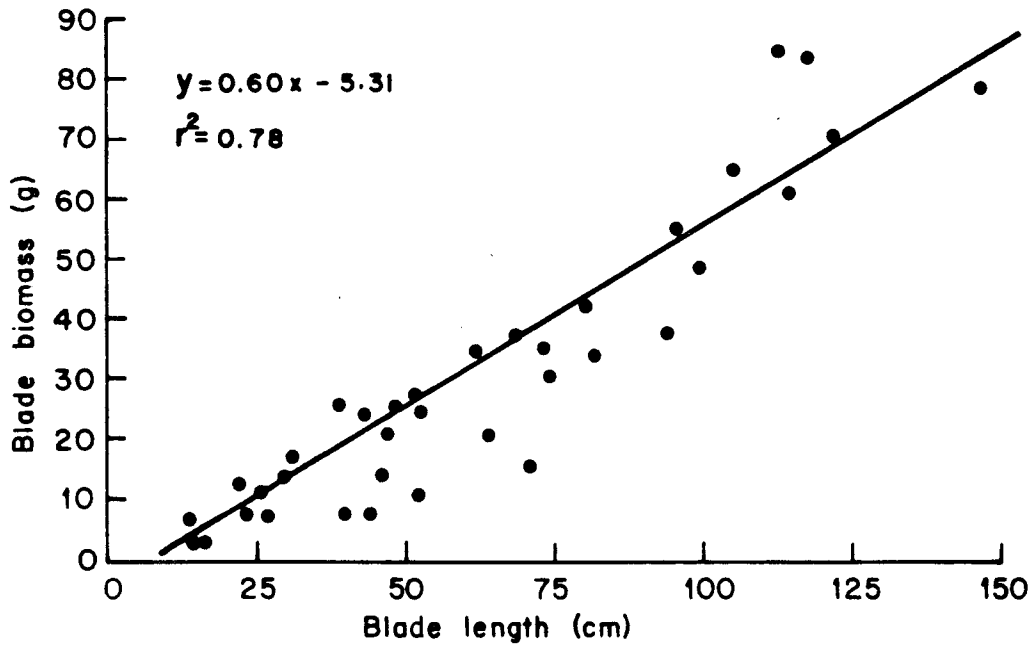


Figure 4. Total plant blade biomass as a function of total blade length (all blade segments and eroded tip) in plants collected in November 1979, 1980, and 1981 (not all data points shown); correlation coefficient, 0.88.

The productivity of the plants collected at DS-11 and DS-11A based on the length-to-biomass correlations is shown in Table 1. Mean production was about 55% greater in L. solidungula at DS-11A than at DS-11. For the periods from November to May and from November to July, mean biomass production at DS-11 and DS-11A was significantly different ($p < 0.05$). Differences in P:B ratios at the two sites for the period from November to July were not significant ($0.05 < p < 0.10$), mainly due to anomalously high P:B ratios for some plants at DS-11. Plants at DS-11 produced additional tissue between May and July, but no tissue production was noted for plants at DS-11A during the same period. The lack of growth in plants at DS-11A may be explained by a shift to food

TABLE 1. Mean Production ($g \pm 95\%$ confidence limits) and P:B Ratios of Plants Collected at DS-11 (turbid ice canopy) and DS-11A (clean ice canopy) in gwyr 1979. Number of observations in parentheses.

Site	15 November to 22 May	15 November to 25 July	PB ¹	PB ²
DS-11	10.12 \pm 1.16 (56)	11.98 \pm 1.28 (42)	0.80 \pm 0.27 (41)	0.91 \pm 0.22 (15)
DS-11A	21.77 \pm 1.86 (51)	21.42 \pm 2.64 (41)	1.26 \pm 0.44 (40)	-----

¹ Does not include biomass increment for last quarter (19 July to 15 November) for gwyr 1979.

² P:B for entire gwyr 1979.

storage starting in May, when nutrient concentrations begin to drop, but I have no data on tissue density to support this hypothesis. The mean production-to-biomass (P:B) ratio by late July was 1.26 at DS-11A compared to 0.80 at DS-11. The P:B ratio for the entire growth year (gwyr 1979) at DS-11 was 0.91, an increase of 14% from July. Since I did not return to DS-11A in November, it was not possible to calculate the P:B for gwyr 1979 at this site.

Consumption of kelp by the chiton *Amicula vestita*

Amicula vestita appears to be the only herbivore in the Boulder Patch that noticeably consumes kelp blades. The animal has a mean density of 16 individuals m^{-2} and a biomass of 11 g m^{-2} on rock substrata at DS-11 (Dunton et al., 1982). Of this biomass, 86% is represented by animals whose individual wet weights are greater than 1 g. The mean biomass of this group is 2.11 g.

The daily rate of consumption of kelp blades by the same three chitons during three different periods is shown in Figure 5. The daily rate of feeding varied from 13 to 46 mg of fresh kelp per day and was related to live body biomass. The mean annual consumption-to-biomass ratios for the three animals were similar (3.82, 3.34, and 2.73), giving an average of 3.3. No changes in the wet weights of the animals were found.

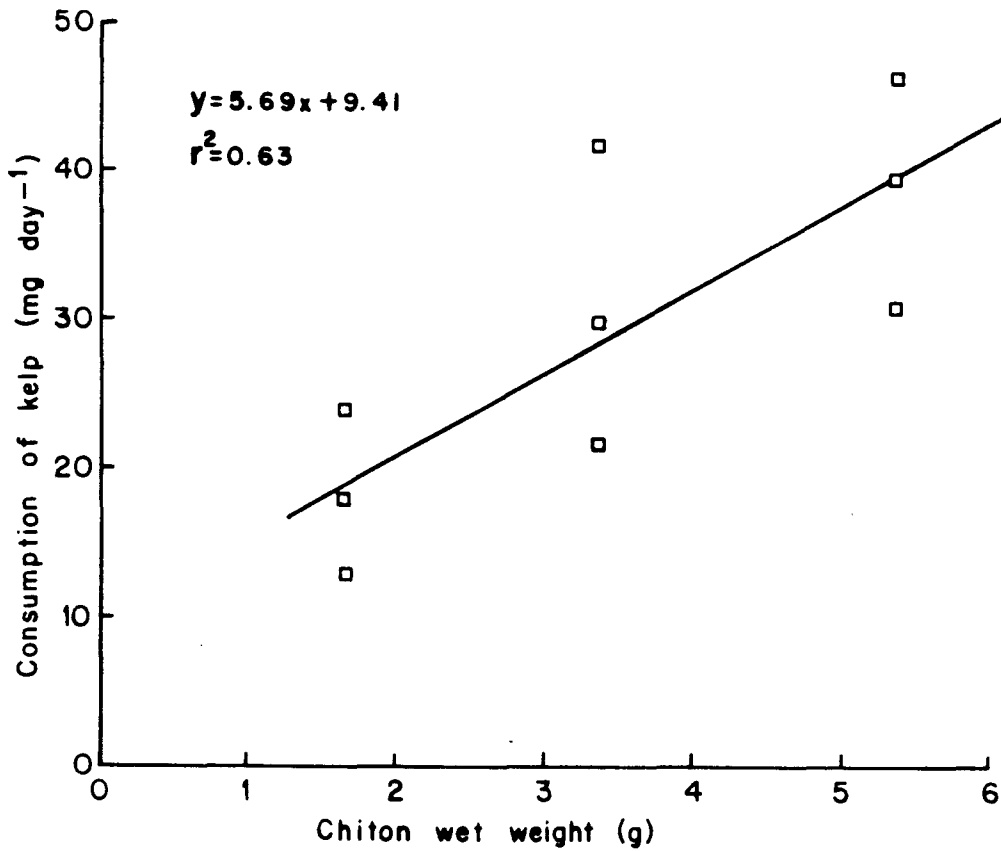


Figure 5. Relationship between herbivore biomass and consumption of kelp (mg day⁻¹) for Amicula vestita. Each point represents mean consumption in three chitons weighing 1.7, 3.3 and 5.2 g over time periods ranging from 51 to 67 days; correlation coefficient, 0.79.

These data allow a calculation of the annual consumption of kelp by A. vestita. The biomass of A. vestita per m^2 of seafloor is 4 g m^{-2} (11 g m^{-2} multiplied by 0.86, the percentage of animals greater than 1 g wet weight, and 0.42, the percentage rock cover at DS-11). From Figure 6, the C:B ratio of an average chiton (wet weight, 2.11 g) is 3.71. Assuming that carbon comprises 5.3% of a kelp's wet weight (Dunton et al., 1982), the annual ingestion of kelp by A. vestita is roughly 0.8 g C m^{-2} .

Benthic microalgal production

Benthic diatoms appeared in 62% of the benthic samples collected. Mean biomass (wet weight) was 3.4 g m^{-2} . The percentage dry weight to wet weight of the diatoms was 21%, and the percentage carbon of dry weight was 8%. Based on these data, the mean standing crop of benthic diatoms is approximately 0.6 g C m^{-2} . I found no correlation between biomass and month of collection over the three-year period. Filamentous diatoms consisted primarily of Amphipleura. These were most common on bryozoans, hydroids, and branched and foliose red algae, such as Rhodomela confervoides, Phyllophora truncata and Phycrodryis rubens.

DISCUSSION

Annual kelp carbon production

Beneath clean ice, and in response to increasing day length in the late winter and early spring, linear growth in L. solidungula is about 55% greater than under turbid ice, resulting in a substantial increase in the standing crop of these plants. The mean P:B ratio of plants exposed to light (under clean ice) measured in July was 1.26, compared to a ratio of 0.80 for plants exposed to dark (under turbid ice). The measured increase of the P:B ratio in dark-exposed plants between July and November was about 14%. Applying this increase to plants at DS-11A (subject to the same late summer and early fall light conditions), an annual P:B ratio of 1.44 was obtained. Using this P:B ratio, the productivity of the kelp was ca $10.4 \text{ g C m}^{-2}\text{yr}^{-1}$. This compares to about $6.6 \text{ g C m}^{-2}\text{yr}^{-1}$ under normal winter conditions of darkness under the ice canopy. Since turbid ice is patchily distributed in Stefansson Sound, it is likely that the average productivity of the kelp bed (with a density similar to DS-11) falls between the minimum and maximum values listed above.

The P:B ratios of L. solidungula in the Boulder Patch ranged from 0.9 to 1.4; this is considerably lower than other species of Laminaria in more temperate regions. In St. Margaret's Bay, Nova Scotia, for example, the P:B ratio of L. longicruris ranges from 7.2 to 10.7 (Mann, 1972) -- almost an order of magnitude greater.

In a kelp bed off the coast of South Africa near Cape Town, the P:B ratio of L. pallida is about four times greater than L. solidungula (Newell et al., 1982). But despite the much lower production in the Boulder Patch compared to kelp beds in temperate regions, the proportional split between phytoplankton and kelp production remains nearly the same. In the Beaufort Sea, the presence of an isolated source of kelp carbon provides a unique opportunity to assess its importance to both invertebrate and vertebrate animals.

A portion of this annual production is consumed directly by Amicula vestita. On an individual basis, Amicula consumes nearly four times its weight in fresh kelp annually, which likely accounts for most (but not all) of its dietary intake. Based on its observed density, the kelp carbon utilized by Amicula ($0.8 \text{ g m}^{-2} \text{ yr}^{-1}$) represents between 8 and 12% of annual production by L. solidungula, depending on the character of the ice canopy. Off the coast of Nova Scotia, Miller et al. (1971) found that the annual consumption of kelp by herbivores (sea urchins and snails) was about 9% of total kelp production. Newell et al. (1982) calculated that urchins consumed about 12% of total kelp production off the west coast of South Africa. The fraction of kelp not consumed by herbivores enters the foodweb in dissolved or particulate form where it becomes a detrital source of carbon to benthic consumers.

An annual carbon budget for the Boulder Patch

In years characterized by the presence of a turbid ice canopy, only three sources of marine carbon are available to consumers in the Boulder Patch -- kelp, phytoplankton, and benthic microalgae. The spring bloom of ice microalgae, which is common in most arctic coastal areas (Alexander, 1974; Hsiao, 1980) does not occur because of the lack of light caused by the presence of turbid ice. But in the absence of turbid ice in Stefansson Sound, productivity of the ice algae is about $5.2 \text{ g C m}^{-2}\text{yr}^{-1}$ (Schell et al., 1984).

The productivity of benthic microalgae in the absence of turbid ice is about $0.4 \text{ g C m}^{-2}\text{yr}^{-1}$, based on a P:B ratio of 7 (Chapman, 1981). Although it seems unlikely that this P:B ratio would hold for arctic regions, Matheke and Horner (1974) reported high productivities for benthic microalgae near Barrow, in which chlorophyll a concentrations increased nearly an order of magnitude during a three-month summer period. Since measured productivity rates in the benthic microalgae are undetectable under the ice canopy (Horner and Schrader, 1981), carbon production occurs only during the summer open-water months, between July and October. In the presence of turbid ice, which is accompanied by extremely high water turbidity during breakup and freeze-up, I assume that annual benthic microalgal productivity is cut by about 25 percent. The carbon contribution made by the phytoplankton is about $8.0 \text{ g m}^{-2}\text{yr}^{-1}$ in the Boulder Patch (Schell et al., 1984) and is largely unaffected by turbid ice. Based on these data, it is

possible to compare the sources of carbon and their magnitudes, either in the presence or absence of turbid ice (Figure 6).

In both cases, kelp clearly contributes a major source of carbon to consumers in the Boulder Patch. Carbon derived from phytoplankton, ice algae, and benthic microalgae match the input from kelp, but the benthic microalgal component is relatively unimportant. Annual growth increments in L. solidungula support observations that turbid ice is a frequent occurrence in the Boulder Patch (Dunton et al., 1982). Thus, it appears that 98% of the carbon available to consumers is derived from either kelp or phytoplankton in most years. Particulate organic matter (the fragmented portion) derived from kelp is about 60% of the total released to the environment (Newell et al., 1982). The importance of this fraction to consumers in an isolated community dominated by filter feeders, which comprise 65% of the total standing stock (Dunton et al., 1982), is now being investigated.

Recent work has shown that the carbon in the particulate fraction is converted into bacterial biomass with an efficiency of between 8 and 11% (Stuart et al., 1981; Robinson et al., 1982). But it is not known to what extent consumers depend on the protein enrichment of fragmented kelp by bacterial mineralization, although Newell et al. (1982) reported that bacterial degradation of detritus is important to a kelp community on the west coast of South Africa. Findlay and Tenore (1982) recently demonstrated that a polychaete detritivore derived a major portion of its nitrogen directly from seaweed detritus, not the microbial

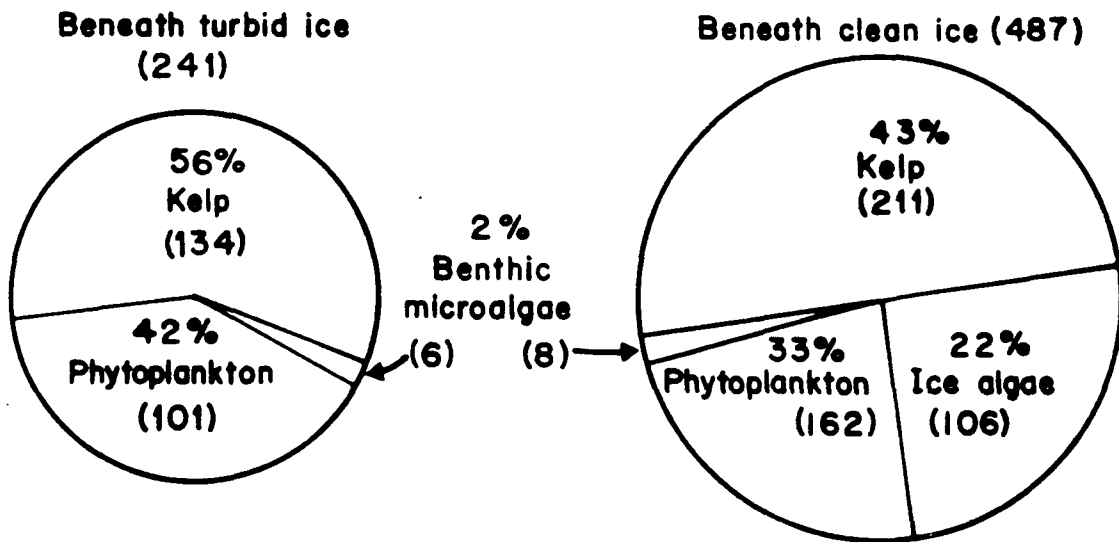


Figure 6. The sources of carbon ($\text{g} \times 10^6$, in parentheses) and their percent inputs to the Stefansson Sound Boulder Patch in years characterized by either turbid ice or clean ice (total area $2.03 \times 10^7 \text{ m}^2$).

population that colonized the detritus. It is possible that in the Boulder Patch, the relatively lower carbon flux (in comparison to temperate latitudes) may force many consumers to develop a high assimilatory efficiency for kelp detritus. Consumers so adapted would also be able to utilize a year-round source of kelp carbon, especially during the period of total ice cover, when phytoplankton production virtually ceases. On the other hand, it is more likely that most of the kelp detritus enters a microbial foodweb, and does not become available to macroconsumers, but instead is regenerated as biogenic CO₂. In the following chapter I will discuss how Laminaria solidungula allocates its carbon reserves to survive the dark ice-covered period and still show an 80% net gain in annual carbon production.

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CHAPTER 4. A SEASONAL CARBON BUDGET FOR THE KELP LAMINARIA
SOLIDUNGULA IN THE ALASKAN HIGH ARCTIC

SUMMARY

On the north arctic coast of Alaska, Laminaria solidungula is the dominant member of a kelp bed community that is subject annually to eight months of darkness under a turbid ice canopy. Seasonal changes in total tissue carbon were measured for 24 sporophytes incubated in situ for one year. Net annual production was calculated from these measurements and compared to carbon fixation rates from in situ ^{14}C uptake experiments. During the period of rapid growth, from November to late April, L. solidungula is in a carbon deficit. About 25% of the plant's original carbon content is depleted before photosynthetic production can resume at breakup in June or early July. The daily rate of carbon loss ($0.7 \mu\text{g}$ per mg of frond dry weight) is greatest between November and late February; it is less ($0.2 \mu\text{g C mg}^{-1} \text{ day}^{-1}$) between February and late April due to photosynthesis at extremely low light levels. The main summer carbon fixation rate measured by ^{14}C uptake experiments was $0.09 \mu\text{g mg}^{-1} \text{ hr}^{-1}$. This rate of production, when extrapolated for the summer open-water period, matched net carbon production for experimental plants grown in situ, leaving no assimilatory surplus. The plants reallocate stored reserves to produce new frond tissue during the ice-covered period that replaces about 80% of their previous year's carbon content.

INTRODUCTION

Laminaria spp. depend to varying degrees on stored food reserves for growth when light levels reach their annual minima during the late fall and early winter. In the Canadian High Arctic, where seaweeds must endure a winter dark period of at least three months, Chapman and Lindley (1980) found that L. solidungula accumulated carbon reserves (as reflected in both laminarin content and tissue density) during summer when growth rate was lowest. They noted these reserves were subsequently reduced through the winter, presumably to support growth during the period of low light.

Unaware of the simultaneous work of Chapman and Lindley (1980, 1981) on L. solidungula in arctic Canada, Dunton et al. (1982) noted that L. solidungula plants on the north arctic coast of Alaska produced a new blade and completed nearly 90% of its annual linear growth in complete darkness under a turbid ice canopy that occluded light completely from late October until June. They found nearly identical seasonal changes in linear growth and tissue density as did Chapman and Lindley (1980), but growth rates, standing crop and productivity were two-to-four times lower than the Canadian population (Dunton et al., 1982; Dunton, 1984). However, no data on carbon flux within this plant have been presented by either the Canadian or Alaskan group.

In northern European waters, reserves of photosynthate accumulated in the frond of L. hyperborea during summer, its period of slow growth, support the formation and growth of a new blade the following spring (Luning, 1969). In contrast, little accumulation of reserve carbohydrates occurs in L. digitata which exhibits rapid, sustained summer growth (Luning, 1979). Johnston et al. (1977) found that large concentrations of laminarin and mannitol are synthesized by L. saccharina during the summer months. But they noted that these photosynthates were not only unnecessary (because the carbon fixed during winter matched the plant's energy requirements), but such reserves were not available due to distal tissue loss in autumn and winter.

Gagne et al. (1982) compared the growth strategies employed by L. longicruris at three sites differing in respect to the availability of inorganic nitrogen. He found that summer storage of carbohydrates and autumn growth were greatest in L. longicruris plants living at the Nova Scotia site where nitrogen was abundant only in winter. Storage was least where nitrogen was available year round, and intermediate where nitrogen was limiting only in the late spring and summer.

Only two previous studies have specifically addressed seasonal carbon budgets and carbon allocation in Laminaria spp. Hatcher et al. (1977) examined L. longicruris in Nova Scotia and Johnston et al. (1977) worked on L. saccharina in Scotland. Both studies showed that the species were able to produce a photosynthetic

surplus throughout the winter and possess a large annual assimilatory surplus that could not be accounted for in terms of growth or accumulation of stored material. Both Johnston and Hatcher concluded that this surplus, 25-35% of net carbon fixation, was due to extracellular release of dissolved organic matter.

Do kelp populations living in light limited arctic environments also produce such an assimilatory surplus? To answer this question for L. solidungula, I constructed an annual carbon budget based on ^{14}C uptake experiments and the weight gains of plants grown in situ. Seasonal visits to our study site also allowed me to clarify how L. solidungula allocates its limited carbon supply during several months of continuous darkness while completing over 90% of its linear growth.

METHODS

Site description

The experiments were conducted at an established study site, dive site 11 (DS-11; 70°19.25'N, 147°35.1'W), in an area known as the Boulder Patch in Stefansson Sound, 20 km northeast of Prudhoe Bay in the Beaufort Sea off Alaska's north arctic coast (Fig. 1). The Boulder Patch is an area of cobbles and small boulders that cover approximately 20 square kilometers of seabed in an area otherwise characterised by fine-grained sediments of silty sands or

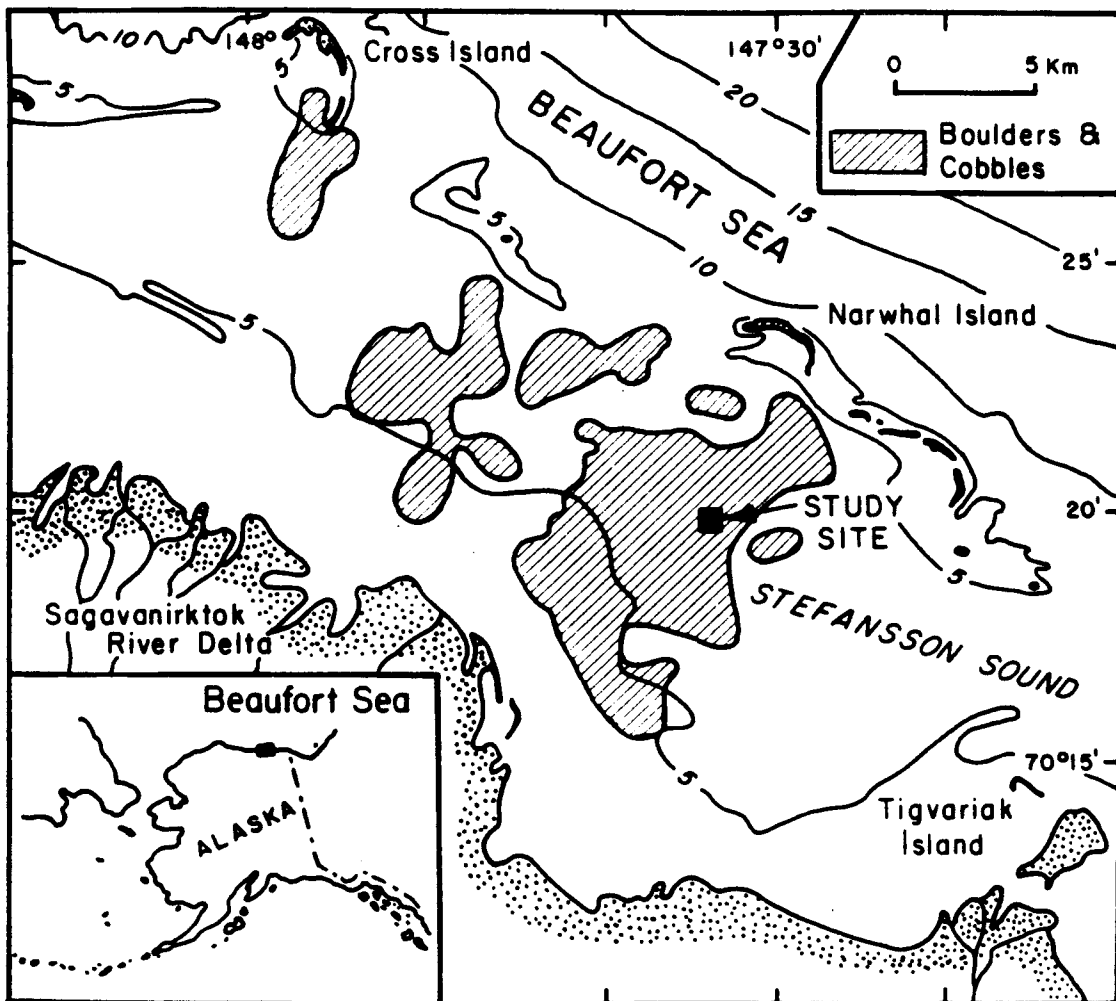


Figure 1. Location of the study site in the Beaufort Sea, Alaska.

mud. The rocks provide a substrate for a diverse assortment of invertebrates and several species of algae, including the predominant brown alga Laminaria solidungula, which constitutes over 90% of the brown algal biomass (Dunton et al., 1982). Water depth at DS-11 ranges from 6 to 7 meters.

Data were collected at DS-11 for this study in November 1979 and in February, April and August of 1980. During the open-water period (early July to late September), we dove from a small boat. During ice-covered periods, we entered the water through holes cut in the ice with augers and ice chisels. A heated, insulated hut (Parcoll, Panebee Ltd., Montreal) placed over the dive hole functioned as a dive shelter and laboratory.

Bottom water temperatures at the site on visits during the ice-covered period were -1.8°C . Temperatures ranged from 0 to 3.5°C in August.

Field measurements on plants

The frond of L. solidungula is divided into distinct ovate blades of different sizes by constrictions that form annually (Fig. 2). The growth of a new basal blade starts in November and continues until the following November, allowing an accurate measurement of the plant's annual production.

In November 1979, 24 plants were carefully removed from their substratum and brought to the surface. I removed the old blades by

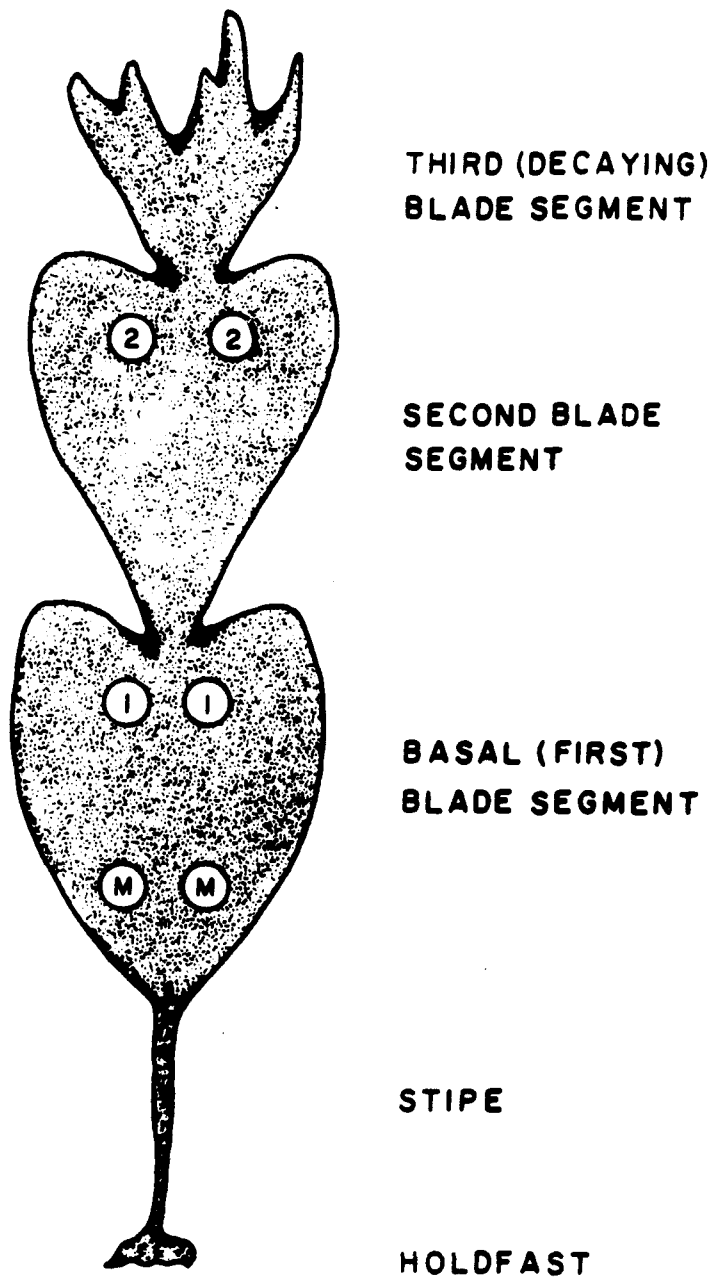


Figure 2. Schematic drawing of sampling in a specimen of Laminaria solidungula for net production using the ^{14}C method. The open circles mark the samples punched out of the meristematic zone of the growing frond (M), the area of the basal blade segment in which most enlargement of the new blade occurs (1), and the second blade segment left from preceding year (2). Samples were punched out following incubations of entire plants in situ.

slicing the frond at the constriction directly above the basal blade. I also checked the condition of each plant to ensure it was healthy and that the remaining basal blade was entire and free of epiphytes and grazing scars. Individual plants were then measured, weighed to the nearest 0.1 g on a top loading Mettler balance and the stipes fastened to a large submerged plastic cage anchored to the seafloor. Plants were handled only by their holdfasts. Blades were never blotted, and most excess water was simply removed by allowing the plants to lie on a clean damp towel for about a minute.

On each subsequent trip to the site, all plants were retrieved, measured, weighed, and then immediately reattached to their support. Plants were discarded if any blades or stipes were damaged as a result of natural or artificial causes. To obtain the actual weight of the frond, I subtracted the predicted stipe weight based on a stipe length vs stipe weight regression analysis made from 88 plants collected at the site in November 1979, 1980 and 1981 (Fig. 3). In a separate one-year pilot study, I also found that the net weight gain of an entire plant matched the biomass (wet weight) of the basal blade within $\pm 7\%$ in nearly all cases with a mean difference of 0.5% (N = 13). Therefore, I assumed for the purposes of estimating carbon budgets that the wet weights of the distal blades and stipe remained essentially constant.

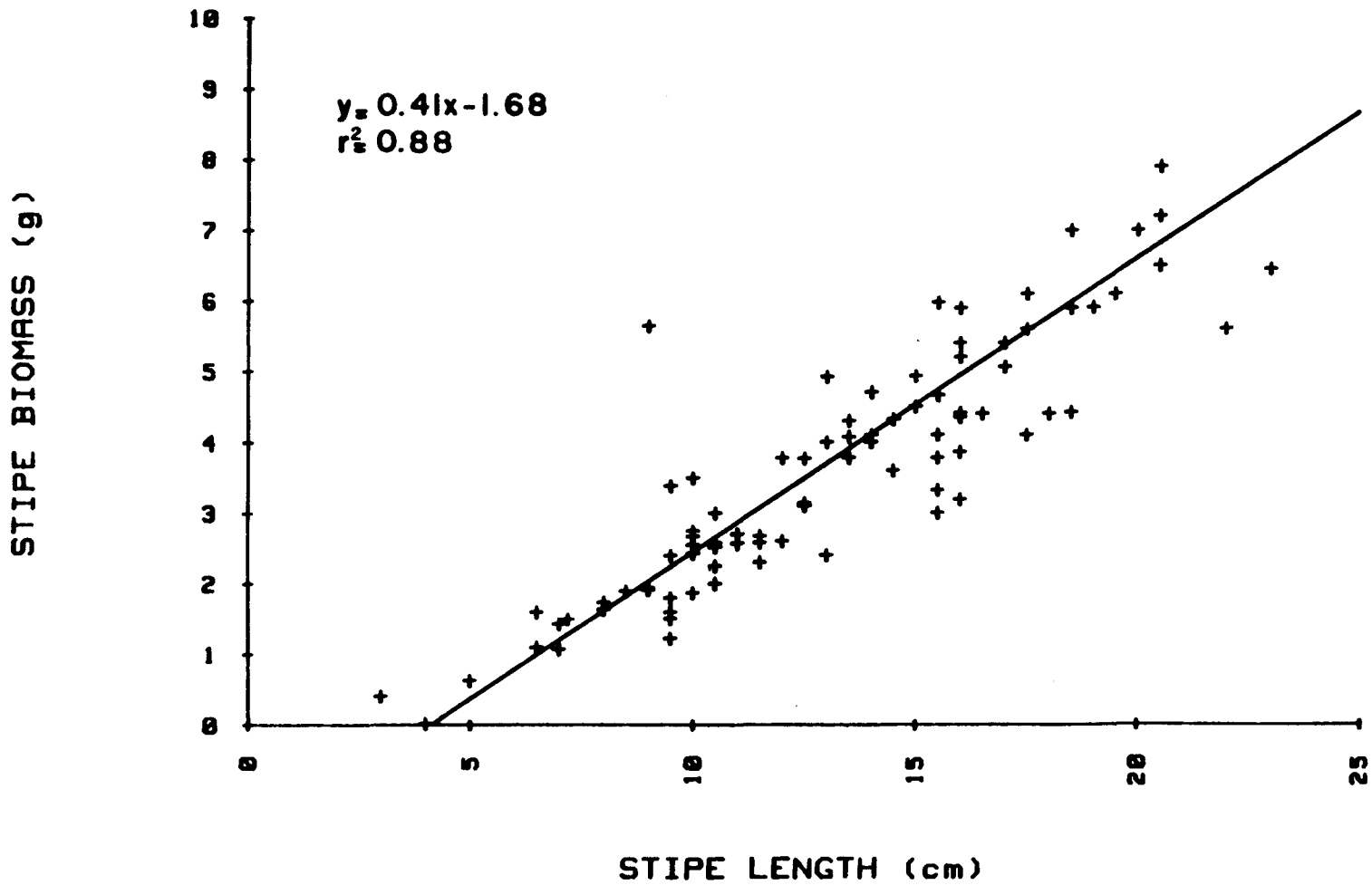


Figure 3. Laminaria solidungula. Stipe biomass as a function of stipe length (N = 88). The 95% CI (individuals) was ± 1.72 and the 95% CI (mean) was ± 0.26 .

Seasonal changes in average N and C content

On each visit to the site, 6 to 11 representative plants were taken for analysis of carbon and nitrogen content. Blade segments were separated, dried to a constant weight at 35°C and ground to a coarse powder in a mill. Subsamples of ground tissue from each blade were weighed on a Kahn 26 Automatic Electro Balance and analyzed for carbon and nitrogen content on a Perkin-Elmer 240C elemental analyzer.

Fronde carbon flux

An example of net carbon production for each blade versus the whole frond is shown for a representative plant in Table 1. The carbon content for each blade was obtained by multiplying the wet weight of the tissue by its density (% dry weight of wet weight) and carbon content per unit dry weight. Seasonal changes in the tissue density of plants collected at the same time of this experiment have been previously reported (Dunton et al., 1982).

¹⁴C uptake

I obtained summer photosynthetic rates of intact mature L. solidungula plants in late July and early August 1980. Each plant was individually enclosed within a 50 x 30 cm clear polyethylene

TABLE 1. *Laminaria solidungula* -- sample calculation of net carbon loss or gain in new and old tissue in experimental plant No. 3.
All weights in grams.

Extrapolation period (1980)	WHOLE PLANT	BASAL BLADE				SECOND BLADE				TOTAL FROND
	Wet weight	Wet weight ^a	Total carbon ^c	Previous period total carbon	Net carbon gain	Wet weight ^b	Total carbon ^c	Previous period total carbon	Net carbon gain or loss	Net carbon gain or loss
start 23 Nov 79	9.7	----	----	----	----	7.7	0.671	----	----	----
23 Nov 79 - 29 Feb	12.75	3.05	0.088	0	0.088	7.7	0.449	0.671	-0.222	-0.134
29 Feb - 23 Apr	12.95	3.25	0.092	0.088	0.004	7.7	0.414	0.449	-0.035	-0.031
23 Apr - 1 Aug	16.31	6.61	0.440	0.092	0.348	7.7	0.461	0.414	0.047	0.395
1 Aug - 4 Nov	19.00	9.30	0.828	0.440	0.388	7.7	0.375	0.461	-0.086	0.302

^a New whole plant weight minus previous.

^b Corrected for stipe biomass of 2 g based on a stipe length of 9.0 cm (see Figure 2).

^c Reflects seasonal changes in wet:dry weight ratios (Dunton et al., 1982) and tissue carbon content (Figure 4).

bag along with 0.75 to 1.0 liter of ambient seawater spiked with 5 μCi of $\text{NaH}^{14}\text{CO}_3$. The open end of each bag was securely fastened with a large rubber band and electrical tape. The experiment consisted of four separate incubations performed over a 5-day period. Each included four to eight experimental plants, one to three dark-incubated plants and one formalin treated plant. Dark-incubated plants had three black polyethylene bags secured over the clear bags. In situ incubations lasted from 24.5 to 27 hours except for one 18 hour incubation.

After incubation, the plants were removed from their bags, rinsed in seawater, placed in an opaque container, and quickly transported to our field station. Duplicate tissue samples from the meristem, new blade and second blade (Fig. 2) were punched out with a cork-borer (area 0.31 cm^2) and dried in darkness.

Each ^{14}C labeled disc was weighed in the laboratory, combusted in a biological material oxidizer (Harvey Instrument Corporation), and the $^{14}\text{CO}_2$ trapped in a liquid scintillation cocktail. The contents were poured into a scintillation vial and counted for 5 minutes on a Beckman LS-100C liquid scintillation counter. Background and standard counts were obtained using equivalent amounts of unlabeled kelp discs and quenched C-14 standards. I express photosynthetic rates as milligrams carbon incorporated per milligram dry weight per hour, using a value of $17.4 \text{ mg total inorganic-C liter}^{-1}$ of seawater (Strickland and Parsons, 1972).

Light measurements

Due to the remoteness of the site and availability of equipment it was only possible to make instantaneous measurements of in situ irradiance. We used a Protomatic underwater photometer (Dexter, Michigan) to obtain total illumination in foot candles (1 foot candle = 10.76391 lux). During the ice-covered period, we made measurements in November, late February and early March.

RESULTS

Fronde carbon and nitrogen content

Seasonal changes in total tissue N and C content in the developing basal blade and mature second blade are shown in Figure 4. In both blades, carbon content decreases through the winter, reaching a minimum in late April. Between November and April, the carbon content in blade two dropped from 36 to 31%, which coincided with the formation and rapid growth of the new basal blade segment. From April onward, percent carbon in blade two increased to 32.5%, but did not regain its original carbon percentage. In the basal blade, the carbon content decreased from 29% in February to 26% in late April, and then rapidly increased to 37% by November.

In contrast to carbon, nitrogen content exhibited distinct seasonal variation in both blades. The nitrogen content in the

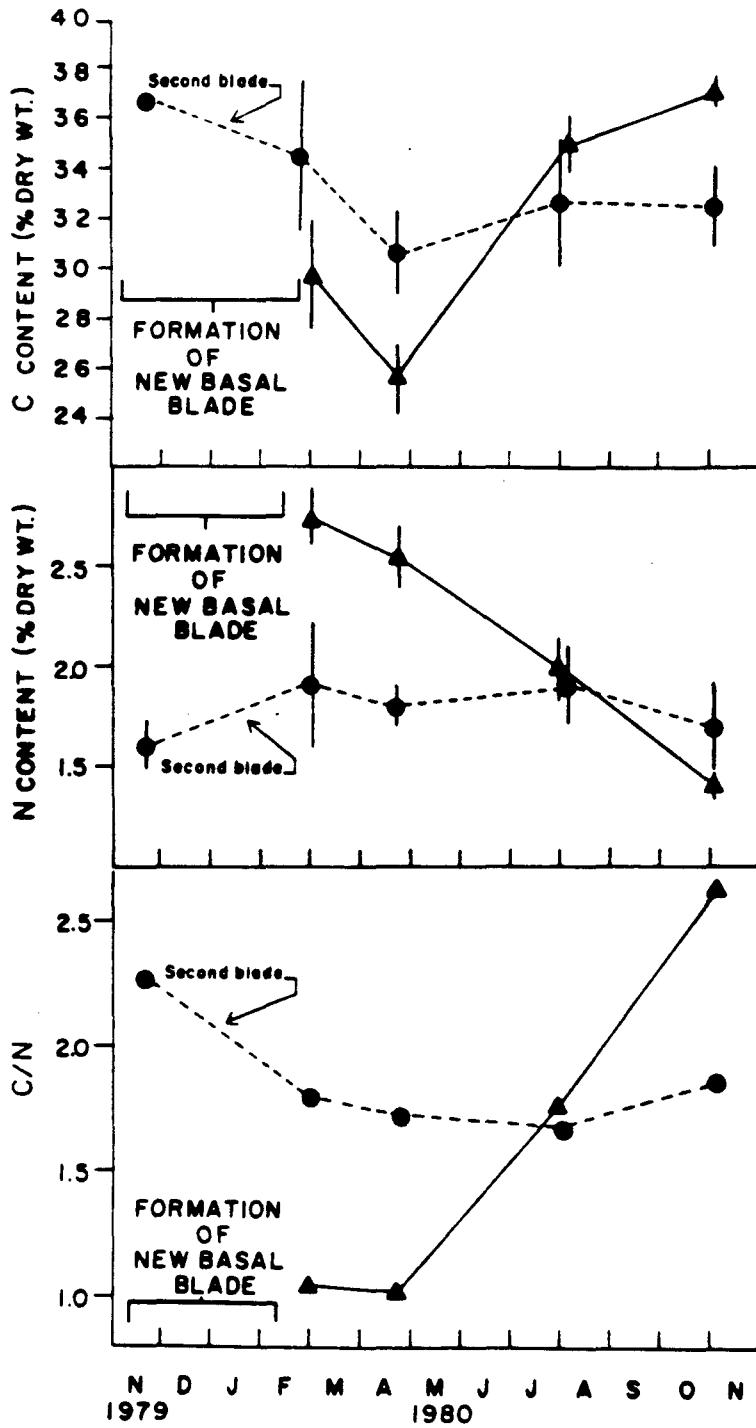


Figure 4. *Laminaria solidungula*. Seasonal changes in total carbon, nitrogen (means $\pm 95\%$ confidence limits) and C/N in the first (closed triangles) and second (closed circles) blade segments of fronds collected at site DS-11.

basal blade dropped steadily through the year while it remained fairly constant (between 1.6 and 1.9%) in the second blade. Nitrogen content was significantly lower ($p < 0.0001$) than total N in the basal blade in February and April. In the basal blade, the drop in tissue N from 2.7% in February to 1.4% in November is reflected in its C/N ratio, which increased from 10 to 26 for the same period. Changes in the C/N ratio for the second blade were small, but showed a decrease of 23 to 17 from November to August.

Growth and carbon flux determinations

A summary of the seasonal pattern of linear growth and tissue carbon flux in the experimental plants in relation to external dissolved inorganic nitrogen concentrations is shown in Figure 5. Linear growth was high between November and February (0.8 mm day^{-1}), the darkest period of the arctic winter. Growth continued to increase until late April, but slowed to 0.6 mm day^{-1} between late April and August. Growth was lowest between August and November (0.1 mm day^{-1}), a largely ice-free period.

This seasonal growth pattern agrees well with previous studies on L. solidungula (Chapman and Lindley, 1980; Dunton et al., 1982). A turbid ice canopy occluded light at this site, as had been the case in past years (Dunton et al., 1982). Irradiance levels on the bottom adjacent to the experimental plants in November and late February ranged from undetectable to 0.16 foot candles (equivalent

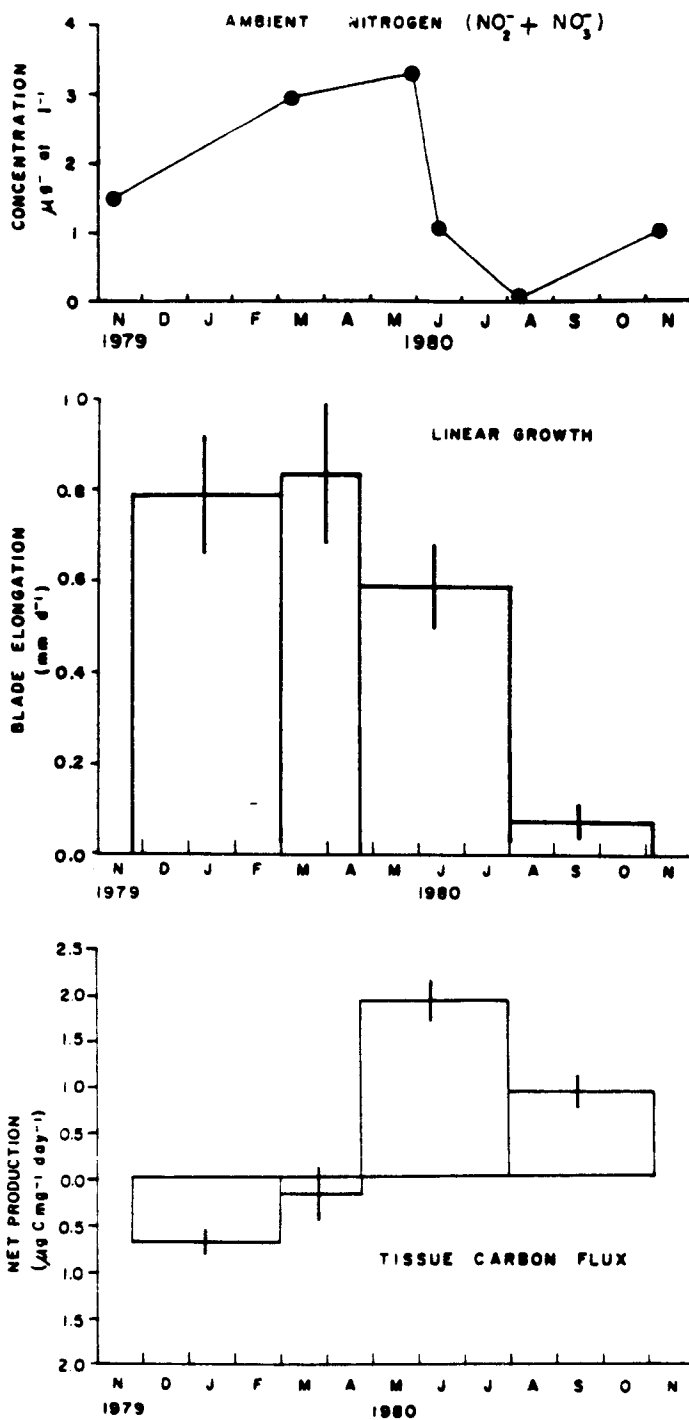


Figure 5. *Laminaria solidungula*. Seasonal variation in ambient inorganic nitrogen, blade growth (means \pm 95% confidence limits) and tissue carbon production at 7 m depth. Ambient inorganic nitrogen data from Dunton et al. (1982).

to less than $0.03 \mu\text{Em}^{-2}\text{s}^{-1}$). In early March, however, we noticed lighter patches under the ice canopy in several locations that appeared to coincide with our previous activities on the ice surface, which included the removal of ice and snow for dive holes and ice camps. Maximum irradiance under these patches was also low, 0.41 foot candles ($0.09 \mu\text{Em}^{-2}\text{s}^{-1}$).

Mean net carbon assimilation in the experimental plants showed a pattern nearly inverse to linear growth. Between November and February, net carbon loss in an average sized plant was about $0.7 \mu\text{g mg}^{-1}\text{day}^{-1}$. Net carbon loss continued until April, but at a slower pace ($0.2 \mu\text{g mg}^{-1}\text{day}^{-1}$). The rate of carbon loss decreased during this period because of carbon fixation resulting from patchy light penetration of the ice canopy. A lower respiratory demand during this period is unlikely, since water temperatures remained constant (-1.8°C), and linear growth rates increased to their highest annual levels.

Net carbon fixation in the experimental plants reached a maximum of $1.9 \mu\text{g mg}^{-1}\text{day}^{-1}$ between late April and August. This marks the period of initial ice canopy deterioration, followed by open water in early to mid-July. From August to November, the period of minimum linear growth, net carbon production in the fronds slowed to $0.9 \mu\text{g mg}^{-1}\text{day}^{-1}$.

Levels of ambient inorganic nitrogen ($\text{NO}_2^- + \text{NO}_3^-$) from the same period at DS-11 have been reported previously (Dunton et al., 1982) and are shown in Figure 5 for comparative purposes. The

concentrations of inorganic nitrogen follow an annual cycle typical of arctic waters (Chapman and Lindley, 1980) and temperate waters (Chapman and Craigie, 1977; Wheeler and North, 1981).

Concentrations increase from 1.5 to 3.3 $\mu\text{gat}\cdot\text{l}^{-1}$ from November to June, followed by a sharp decline in mid-June. The winter linear growth of L. solidungula occurs during higher concentrations of inorganic nitrogen as previously reported by both Chapman and Lindley (1980) and Dunton et al. (1982).

Seasonal variations in frond fresh weight, and the total carbon content of the blades and frond in experimental plant number 3 are shown in Figure 6. It is noteworthy that despite a consistent gain in frond fresh weight from November to April (7.7 to 11 g), the carbon content of the frond dropped from 0.7 to 0.5 g. This loss, about 25% of the initial carbon content of the frond, was typical for most plants. From late April to November, the fresh weight and carbon content of the frond increases. However, the rise in frond carbon content from 0.5 to 1.2 g is almost entirely due to the increase in carbon content of the basal blade. This seasonal variation in fresh weight and carbon content was observed in all the experimental plants.

Annual net photosynthesis - ^{14}C uptake

Total ^{14}C uptake by L. solidungula during four separate incubations from 29 July to 3 August is shown in Table 2.

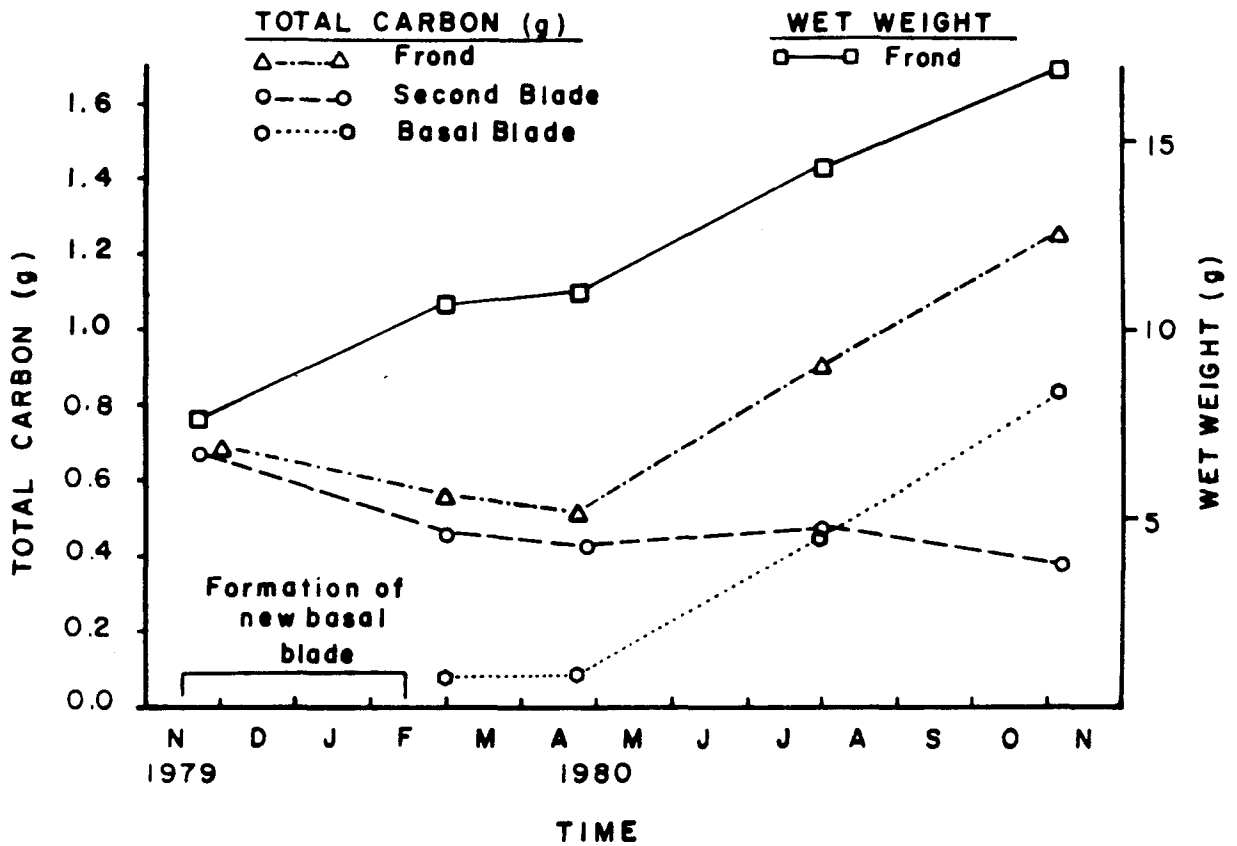


Figure 6. *Laminaria solidungula*. Seasonal variation in frond fresh weight, and total carbon content in the basal blade, second blade segment and total frond as exemplified by one of the 14 experimental plants (number 3) that survived one year fully intact.

TABLE 2. *Laminaria solidungula*. Summary of photosynthetic (PS) and dark fixation (DF) rates (means \pm 95% confidence limits) in different regions of the frond based on uptake of $^{14}\text{CO}_2$ in 29 plants from four separate incubations.

<u>L. solidungula</u>	Carbon fixation ($\mu\text{g C} \times 10^{-3} \text{ mg dry weight}^{-1}\text{hr}^{-1}$)			
	Photosynthesis	Dark fixation	PS - DF	PS:DF
Meristem	0.093 \pm 0.015	0.015 \pm 0.005	0.078	6.2
Basal blade	0.124 \pm 0.014	0.014 \pm 0.004	0.110	8.9
Second blade	0.082 \pm 0.019	0.011 \pm 0.006	0.071	7.4
Whole frond ^a	0.100	0.013	0.086	7.5

^a Frond fresh weight in all plants exceeded 10 g.

Photosynthetic rates were greatest in the young basal blade above the meristematic region and lowest in the second blade. Light-independent carbon fixation (LICF) was highest in the meristematic region, accounting for 16% of the photosynthetic (PS) rate of CO₂ fixation. Over the entire frond, LICF accounted for roughly 13% of its total capacity for light carboxylation. After correction for LICF, average net photosynthetic fixation in the frond is about 0.09×10^{-3} mg C mg dry weight tissue⁻¹hr⁻¹.

In situ light measurements made during the four incubations ranged from nighttime lows of 90-130 foot candles (equivalent to about 20-30 $\mu\text{Em}^{-2}\text{s}^{-1}$) to daytime highs of 400-600 foot candles (equivalent to 80-130 $\mu\text{Em}^{-2}\text{s}^{-1}$). Continuous light meter measurements made at a nearby site in early August 1984 (Dunton et al., 1985) reflect photon flux densities of the same magnitude (Table 3). During this four-day period, the mean hourly minimum ranged between 40 and 60 $\mu\text{Em}^{-2}\text{s}^{-1}$, and mean hourly maximums varied between 110 and 210 $\mu\text{Em}^{-2}\text{s}^{-1}$.

Annual carbon budget

On an annual basis, net carbon production in an average sized kelp plant is 0.7 g, for an approximate P:B ratio of 0.8 (Table 4). The total carbon gain in new tissue (the entire basal blade) is 1.1 g (P:B = 1.2), a difference of about 35%. The overestimate of

TABLE 3. Laminaria solidungula. Summary of light data collected continuously over a four-day period in early August 1984 at a site in the Boulder Patch (data summarized from Dunton et al., 1985).

Measurement date (August 1984)	Quantum Irradiance ($\mu\text{E m}^{-2}\text{s}^{-1}$)			Day total ($\times 10^6$)
	Mean hourly maximum	Mean hourly minimum	Hourly mean	
10	208.2	59.9	121.3	10.5
11	127.0	43.4	81.0	7.0
12	107.8	40.1	62.7	5.4
13	118.0	44.9	66.5	5.7

TABLE 4. *Laminaria solidungula*. Total annual weight gains and calculated summer productivities of 14 plants in two size classes that survived one complete year in situ.

Size class	Initial frond fresh weight (g)	N	Basal Blade		Whole Plant		
			Total carbon (g)	P:B ratio	Net annual carbon production (g)	P:B ratio	Calculated summer productivity ^a (means \pm 95% confidence limits, $\mu\text{g C mg}^{-1}\text{hr}^{-1}$) ^b
Small	1-5	6	0.467	1.7	0.355	1.3	0.119 \pm 0.022
Medium	7-15	8	1.063	1.2	0.680	0.8	0.085 \pm 0.012

^a Based on 2,264 hours of available light (Schell et al., 1984).

^b Carbon production per mg dry weight of total summer frond tissue.

annual carbon production based on basal blade weight alone is explained by the stored food reserves. These reserves are used for both the growth and respiratory requirements of the plant, and are located in the second blade. Therefore, the difference in annual carbon production noted above is attributed to the growth of the new basal blade at the expense of the remainder of the plant.

Based on net annual carbon production in an average sized plant, and assuming that photosynthesis is minimal during the ice-covered period (November to June), I calculated summer carbon production on an hourly basis. I obtained the number of summer hours available for photosynthesis from Schell et al. (1984), who estimated available summer daylight at 2,264 hours to calculate phytoplankton productivity in arctic Alaskan nearshore waters. The result, $0.085 \mu\text{g C mg dry weight}^{-1}\text{hr}^{-1}$ (Table 4), is in excellent agreement with the hourly net carbon production estimate found in the C-14 uptake experiment (Table 2).

In light of these results, annual net carbon production of a L. solidungula population (standing crop of 140 g m^{-2} , Dunton et al., 1982) exposed to a winter turbid ice canopy is about 6 g C m^{-2} . This figure is slightly lower than I have previously reported for L. solidungula in the Boulder Patch, since the earlier calculations were based solely on basal blade production (Dunton et al., 1982). In the absence of turbid ice, productivity climbs to $10 \text{ g C m}^{-2}\text{yr}^{-1}$ (Dunton, 1984), and so annual production probably lies between 6 and 10 g C m^{-2} .

DISCUSSION

Winter carbon deficit

It appears that during the eight months under a turbid ice canopy, L. solidungula experiences a carbon deficit in which up to 30% of its original total carbon content is depleted. At the same time, however, the plant undergoes rapid linear growth, producing a new blade and completing nearly 90% of its annual linear growth before the photosynthetic season begins.

During the initial part of the ice-covered period, November to February, tissue density (a reflection of total tissue carbon) in the second blade drops from 24 to 17% as stored photosynthate is translocated to the developing basal blade (Dunton et al., 1982). In the subsequent two months, from late February to April, there is very little gain in plant wet weight (Figure 6) and little change in tissue density (Dunton et al., 1982). Yet the plant's carbon deficit continues to accrue as the percent carbon content of dry weight drops significantly ($p < 0.01$) by 3-4% in both blades. The carbon content is replenished between late April and early August. I suspect that this increase does not start until June, however, when breakup of the ice canopy begins. Elevated levels of carbon occur through the summer and fall. Such a distinct seasonal pattern in carbon content has not been noted before in kelp.

Little seasonal variation is reported for either L. longicuris (Mann, 1972) or Macrocystis pyrifera (Wheeler and North, 1981).

The presence of a fall or winter carbon deficit when irradiance is below the compensation point has also been shown for short periods in L. longicuris (Hatcher et al., 1977) and apparently in L. saccharina as well (Johnston et al., 1977). Hatcher et al. found carbon assimilation was negative in November and that stored carbon was needed to support the growth of L. longicuris from October to early January. In L. saccharina, the question of a winter carbon deficit is more complicated since Johnston et al. (1977) believed that the carbon requirements for growth and respiration were met by light plus dark (LICF) fixation. I find this difficult to accept for the same reasons outlined by Gagne et al. (1982). These include: (1) the Calvin cycle is the dominant pathway and the only light-dependent one for CO₂ fixation in the Phaeophyta (Kremer, 1981); and (2) a net gain of carbon by dark fixation is not possible without the input of energy; e.g., the glycolytic catabolism of reserve carbohydrate (Willenbrink et al., 1975; Kremer, 1981). This is the basis for the subtraction of the dark fixation rate from total net photosynthetic ¹⁴C uptake as originally prescribed by Steemann Nielsen (1952) -- but later questioned by Morris et al. (1971) before the pioneering work on LICF in brown algae had been completed by Akagawa et al. (1972).

If the correction for dark fixation is applied to the ¹⁴C light fixation rates for L. saccharina (Johnston et al., 1977), we

find that the respiratory requirement of the plant exceeds photosynthetic carbon assimilation for three months, from November to January. The dependence of L. saccharina on stored photosynthate during this period is not clear, since Johnston et al. indicate that most reserves are lost via distal frond erosion in October and November.

None of the Laminaria spp. studied to date appear to possess the traits necessary for sustained growth at light levels well below the compensation point for periods of six months or longer. For both L. solidungula and L. hyperborea, which are morphologically similar, this includes cessation of linear growth by early summer and storage of photosynthate as reflected in tissue densities of 24 to 27% (Luning, 1971; 1979; Dunton et al., 1982). While L. saccharina also occurs alongside L. solidungula in the Boulder Patch, it possesses a distinctly different pattern of growth that suggests an inability to use stored carbon reserves (Chapter 5). If such is the case, it has important implications with respect to the current controversy regarding the role of genetic and environmental factors in regulating growth of Laminaria.

Role of dark fixation

It is now generally accepted that translocation plays a vital role in the growth of Laminaria spp., for both the transport of

photosynthate to meristematic tissue during periods of rapid growth, and for the transport of stored materials for growth and metabolism when light is below the compensation point (Luning et al., 1973; Johnston et al., 1977; Hatcher et al., 1977).

Translocation is a common feature in the Laminariales, and all species studied so far possess a long-distance transport system in the medulla (Schmitz, 1982). The composition of the translocate consists of high amounts of both amino acids and mannitol (Luning et al., 1972).

In brown algae, the carboxylating enzyme of dark carbon assimilation is phosphoenolpyruvate carboxykinase (PEP-CK), yielding oxalacetate, aspartate and malate (Akagawa et al., 1972). The substrate of PEP-CK, phosphoenolpyruvate (PEP) is provided by an intermediate of the reductive pentose phosphate cycle in the light, and by glycolytic catabolism of reserve carbohydrate in the dark (Kremer, 1981). Several workers have shown that, relative to photosynthetic assimilation, the rates of dark fixation and PEP-CK activity in the young growing parts of the frond are four to five times greater than in older portions (Willenbrink et al., 1975; 1979; Koppers and Kremer, 1978). In L. solidungula, we found dark fixation rates only 10-20% higher in the meristematic region, but these rates were obtained during the period of slowest tissue production in L. solidungula. In all, dark fixation accounted for approximately 13% of the total carbon fixed in L. solidungula,

compared to 13 to 85% in L. hyperborea and 5 to 17% in L. saccharina (Kuppers and Kremer, 1978).

Kuppers and Kremer (1978) found that the absolute amounts of nitrogenous compounds were highest in meristematic tissue where maximum activities of PEP-CK and dark fixation were observed. In L. solidungula the highest N content and lowest C:N ratio occur in the basal blade between February and April (Figure 4). This corresponds to the period of rapid linear growth in L. solidungula and the occurrence of higher ambient inorganic nitrogen concentrations. But the higher concentrations of inorganic nitrogen ($3.3 \mu\text{g}\cdot\text{at l}^{-1}$) are not responsible for the higher internal nitrogen levels recorded in this plant. Chapman et al. (1978) found that an increase in external NO_3^- concentration from 0 to $3 \mu\text{g}\cdot\text{at l}^{-1}$ only raised the total N content 0.15% and changed the C/N ratio one integer in L. saccharina. Thus, L. solidungula appears to be actively concentrating its nitrogen reserves in the young basal blade. Such elevated concentrations of tissue N in actively growing regions of plant tissue have been noted before (Wheeler and North, 1981). The coincidence of a high nitrogen content in active meristematic tissue constantly supplied with reduced material, such as mannitol, suggests that LICF may account for the vigorous growth that results in a net carbon deficit in L. solidungula during the dark ice-covered months.

Carbon budget

Most, if not all, of the carbon required by L. solidungula to produce a new blade during the ice-covered period is derived from food reserves in the second blade. Actual gains in carbon content via photosynthesis do not occur until late spring or early summer. But net summer carbon production, as estimated by ^{14}C uptake experiments, nearly matches the net annual carbon gain of experimental plants grown in situ, leaving little left over for winter respiration between November and February (photosynthetic carbon fixation due to some light penetration of the ice canopy appears almost to offset respiratory requirements after February; see Figure 5). The carbon fixation rates reported here using ^{14}C uptake experiments (0.08 to $0.12 \mu\text{g C mg}^{-1}\text{hr}^{-1}$) are in good agreement with those found by Koppers and Kremer (1978) for L. hyperborea (0.08 to $0.2 \times 10^{-3} \mu\text{g C mg}^{-1}\text{hr}^{-1}$). For L. saccharina, fixation rates ranging from 0.2 to $0.8 \mu\text{g C mg}^{-1}\text{hr}^{-1}$ have been reported (Johnston and Cook, 1968; Johnston et al., 1977; Koppers and Kremer, 1978).

Underestimation of the number of hours available for summer photosynthesis probably accounts for most of the missing carbon needed to satisfy winter respiratory requirements. The number of hours used to calculate summer productivity in Table 4 is estimated for arctic phytoplankton (Schell et al., 1984) which are light saturated at about $200 \mu\text{E m}^{-2}\text{s}^{-1}$ (Platt et al., 1980). In

contrast, L. solidungula appears to be light saturated at much lower levels, about $40\text{-}60 \mu\text{E m}^{-2}\text{s}^{-1}$ (Chapman and Lindley, 1980). For comparison, light saturation in L. saccharina off the coast of Scotland is about $120 \mu\text{E m}^{-2}\text{s}^{-1}$ (Johnston et al., 1977), $80 \mu\text{E m}^{-2}\text{s}^{-1}$ for L. hyperborea in the North Sea (Willenbrink et al., 1975), and about $40 \mu\text{E m}^{-2}\text{s}^{-1}$ in the giant kelp Macrocystis integrifolia and Nereocystis leutkeana off British Columbia (Willenbrink et al., 1979). In the Boulder Patch, the lowest mean hourly irradiances recorded daily in early to mid-August were $40 \mu\text{E m}^{-2}\text{s}^{-1}$ (Table 3). This indicates L. solidungula was light saturated nearly 24 hours a day, although Schell et al. (1984) report only 20 photosynthetically useful hours per day in August. In September, only fifteen 12-hour days are budgeted, although open water persists for nearly the whole month, and sometimes into October. If these hours are taken into account, the carbon available for winter respiration is increased considerably.

In contrast to the carbon budgets constructed for L. longicruris (Hatcher et al., 1977) and L. saccharina (Johnston et al., 1977), L. solidungula does not possess an assimilatory surplus during a major portion of the year. Whereas both Hatcher and Johnston searched for an additional carbon sink to account for a carbon surplus for each species (about 25-35% of net annual productivity), no such dilemma occurs in the case of L. solidungula. The release of dissolved organic matter by this plant must amount to a very small percentage of the total carbon fixed.

In summary, the ability of L. solidungula to reallocate carbon reserves to survive over eight months of continuous darkness annually, and yet still replace 80% of its carbon content, should qualify it for a phycological commendation. In the next chapter I will discuss how the pattern of growth in L. solidungula differs from L. saccharina under the same conditions in the Boulder Patch.

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CHAPTER 5. GROWTH OF DARK-EXPOSED LAMINARIA SACCHARINA AND L. SOLIDUNGULA (LAMINARIALES, PHAEOPHYTA) IN THE ALASKAN BEAUFORT SEA

SUMMARY

Linear growth of Laminaria saccharina sporophytes exposed for nine months of darkness under a turbid ice canopy was compared to that of L. solidungula for a two-year period in the Alaskan Beaufort Sea. Peak growth in L. solidungula (1.4 mm day^{-1}) occurred between late February and late April. During the dark period, from November to late April, linear growth was 1.5 to 8 times greater than that of L. saccharina. In contrast, L. saccharina completed nearly all of its annual growth between late April and late July, when light penetrates the water column as a result of breakup of the ice canopy. Average elongation rate during the period of rapid growth, which started four to five months later than plants found at temperate latitudes, was 4.7 mm day^{-1} . The seasonal pattern of linear growth in the two species differs because L. saccharina depends on light for winter and spring growth, while L. solidungula utilizes stored carbon reserves during the same period. The delay of growth in the ubiquitous L. saccharina to late spring reflects a different growth strategy than that found in L. solidungula, and indicates the ability of L. saccharina to survive in the Arctic without a fundamental change in its genome.

INTRODUCTION

There are few published accounts on the growth of kelp in arctic regions. Growth and productivity measurements are reported only for Laminaria solidungula J. Agardh (Chapman and Lindley, 1980, 1981; Dunton et al., 1982; Dunton 1984), an alga restricted primarily to arctic and subarctic waters. The growth of L. saccharina (L.) Lamour. in the Arctic has not been reported, although this ubiquitous alga occurs throughout the Arctic and is often found both interspersed with L. solidungula and in pure stands at several locations in the Alaskan Beaufort Sea (Dunton et al., 1982).

Perhaps the most compelling reason to study the pattern of growth of Laminaria saccharina in the Alaskan Beaufort Sea is to examine its response to long periods of complete darkness caused by a turbid ice canopy. In an area known as the Boulder Patch in the Beaufort Sea, a three-year study of L. solidungula showed that the plant depended heavily on stored food reserves to complete over 90% of its annual linear growth during eight to nine months of complete darkness (Dunton et al., 1982). It is unknown whether L. saccharina also depends on stored food reserves for winter growth in areas characterized by continuous darkness (such as the Boulder Patch). Johnston et al. (1977) concluded that L. saccharina did not depend on stored materials for growth, since these reserves

were lost by distal blade erosion during autumn storms prior to the period of rapid growth.

There is also disagreement concerning the mechanisms responsible for the observed seasonality of growth in laminarian species. Luning (1979) believes that differences in the seasonal growth pattern among Laminaria species are genetically determined for the most part, while Chapman and Craigie (1977) believe that environmental factors, such as the seasonal availability of nutrients or light, play the dominant role. In this study, I examined seasonal growth rates of L. saccharina and L. solidungula over a two-year period in the Alaskan Beaufort Sea. In both years, the plants were exposed to nearly nine months of continuous darkness caused by the presence of a turbid ice canopy. This permitted a comparison of linear growth in both species under identical seasonal conditions of light and nutrient limitation.

MATERIALS AND METHODS

Study site

Field studies were conducted at an established study site, dive site 11 (DS-11; 70°19.25'N, 147°35.1'W), on the eastern side of the Boulder Patch in Stefansson Sound, Alaska (Fig. 1). The Boulder Patch is an area of cobbles and small boulders (generally less than 1 m in diameter) that covers approximately 20 square

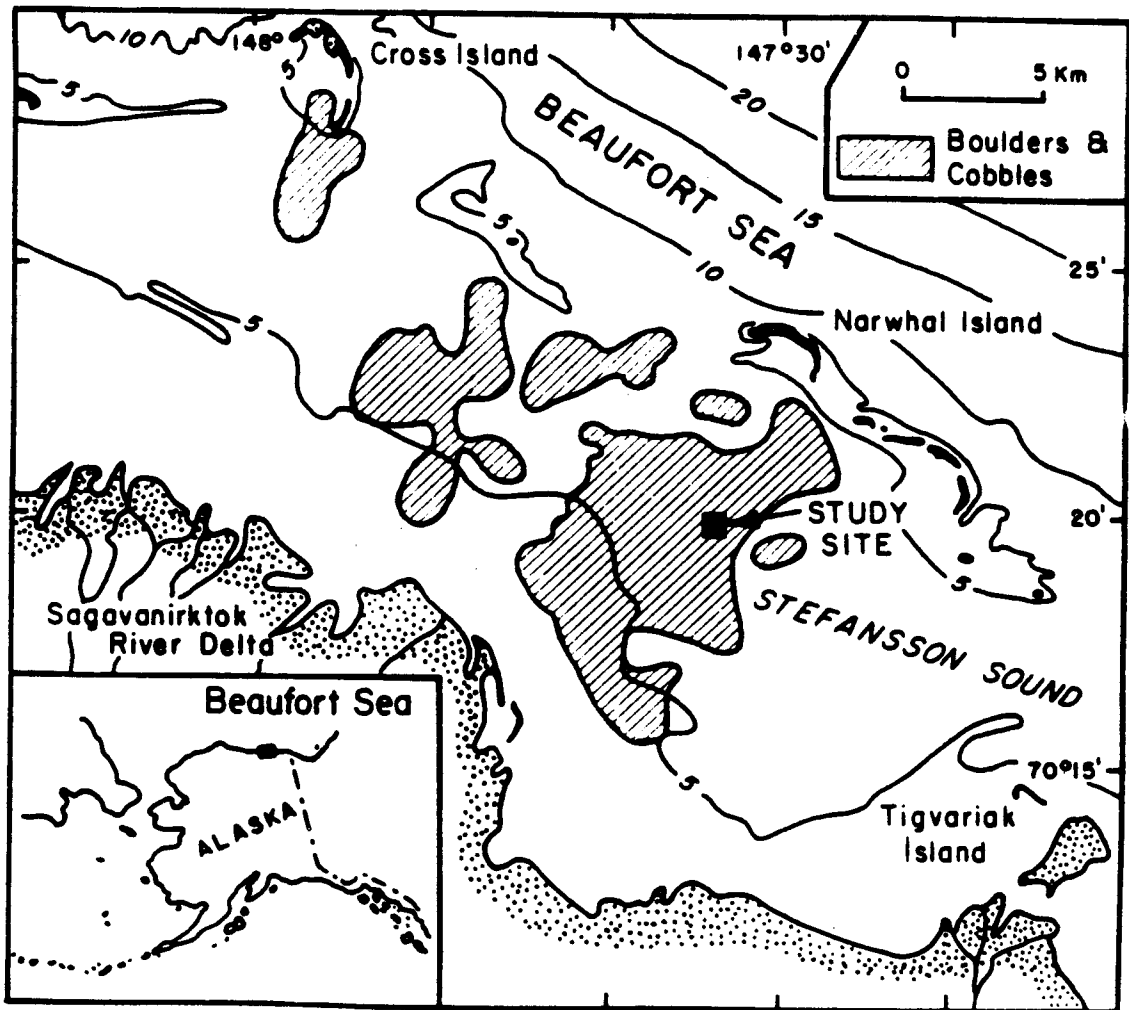


Figure 1. Location of the study site in Stefansson Sound, Alaska.

kilometers of seabed. The Boulder Patch is a unique feature of the Alaskan Beaufort Sea shelf, which is otherwise characterized by fine-grained sediments of silty sands or mud. The rocks provide a substrate for a diverse assortment of invertebrates and several species of algae (Dunton et al., 1982). The predominant brown alga is Laminaria solidungula, which constitutes over 90% of the brown algal biomass.

Water depth at DS-11 ranges from 6 to 7 meters. Freezup is usually complete by mid-October, and breakup begins in late June or early July. Bottom water temperatures at DS-11 range from a nearly constant -1.8°C under the ice canopy to 7°C during the summer open-water period. Salinity ranges from 14 ‰ in summer to 35 ‰ in winter (Barnes et al., 1977). Divers entered the water through holes cut in the ice using augers and ice chisels during ice-covered periods. In situ linear growth measurements were made at approximately three-month intervals by a team of divers between July 1979 and July 1981.

During the period that growth measurements were collected, the ice canopy contained large amounts of sediment (incorporated during ice formation in October) which blocked light transmission completely, even during periods of 24-hour daylight. Photon flux density on the bottom of DS-11 under this "turbid ice" was less than $0.05 \mu\text{E s}^{-1}\text{m}^{-2}$ (Dunton et al., 1982). Thus, plants at DS-11 were exposed to complete darkness for nearly nine months annually,

and turbid ice appears to be a widespread and frequent occurrence in Stefansson Sound (Dunton, 1984).

Field studies

Thirteen mature, healthy individuals (30-90 cm long) of Laminaria saccharina were collected by divers for the growth experiment, tagged and then attached to a roll of 1 cm mesh plastic net anchored to the seafloor. Holdfasts were attached to the net using small plastic cable ties. Within six months, the algal holdfasts had become firmly attached to the plastic mesh by outgrowths from old haptera as well as by new haptera. Due to the extremely low abundance of L. saccharina at the study site, it was not possible to collect plants for stored carbon tissue analyses.

Laminaria solidungula plants were tagged in place, and linear growth was followed by punching holes in the base of the blade, above the meristematic region (Dunton et al., 1982). Holes were punched in L. saccharina at both 5 and 10 cm above the junction of lamina and stipe. The similar morphology of both species allowed accurate measurement and comparison of linear growth. The lamina is divided into distinct segments of different sizes by constrictions that are produced annually. The constriction appears as a taper in blade width in L. saccharina, but it is more pronounced in L. solidungula, resulting in distinct ovoid-oblong blade segments. In both species, the constrictions form during

November, a period of extremely slow growth. These constrictions have formed annually in all plants examined without exception. The growth of a new basal blade starts in November and continues until the following November, allowing an accurate measurement of the plant's annual production at any time during the year. Annual growth was also measured by determining blade segment lengths. Comparisons of the two methods (measurement of hole movement versus blade segment length) yielded differences no greater than ± 1 cm. Inorganic nitrogen (nitrate and nitrite) was measured in water samples collected 1 to 3 meters above the seafloor near DS-11 using the automated technique of Strickland and Parsons (1972).

RESULTS

Linear growth

Linear growth in Laminaria solidungula in the Boulder Patch was similar to rates previously reported by Dunton et al. (1982) between August 1978 and November 1980. Figure 2 shows the results of growth measurements taken from November 1979 to July 1981. L. solidungula exhibited the lowest rate of linear growth (0.25 mm day^{-1}) in 1980 during the ice-free period from July to November. Maximum growth rates in 1980 were recorded between February and April (1.41 mm day^{-1}). L. saccharina exhibited the lowest rate of linear growth between November 1979 and February 1980 (0.12 mm day^{-1}). The highest growth rate

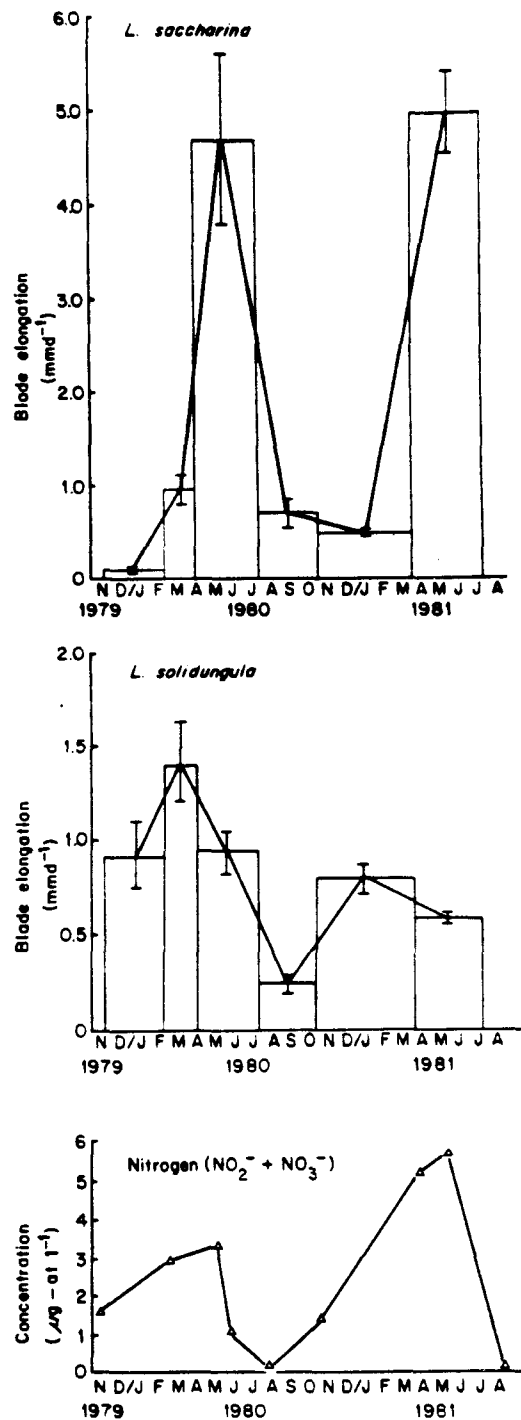


Figure 2. Linear growth rate (mean \pm 95% confidence limits) in L. saccharina and L. solidungula related to ambient inorganic nitrogen concentrations. Plants are exposed to complete darkness from approximately mid-October to mid-June.

occurred between late April and late July 1980 (4.69 mm day^{-1}). Similar results were obtained for 1981, but the periods of maximum and minimum growth are not as well defined because of one less visit to the study site. Since the turbid ice canopy in Stefansson Sound prevented penetration of light from October to June, L. solidungula completed most of its annual linear growth in absolute darkness. In contrast, L. saccharina completed much of its growth during the period when light starts to penetrate the ice canopy as a result of breakup in June.

Concentrations of inorganic nitrogen in the form of NO_2^- and NO_3^- in the seawater are shown beneath the growth curves for both species of Laminaria in Figure 2. The concentrations of inorganic nitrogen follow an annual cycle typical of arctic (Chapman and Lindley, 1980) and temperate waters (Chapman and Craigie, 1977; Wheeler and North, 1981), and are shown here for the period between November 1979 and August 1981. Levels of inorganic-N are lowest in summer (less than $0.1 \mu\text{g-at l}^{-1}$), increase through the fall and winter months, and peak in late May (3.31 to $5.7 \mu\text{g-at l}^{-1}$). Periods of highest linear growth in both L. solidungula and L. saccharina occur during higher concentrations of inorganic nitrogen. A similar pattern between growth and nitrogen availability has also been documented for L. solidungula in the Canadian High Arctic by Chapman and Lindley (1980) and observed previously by Dunton et al. (1982) for this species in the Boulder Patch.

DISCUSSION

Contrary to Laminaria solidungula, the period of rapid growth in L. saccharina occurs between late April and late July. This period is characterized by a peak in inorganic-N concentrations during late May and the start of breakup in June. Breakup lasts from about mid-June to early July, and during this time increasing amounts of light reach the seafloor as the turbid ice canopy deteriorates. Specimens of L. saccharina did produce a small new blade segment during the dark winter period, but little linear growth occurred between November and late April. In contrast, L. solidungula completes most of its linear growth between November and late April, with peak growth occurring between February and late April. From May onward, linear growth slows dramatically. In fact, daily growth rates recorded in the same plants from late May to late July (Dunton et al., 1982) are less than half that of the period from February to April, even in plants exposed to light beneath the ice canopy from February into spring and summer (Dunton, 1984).

The period of rapid growth in Laminaria saccharina in the Boulder Patch starts four to five months later than in temperate regions due to the darkness caused by the turbid ice canopy. Parke (1948) found that linear growth in L. saccharina on the Devon and Argyll coasts of Great Britain was greatest from February to June. Working in a Scottish sea loch, Johnston et al. (1977) noted marked linear growth from February to April, sometimes extending to June. On the northeastern coast of the

United States, Brady-Campbell et al. (1984) found that rapid growth in L. saccharina began in January and reached a maximum of 2 cm day⁻¹ by late May. In St. Margaret's Bay, Nova Scotia, growth in L. longicruris -- a species thought to be conspecific with L. saccharina (Chapman, 1974; Kain, 1979) -- begins to accelerate between December and January, and reaches a level roughly twice the minimal rate before reaching its annual maximum in June (Mann, 1972; Chapman and Craigie, 1977; Gagne et al., 1982). In every case, elongation rates begin to decline by July, with minimal growth from September to December. I found the decline in linear growth rate in L. saccharina begins by late July or early August, with minimal growth occurring from November to late April.

Unfortunately, I cannot provide conclusive evidence that most of the annual linear growth in Laminaria saccharina occurs after breakup in June, when light is available. From about mid-May to July, it is nearly impossible to conduct safe diving operations, either from vessels or from the deteriorating broken ice canopy. Nonetheless, there is a conspicuous delay in rapid linear growth in L. saccharina until the open water period. I attribute this delay to the species' inability to use stored carbon reserves for appreciable winter growth during most, if not all, of the ice-covered period. Although present in the frond, carbon reserves have not been shown to be important for growth in populations of L. saccharina and L. longicruris from January on since photosynthetic carbon fixation matches or exceeds the carbon demand for growth (Hatcher et al., 1977; Johnston et al., 1977). In addition, both Johnston et al.

and Brady-Campbell et al. (1984) found significant loss of distal frond tissue during the autumn and early winter months. This blade loss may considerably limit the amount of carbon available for winter growth. In the Boulder Patch, L. saccharina suffers a similar blade loss.

The long linear frond produced by Laminaria saccharina in late spring and early summer is particularly susceptible to erosion -- more so than the fronds of L. solidungula. These ovate blades are considerably thicker and usually lie close to the seafloor where current velocities are slower. Also, the highest concentrations of stored carbon reserves in L. solidungula are not located throughout the frond or in the distal tissue as in L. saccharina (Johnston et al., 1977), but in the basal blade segment of a multisegmented frond.

A strong contrast is apparent in the seasonal growth patterns of these two species. The adaptation made by L. solidungula guarantees maximum linear growth during a period of favorable nutrient (inorganic-N) availability. Winter and early spring linear growth in dark-exposed L. solidungula plants also allows them almost to double their photosynthetic potential when light first becomes available in June during breakup. Moreover, if turbid ice is absent, light penetrates the ice canopy during winter and early spring, and linear growth increases significantly, by up to 60% (Dunton, 1984).

The strategy employed by Laminaria saccharina, of rapid growth during a period of light and nutrient availability, is not

different from its growth pattern in temperate systems. If, however, the onset of rapid linear growth in L. saccharina begins at ice breakup in mid-June as hypothesized, it coincides with plummeting inorganic-N concentrations. In the Boulder Patch, L. saccharina occurs infrequently. Plants are seldom more than 1.5 m in length, but small isolated populations of large (1-3 m long) healthy individuals can be found in quiet, more sheltered waters where turbid ice is least likely to occur (Dunton et al., 1982). In these areas, the kelp probably grows most rapidly between February and June, as conspecifics in temperate regions.

In contrast to Laminaria solidungula, L. saccharina is not optimally adapted to long periods of poor light conditions typical of arctic environments. Most linear growth appears to be delayed until light is available for photosynthesis, regardless of nutrient concentrations. This supports the hypothesis that the strategy of growth and the pattern of carbon allocation in Laminaria may be genetically determined (Luning, 1979; Gagne et al., 1982). If so, genotypic restrictions in L. saccharina explain the lack of a significant change of growth strategy in response to extended dark periods. In the following chapter I will address the importance of kelp carbon produced by Laminaria spp. in the Boulder Patch to the resident benthic fauna.

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CHAPTER 6. DEPENDENCE OF CONSUMERS ON MACROALGAL (LAMINARIA
SOLIDUNGULA) CARBON IN AN ARCTIC KELP COMMUNITY: $\delta^{13}\text{C}$
EVIDENCE

SUMMARY

Stable carbon isotope measurements ($\delta^{13}\text{C}$) were used to assess the importance of kelp carbon (-15 to -16 ‰) versus phytoplankton carbon (-25 to -26 ‰) to resident fauna of an isolated kelp bed community on Alaska's north arctic coast. The predominant kelp, Laminaria solidungula, showed some seasonal variation in $\delta^{13}\text{C}$ which was correlated with changes in the carbon content of the tissue. Animals that showed the greatest assimilation of kelp carbon (>50%) included macroalgal herbivores (gastropods and chitons, -16.7 to -18.1 ‰), a nonselective suspension feeder (an ascidian, -18.8 ‰) and a deposit feeding polychaete (-17.3 ‰). Animals that showed the least incorporation of kelp carbon into body tissues (<7%) included selective suspension feeders (bryozoans, hydroids and soft corals, -22.6 to -23.8 ‰). Sponges, gastropod omnivores and crustaceans exhibited an intermediate dependence on kelp carbon (25 to 40%). Within some taxonomic groups, species exhibited a broad range in isotopic composition which was related to differences in feeding strategies. In the polychaete group alone, $\delta^{13}\text{C}$ values identified four major feeding habits: deposit feeders (-17.3 ‰), omnivores

(-20.3 ‰), predators (-22.0 ‰) and microalgal herbivores (-22.9 ‰). Distinct seasonal changes in the $\delta^{13}\text{C}$ values of several animals indicated an increased dependence on kelp carbon during the dark winter period when phytoplankton was absent. Up to 40% of the body carbon of mysids and euphausiids, which are key prey species for birds, fish and marine mammals, was composed of carbon derived from kelp detritus during the ice covered period.

INTRODUCTION

Kelp beds dominate rocky shores throughout the world, from the tip of South Africa (Dieckmann, 1980) to the High Arctic (Chapman and Lindley, 1981; Dunton et al., 1982). Their productivity per unit area is often an order of magnitude higher than that of the surrounding phytoplankton in the adjacent water column (Mann, 1973), with most of this production released as dissolved or particulate matter into the environment (Johnston et al., 1977; Newell et al., 1982). On this basis they are thought to be an important dietary carbon source for many benthic and epibenthic animals (in addition to the macroalgal herbivores) via detrital food chains (Mann, 1975; Newell, 1984).

It has been difficult, however, to provide quantitative information on the dependence of various benthic consumers on the fragmented and partially decomposed kelp material, or the dissolved components which result from leaching and decomposition of the fronds. Examination of animal gut contents is tedious and difficult, and especially hard in suspension feeders that lack a digestive tract, such as sponges and hydroids. Evidence for the utilization of kelp detritus in field collected animals is scarce, although one set of laboratory studies has shown that a benthic filter feeding bivalve is capable of absorbing kelp detritus (Stuart et al., 1982a). Other laboratory studies have revealed that macroalgal detritus is more rapidly assimilated over other

more decay-resistant macrophytes (e.g., the marshgrass Spartina, and Capitella capitata (Tenore, 1977a; 1977b; 1981). Field and laboratory investigations have also addressed the potential nutritional value of kelp detritus and the conversion efficiency of kelp detritus to bacterial biomass (Newell et al., 1980; Lucas et al., 1981; Newell et al., 1982; Stuart et al., 1982b; Robinson et al., 1982b; Newell and Field, 1983). No information is available, however, on the relative amount of kelp carbon assimilated by various invertebrate consumers compared to other carbon sources, such as phytoplankton in a natural ecologic setting.

In recent years, questions of this nature have been addressed by using naturally occurring stable carbon ratios ($^{13}\text{C}/^{12}\text{C}$ or $\delta^{13}\text{C}$), which enables tracing of plant carbon sources to the consumer level (Incze et al., 1982; Stephenson and Lyon, 1982). Through $\delta^{13}\text{C}$ analyses of aquatic flora and fauna, the technique has provided valuable insights into the structure and dynamics of marine and freshwater food webs (reviewed by Fry and Sherr, 1984). Although $^{13}\text{C}/^{12}\text{C}$ ratios have not been used to track carbon flow in kelp beds, the methodology has been applied to salt marshes (Haines, 1976a, b, 1977; Hackney and Haines, 1980; Fry, 1984a) and seagrass meadows (Fry and Parker, 1979; McConnaughey and McRoy, 1979a; Fry et al., 1982, 1983; Fry, 1984b) in attempts to allocate the major carbon source importances to various invertebrate and vertebrate consumers.

While this technique has been used successfully in many food web studies, its application to delineating the importance of different carbon sources to benthic consumers is complicated by two major factors: (1) the presence of multiple carbon sources and (2) overlap in the $\delta^{13}\text{C}$ values of the different carbon sources. Nearshore food webs generally receive a variety of carbon inputs as macrophyte detritus -- these include material from terrestrial, salt marsh, seagrass and marine littoral habitats (Schwinghamer et al., 1983; Simenstad and Wissmar, 1985). This prevented clear assessment of the role of macroalgae in seagrass meadows studied in Alaska (McConnaughey and McRoy, 1979a), Washington (Simenstad and Wissman, 1985), Florida (Fry, 1984b), the Caribbean (Fry et al., 1982) and northern Australia (Fry et al., 1983). Similarly, the presence of multiple carbon sources in Georgia and Mississippi estuaries has presented difficulties in interpreting the role of marsh plant detritus as a food source for resident animals (Haines and Montague, 1979; Hackney and Haines, 1980; Hughes and Sherr, 1983). In recognition of these limitations, other food web studies have focused on the combined use of the stable isotopes of sulfur, carbon, hydrogen, or nitrogen (Macko et al., 1983b; Peterson et al., 1985) and dual carbon (^{13}C and ^{14}C) natural isotopic abundances (Schell, 1983) to distinguish between multiple food sources.

Food webs that are less complex in respect to their carbon inputs enable more accurate resolution of the relative dependence

of consumers on the available food sources. By combining isotopic data with data on the magnitude of the carbon inputs and the feeding behavior of various organisms, Kitting et al. (1984) documented the importance of epiphytic algae to invertebrates in a Texas seagrass meadow, and Suchanek et al. (1985) assessed the importance of seagrass detritus to Caribbean deep sea macrofauna. Clearly, the success of any single tracer isotopic study involving nearshore food webs, known for their spatial and temporal variability in multiple carbon inputs (Simenstad and Wissmar, 1985), will depend on verifying the existence of a two-carbon source dominated system.

In this context, the discovery of an isolated kelp community on Alaska's north Arctic coast is fortuitous (Dunton et al., 1982). Known as the Boulder Patch, the presence of large numbers of cobbles and boulders on the seabed provide a substrate for a diverse assortment of invertebrates and several species of algae, including the predominant brown alga Laminaria solidungula, which constitutes over 90% of the brown algal biomass (Dunton et al., 1982). The Boulder Patch covers approximately 20 km² of seabed and is a unique feature of the Alaskan Beaufort Sea shelf, which is otherwise characterized by fine-grained sediments of silty sands and muds (Barnes and Reimnitz, 1974). Although scattered macroalgae are found on attached pebbles and gravel at Pt. Barrow, about 375 km to the west (Mohr et al., 1957), assemblages of kelp and epilithic invertebrates similar to those of the Boulder Patch

probably occur no closer than the Canadian archipelago, about 1,000 km to the east (R.T. Wilce, pers. comm.).

Because of the isolation of the Boulder Patch and its occurrence in an ocean characterized by nearly nine months of ice cover, the sources and magnitudes of carbon inputs are limited. The carbon budget constructed by Dunton (1984) for this community, showed that virtually all of the carbon available to consumers consists of nearly equivalent inputs of kelp and phytoplankton. Terrestrial inputs of peat carbon, identified by their distinct depressions in ^{14}C activity, are not assimilated by arctic marine fauna which exhibit modern ^{14}C activities (Schell, 1983). The Boulder Patch appeared, therefore, to be an ideal community in which to assess the role of kelp carbon versus phytoplankton carbon to resident fauna using the $\delta^{13}\text{C}$ methodology.

MATERIALS AND METHODS

Field collections

Samples were collected using Scuba from site DS-11 near the center of the Boulder Patch in Stefansson Sound from 1979 to 1983 (Fig. 1). In addition, I obtained samples at site BF-37 on the western fringe of the Boulder Patch (Fig. 1), and distant from the Boulder Patch, at site PB, about 30 km west of DS-11 in Stefansson

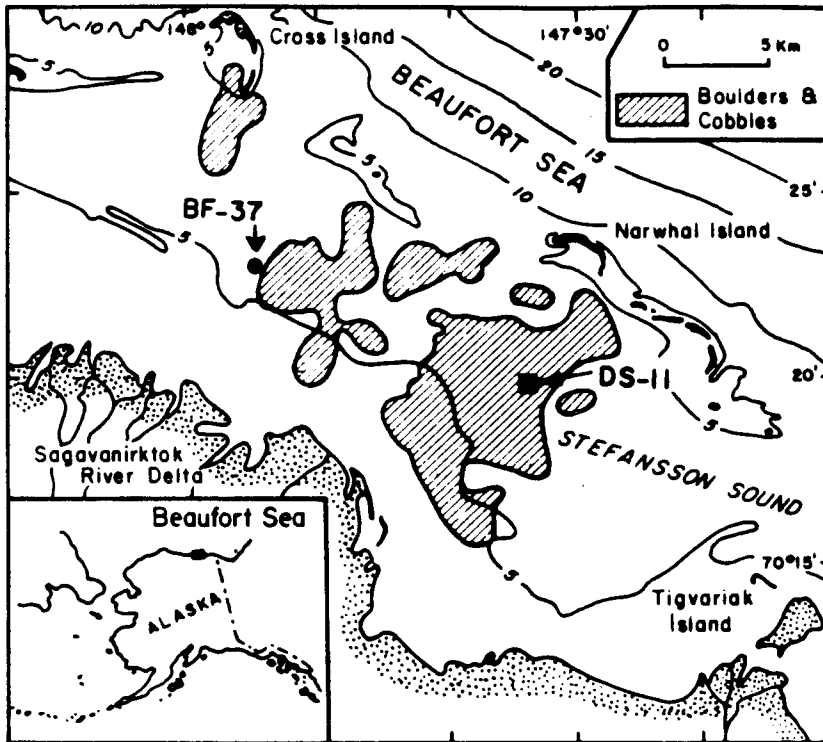


Figure 1. Location of study sites in the Boulder Patch.

Sound. All organisms were collected in water depths ranging between 3 and 6 m.

In the field, invertebrates were washed of debris and generally held alive for several hours to clear their guts before being dried in aluminum dishes. Some animals for $\delta^{13}\text{C}$ analysis were obtained from quantitative samples used to provide data on animal abundance (Dunton et al., 1982). These samples were preserved in formalin. All samples were subsequently soaked in 1 N HCl for 4-6 hours (or until bubbling stopped) to remove carbonates, rinsed in distilled water, and then dried at 50°C. The procedure was the same for preserved specimens, except they were submerged in distilled water for 24 hours to leach formalin from body tissues (Mullin et al., 1984) following the HCl bath.

In many instances, small individuals of the same species collected at one time were pooled into one sample to obtain sufficient material for isotopic analysis. These composites consisted of at least three individuals and included several polychaete and crustacean species. The $\delta^{13}\text{C}$ values of formalin-treated animals were not compared to the values of dried specimens, because leaching may not remove all isotopically light formalin that is bound in animal tissue.

For Laminaria solidungula, I removed the entire blade segments from two plants collected on each of five seasonal visits to DS-11 from November 1979 to November 1980. The frond of L. solidungula is divided into distinct ovate blades of different sizes by

constrictions that form annually (Fig. 2). The growth of a new basal blade starts in November and continues until the following November. I analyzed only the two lowermost blade segments, representing present and previous years' growth (Dunton et al., 1982), and the distal blade segment. Small discs of tissue (2 cm diameter) were also removed at different locations along the frond of two other plants to examine small scale spatial variation in isotopic abundance. The individual blade segments and discs were then ground to a fine powder. An average $\delta^{13}\text{C}$ value of L. solidungula fronds was estimated from the ground tissue of approximately 25 plants collected in summer.

Isotopic analyses

Subsamples of each organism (8-10 mg) were manually ground in the presence of copper oxide and individually combusted in evacuated sealed borosilicate glass tubes at 590°C for two hours. After combustion, the tube was placed on a vacuum line and cracked using a Cajon flexible stainless steel tube fitting (Des Marais and Hayes, 1976). The carbon dioxide gas resulting from the combustion was isolated and purified cryogenically using a -50°C alcohol bath and liquid nitrogen. Isotope measurements were performed on a SIRA 9 dual inlet, triple collector isotope ratio mass spectrometer. Results are expressed as $\delta^{13}\text{C}$ values relative to the limestone standard PDB (Craig, 1957) where

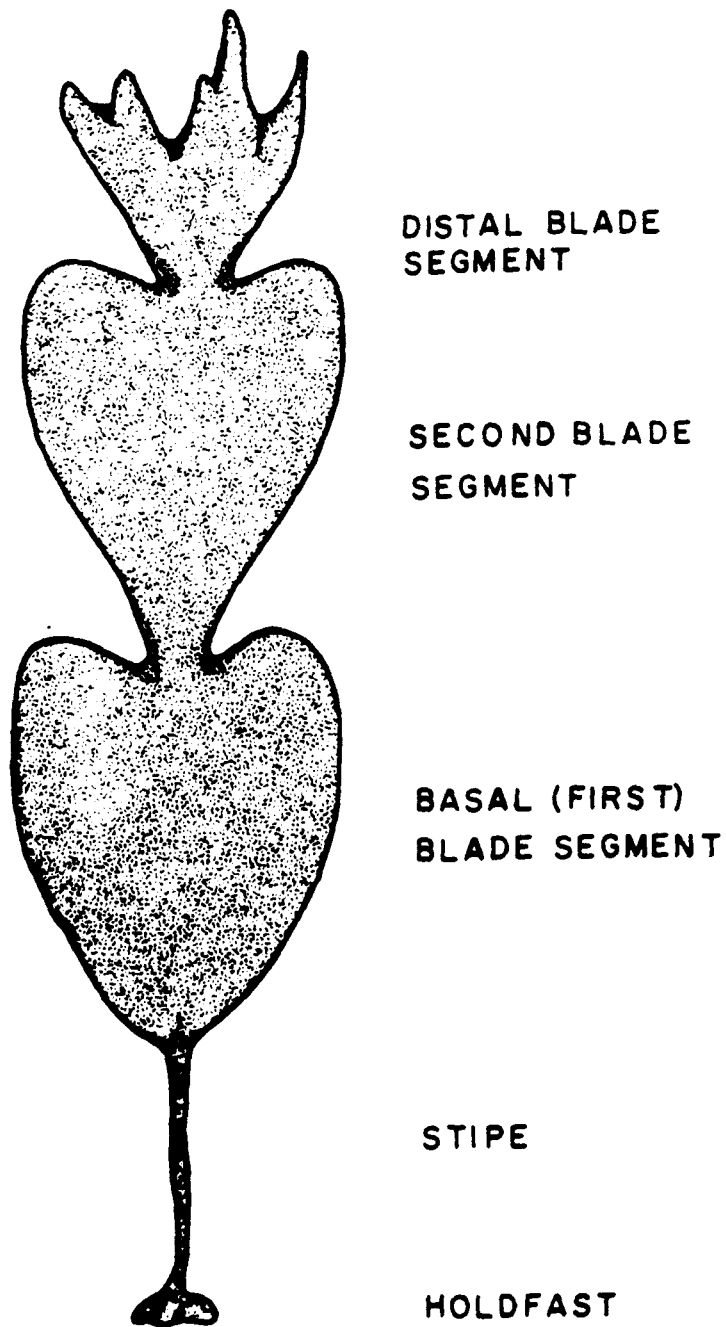


Figure 2. Schematic drawing of a specimen of Laminaria solidungula collected from the Boulder Patch. Each blade segment represents one year of growth.

$$\delta^{13}\text{C} = \left\{ \left[\frac{(^{13}\text{C}/^{12}\text{C})_{\text{sample}}}{(^{13}\text{C}/^{12}\text{C})_{\text{standard}}} \right] - 1 \right\} \times 10^3$$

Results were corrected for ^{17}O contributions and were consistent with replicate samples analyzed separately by Coastal Science Laboratories, Inc., within ± 0.2 ‰ in nearly all cases. My results were usually reproducible to within ± 0.3 ‰.

RESULTS

Isotopic composition of *Laminaria solidungula*

The $\delta^{13}\text{C}$ values of entire blade segments from *L. solidungula* plants collected at different times ranged from -13.4 to -16.3 ‰ (Table 1). I found distinct seasonal variations in the mean $\delta^{13}\text{C}$ value for the basal blade segment, which was isotopically lightest in April (-16.3 ‰) and heaviest in November (-13.4 ‰). A less distinctive, but similar seasonal trend was apparent in the second blade, but not in the distal blade segment. The second and distal blade segments also exhibited higher plant-to-plant isotopic variability. This increased variability was reflected in the standard deviations of the mean, which was ± 0.1 in blade one, and not less than ± 0.2 in the second and distal blade segments. No distinct spatial trend in the isotopic composition of the blade segments was apparent.

TABLE 1. Laminaria solidungula. Seasonal variation in $\delta^{13}\text{C}$ values ($^{\circ}/_{\text{oo}}$) of first, second and distal blade segments of plants collected seasonally at DS-11. Values are $x \pm \text{SD}(n=2)$.

Month	Blade 1	Blade 2	Distal Blade
November 1979	*	-14.6 \pm 0.2	-16.0 \pm 0.8
February 1980	-15.3 \pm 0.1	-14.8 \pm 0.6	-15.8 \pm 0.3
April 1980	-16.3 \pm 0.1	-15.5 \pm 0.3	-15.3 \pm 0.7
August 1980	-15.2 \pm 0.1	-15.4 \pm 1.2	-15.0 \pm 1.6
November 1980	-13.4 \pm 0.1	-15.2 \pm 0.5	-15.3 \pm 0.8

* Growth of the basal blade begins.

Most $\delta^{13}\text{C}$ values for frond tissue ranged between -15 and -16 ‰ (Table 1). The measured mean for 25 plants (minus stipes and holdfasts) was -15.1 ‰ (two replicate determinations). Small 2-cm discs of tissue removed from individual blades of two plants showed isotopic differences of 1.3 to 2.5‰ within a single frond. The $\delta^{13}\text{C}$ values of these discs (Appendix D) generally fell within the range of values reported in Table 1. These data demonstrate that small scale isotopic heterogeneity that exists in the frond, as previously shown in L. longicruris by Stephenson et al. (1984).

$^{13}\text{C}:^{12}\text{C}$ ratios of fauna

The distribution of $\delta^{13}\text{C}$ values of fauna collected at site DS-11 in the Boulder Patch, relative to the two plant carbon sources, is shown in Figure 3. Animal $\delta^{13}\text{C}$ values ranged from -15.3 ‰ for one specimen of a macroalgal herbivore, the gastropod Margarites vorticifera, to -25.9 ‰ for a suspension feeder, the bryozoan Eucrates loricata (Appendix E). These $\delta^{13}\text{C}$ values closely approximate the isotopic composition of two major carbon sources, kelp (-13.4 to -16.3 ‰) and phytoplankton (-25 to -26 ‰; see Chapter 7). A high scatter of $\delta^{13}\text{C}$ values among individuals (e.g., Nereis zonata) indicates a diet of high diversity; little scatter in $\delta^{13}\text{C}$ values (e.g., Spinther alaskensis) indicate an isotopic similarity of diets among the

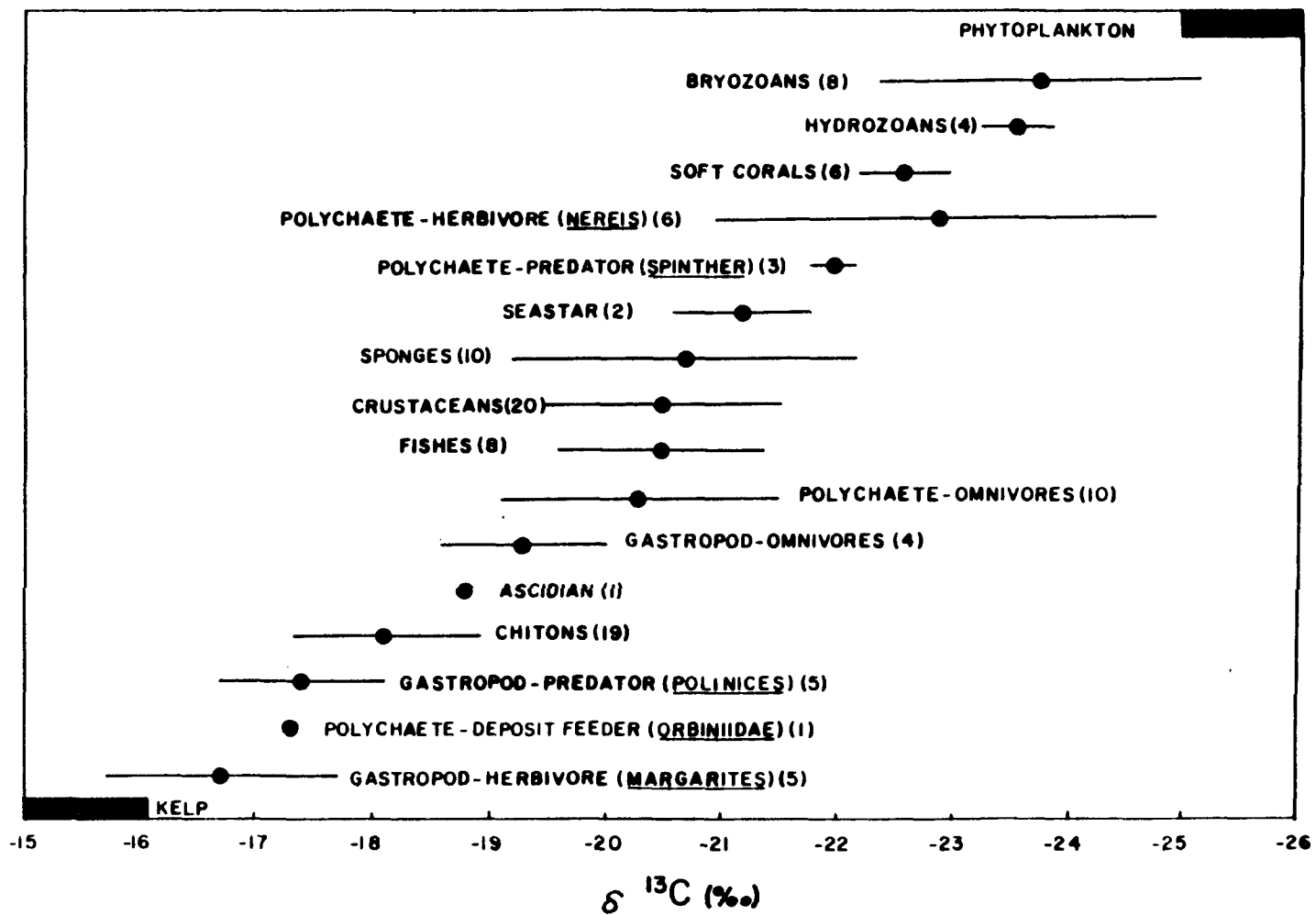


Figure 3. $\delta^{13}\text{C}$ values of Boulder Patch fauna and flora (dried specimens only) collected at site DS-11. Values are $\bar{x} \pm \text{SD}(n)$.

TABLE 2. $\delta^{13}\text{C}$ values ($^{\circ}/\text{oo}$) of fauna (dried specimens only) collected in the Boulder Patch at site DS-11. Values are $x \pm \text{SD}(n)$.

Organism	$\delta^{13}\text{C}$
PORIFERA (sponges)	
<u>Choanites lutkenii</u>	-19.5 \pm 0.7(3)
<u>Haliclona gracilis</u>	-22.4 \pm 1.4(2)
<u>Halichondria panicea</u>	-21.1 \pm 0.7(2)
<u>Phakettia cribrosa</u>	-20.4 \pm 1.7(3)
CNIDARIA	
<u>Sertularia cupressoides</u> (hydroid)	-23.7 \pm 0.2(3)
<u>Thuiaria</u> sp. (hydroid)	-23.3(1)
<u>Gersemia rubiformis</u> (soft coral)	-22.6 \pm 0.4(6)
<u>Lucernaria infundibulum</u> (sessile Schyphozoan)	-19.3 \pm 1.0(3)
NEMERTEA	
<u>Cerebratulus</u> sp.	-18.5(1)
ANNELIDA (polychaetes)	
<u>Antinoella sarsi</u>	-20.8(1)
<u>Brada sachalina</u> ^C	-19.5(1)
<u>Cirratulus cirratus</u> ^C	-21.6 \pm 0.9(2)
<u>Flabelligera affinis</u> ^C	-19.7 \pm 1.3(2)
<u>Harmothoe imbricata</u>	-20.6 \pm 1.6(2)
<u>Nereis zonata</u>	-22.9 \pm 1.9(6)
<u>Nicolea zostericola</u> ^C	-18.8(1)
Orbiniidae ^C	-17.3(1)
<u>Spinther alaskensis</u>	-22.0 \pm 0.2(3)
Terebellidae ^C	-20.1(1)

TABLE 2. (Continued)

Organism	$\delta^{13}\text{C}$
MOLLUSCA	
Gastropods	
<u>Eubranchus</u> sp.	-20.2±1.8(3)
<u>Margarites vorticifera</u>	-16.7±1.0(5)
<u>Neptunea borealis</u>	-18.4(1)
<u>Plicifusus kroyeri</u>	-19.6±0.4(3)
<u>Polinices pallidus</u>	-17.4±0.7(5)
<u>Velutina undata</u>	-22.4(1)
Chitons	
<u>Amicula vestita</u>	-18.4±0.7(12)
<u>Ischnochiton albus</u>	-17.6±0.8(7)
ARTHROPODA - Crustacea	
<u>Hyas coarctatus alutaceus</u> (crab)	-20.2±0.4(3)
<u>Saduria entomon</u> (isopod, 1)	-21.5(1)
<u>Mysis litoralis</u> (mysid) ^C	-20.3±0.9(7)
Amphipods	
<u>Anonyx sarsi</u> (<u>nugax</u>)*	-20.7±1.2(3)
<u>Atylus carinatus</u>	-20.6±1.5(3)
<u>Gammaracanthus loricatus</u>	-20.2(1)
<u>Gammarus setosus</u>	-20.5(1)
<u>Weyprechtia heuglini</u>	-21.0(1)
BRYOZOA	
<u>Alcyonium</u> sp.	-22.6±1.2(2)
<u>Eucratea loricata</u>	-24.9±1.4(3)
<u>Flustra carbasea</u>	-24.0(1)
<u>Flustrella</u> sp.	-23.0±0.8(2)

TABLE 2. (Continued)

Organism	$\delta^{13}\text{C}$
ECHINODERMATA (Seastars)	
<u>Leptasterias groenlandica</u>	-21.2±0.6(2)
UROCHORDATA (Ascidians)	
<u>Mogula griffithsii</u>	-18.8(1)
CHORDATA	
<u>Boreogadus saida</u> (arctic cod)	-21.2(1)
<u>Gymnelis viridis</u> (eelpout)	-19.8(1)
<u>Liparis herschelini</u> (snail fish)	-21.1±0.7(4)
<u>Myoxocephalus quadricornis</u> (four-horned sculpin)	-19.2±0.6(2)

* A. sarsi and A. nugax are taxonomically very similar and undistinguishable as dried specimens

^c Composite sample

individuals sampled. The mean $\delta^{13}\text{C}$ values of all animal species collected at site DS-11 in the Boulder Patch are shown in Table 2.

In nearly all cases, I found that our observations and existing knowledge on the feeding habits of various animals were confirmed by the isotope data. For example, an Orbiniid polychaete, a benthic detrital feeder (Fauchald and Jumars, 1979) had a $\delta^{13}\text{C}$ values of -17.3 ‰, close to kelp carbon (Fig. 3), compared to mean $\delta^{13}\text{C}$ values of -20.3 ‰ for omnivorous polychaete scavengers, and -22 ‰ for the polychaete Spinther alaskensis, known to be ectoparasitic on sponges (Fauchald and Jumars, 1979). The mean $\delta^{13}\text{C}$ value of sponges on which I found S. alaskensis was -20.7 ‰ and my isotopic measurements of different individuals of Spinther reveal a close similarity in diet (± 0.2 ‰). This contrasts the apparent diversity in diet found in Nereis zonata (-22.9 ± 1.9 ‰; Fig. 3), which prefers diatoms (Fauchald and Jumars, 1979).

Other omnivorous epibenthic invertebrates, including gastropods (Neptunea borealis and Plicifusus kroyeri), crustaceans and seastars, ranged from -18.4 to -21.6 ‰ (Table 2). Sessile suspension feeders that feed mainly on phytoplankton and zooplankton, bryozoans and hydroids respectively, commonly ranged from -22.6 to -24.9 ‰. In contrast, an ascidian (a nonselective filter feeder) and sponges (very fine particulate feeders) had values of -18.6 to -22.4 ‰. The $\delta^{13}\text{C}$ value of fishes caught by divers averaged -20.5 ‰, near their predominantly crustacean food sources (Fig. 3). The bottom dwelling four-horned sculpin had

the heaviest mean value (-19.2 ‰) of the four fish species measured (Table 2).

Three animals were often found grazing upon or attached to kelp fronds; they included the gastropod Margarites vorticifera (-16.7 ‰), and the chitons Ischnochiton albus (-17.6 ‰) and Amicula vestita (-18.4 ‰). In contrast, other molluscan animals were isotopically light. The carnivorous gastropod Velutina undata (-22.4 ‰) probably consumes hydroids or bryozoans, as do European species of Velutina (Fretter and Graham, 1962). The eolid nudibranch Eubranchus sp. (-20.2 ‰) were often found feeding on hydrozoans and fish eggs, their major diet (Morris et al., 1980). The heavy $\delta^{13}\text{C}$ value for Polinices pallidus (-17.4 ‰), a boring carnivorous gastropod (Barnes, 1980), indicates that this animal is preying on isotopically heavy bivalves (isotopic composition undetermined).

Distinct seasonal changes in ^{13}C content were displayed by six animals collected at site DS-11 in the Boulder Patch (Table 3). These included a sessile scyphozoan (Lucernaria infundibulum), a polychaete (Flabelligera affinis), an eolid nudibranch (Eubranchus sp.), and three crustaceans, a mysid (Mysis litoralis), a euphausiid (Thysanoessa raschii) and an amphipod, Anonyx sarsi (or nugax). The individuals of these species are small (less than 0.25 g wet weight) and excepting the nudibranchs, were isotopically heavier in April than in August or November. This seasonal isotopic difference ranged between 1.4 and 2.0 ‰ in all six

TABLE 3. $\delta^{13}\text{C}$ values (‰) of organisms that displayed distinct seasonal changes in carbon isotopic content. Values are $\bar{x} \pm \text{SD}(n)$. Samples for Mysis and Thysanoessa are composites.

Organism	August	November	April
<u>Lucernaria infundibulum</u>	-20.3(1)	--	-18.8±0.8(2)
<u>Flabelligera affinis</u> ^c	-20.6(1)	--	-18.8(1)
<u>Eubranchus</u> sp.	-18.3(1)	--	-21.2±0.7(2)
<u>Anonyx sarsi</u> (<u>nugax</u>)	-22.0±0.3(2)	--	-20.0±0.1(2)
<u>Mysis litoralis</u>	-21.0±0.3(4)	-20.0(1)	-19.2±0.3(2)
<u>Thysanoessa raschii</u> ^a	--	-21.6(1)	-20.2(1)

^a Formalin preserved specimen

organisms. The higher $^{13}\text{C}:^{12}\text{C}$ ratios in April compared to August appears to be linked with very low phytoplankton concentrations in the water column from November to April (Schell et al., 1984) and the availability of isotopically heavier kelp detritus. I attribute the low ^{13}C content of eolid nudibranchs in April to their consumption of liparid fish eggs, which contain large amounts of ^{13}C depleted lipids. These eggs are found attached to Laminaria stipes in large numbers during March and April under the ice canopy (Dunton et al., 1982).

To assess the quantitative importance of kelp carbon to various consumers in the Boulder Patch, I compared the isotopic composition of species collected at DS-11 to the same species (or a closely related species) found outside of the Boulder Patch at two sites. Since many of the animals are epilithic, I chose one site on the outskirts of the Boulder Patch (site BF-37) where kelp densities are very low but where some rock substrata are present (Toimil and England, 1982). I found that in nearly all cases, the $\delta^{13}\text{C}$ value of species collected at sites BF-37 and PB were lighter than species at DS-11 (Table 4). The $\delta^{13}\text{C}$ values for organisms collected at sites BF-37 and PB averaged 1.5 ‰ lighter than the same animals collected at DS-11. The benthic animals showing the greatest isotopic difference between sites included the nemertean Cerebratulus (2.4 ‰), the polychaetes Nicolea zostericola (3.0 ‰) and Nereis zonata (1.4 ‰), the gastropod Neptunea (3.7 ‰) and two related species of carnivorous boring gastropods,

TABLE 4. Comparison of $\delta^{13}\text{C}$ values (‰) of organisms collected at the same time of year at DS-11, BF-37 (on the fringes of the Boulder Patch) and site PB (30 km west of the Boulder Patch). Values are $\bar{x} \pm \text{SD}(n)$.

Organism	DS-11	BF-37	PB
Soft Coral			
<u>Gersemia rubiformis</u>	-22.6±0.4(6)	-23.3(1)	--
Nemertean			
<u>Cerebratulus</u> sp.	-18.5(1)	-19.4(1)	-20.9(1) ^a
Polychaetes			
<u>Chaetozone setosa</u> ^{a,c}	-21.6(1)	--	-21.3(1)
<u>Terebellides stroemi</u> ^{a,c}	-21.7(1)	--	-21.6±0.1(2)
<u>Nereis zonata</u>	-23.0±2.1(5)	-24.4(1)	--
<u>Nicolea zostericola</u> ^c	-18.8(1)	-21.8(1)	--
Gastropods			
<u>Neptunea</u> spp.	-18.4(1)	-22.1(1)	--
<u>Polinices pallidus</u>	-17.8±1.1(2)	--	--
<u>Natica clausa</u>	--	-22.2(1)	--
Crustaceans			
<u>Anonyx sarsi</u> (nugax)	-22.0(1)	--	-22.6±1.8(2)
<u>Atylus carinatus</u>	-20.6±1.5(3)	-20.3(1)	--
<u>Gammaracanthus loricatus</u>	-20.2(1)	-20.5(1)	-21.4(1)
<u>Mysis litoralis</u>	-21.0±0.3(4)	--	-23.8±0.8(2)
<u>Saduria entomon</u>	-21.5(1)	--	-22.5(1)
<u>Thysanoessa raschii</u> ^{a,c}	-21.6(1)	--	-22.9(1)
Ascidian			
<u>Mogula griffithsii</u>	-18.8(1)	--	--
<u>Rhizomogula globularis</u>	--	--	-25.1±0.3(2) ^b
Fish			
<u>Boreogadus saida</u> (juv.)	-21.2(1)	-21.9(1)	--

^a Formalin preserved specimen.

^b Collected at site CB, 90 km east of DS-11.

^c Composite sample

Polinices pallidus and Natica clausa (4.4 ‰). Other species showing notable changes between sites included an ascidian (6.3 ‰) and the crustaceans Mysis littoralis (1.6 ‰), Thysanoessa raschii (1.3 ‰), Gammaracanthus loricatus (1.2 ‰) and Saduria entomon (1.0 ‰). Animals that were isotopically similar between sites included two polychaetes (Chaetozone setosa and Terebellides stroemi) and the amphipod Atylus carinatus. The remaining species, the soft coral Gersemia rubiformis, the amphipod Anonyx sarsi (nugax) and juveniles of the arctic cod (Boreogadus saida) showed between site isotopic differences of about 0.7 ‰ (Table 4).

DISCUSSION

Seasonal isotopic variability in Laminaria solidungula

The seasonal pattern in the isotopic composition of the first and second blade segments in L. solidungula appears to correspond to changes in the biochemical composition of the tissues. This is supported by the correlation between the $\delta^{13}\text{C}$ value of the blade tissue with that of its reported carbon content (Chapter 4). The decrease in ^{13}C in the basal (first) blade from November to a minimum in April matches the decrease in the carbon content of this tissue over the same period (Fig. 4). A similar but less pronounced relationship is apparent in the second blade segment.

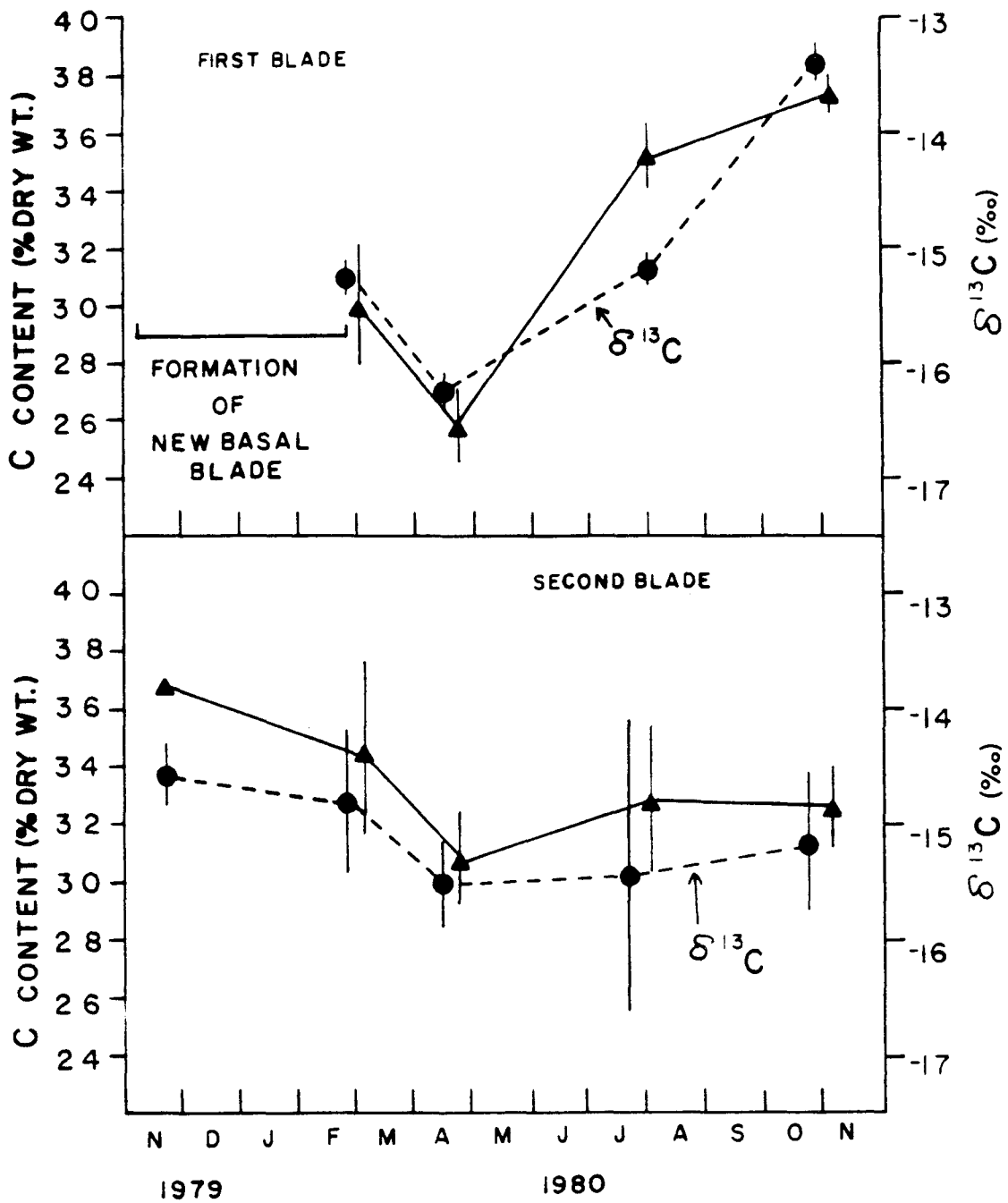


Figure 4. *Laminaria solidungula*. Seasonal variation in carbon content ($x \pm 95\%$ confidence limits) and $\delta^{13}C$ values ($x \pm SD$, $n=2$) of first and second blade segments, Stefansson Sound, Alaska. Tissue carbon data from Chapter 4.

These data support the hypothesis of Stephenson et al. (1984), who attributed the isotopic variability in L. longicuris to the differential storage of biochemical components, but who was unable to provide the tissue measurements to support this idea. Isotopic analyses of the tissue constituents in L. solidungula should provide further insight into the cause of this seasonal trend.

Isotopic analyses of the blade segments in Laminaria solidungula indicate that the $\delta^{13}\text{C}$ value of kelp carbon lies between -15 and -16 ‰. This range includes relatively old material (greater than 3 years) being eroded from the tip of frond as well as that being currently produced as new tissue at the base (Table 1). Although spatial heterogeneity in the isotopic composition of the frond exists in this plant as in L. longicuris (Stephenson et al., 1984), I assume that most of the kelp available to animals is consumed randomly and is well mixed in detrital form. In addition, the isotopic heterogeneity in L. solidungula does not appear to be great (Appendix D). Thus, for the purposes of this study, I assume that the $\delta^{13}\text{C}$ of kelp carbon available to molluscan herbivores is -15.1 (the mean $\delta^{13}\text{C}$ value of first and second blades, all seasons). For kelp detritus I have assigned a $\delta^{13}\text{C}$ value of -16.1 ‰, the mean isotopic composition of distal blades in February and April, since the availability of kelp detritus is greatest during the late winter and early spring when very weak currents occur under the ice canopy. In contrast, summer and fall months are characterized by much higher current velocities (Dunton

et al., 1982) which could carry a large proportion of kelp particulate matter out of the Boulder Patch.

Isotopic evidence for consumer feeding strategies

The difference in $\delta^{13}\text{C}$ values of animal species collected within and outside of the Boulder Patch, together with the observed seasonal trends in $\delta^{13}\text{C}$ noted for some animals, support the hypothesis that many organisms assimilate carbon derived from kelp. Analysis of additional samples may provide sufficient data to determine if these differences and trends are statistically significant, but that is not possible at this time. Equally important, however, is that some animals exhibit a selectivity for food that results in little or no incorporation of detrital kelp carbon. Overlooked in previous isotopic studies is the fact that some suspension feeders can be excellent macroscopic indicators of phytoplankton or zooplankton isotopic composition.

Phytoplankton are the major food source for bryozoans, whose food is limited to less than 50 μm in diameter, the average size of the bryozoan mouth (Winston, 1977). In the Boulder Patch, the mean $\delta^{13}\text{C}$ value of Eucreatea loricata (-24.9 ‰) matches the isotopic composition of the phytoplankton, predicted to be in the -25 to -26 ‰ range (Chapter 7). The $\delta^{13}\text{C}$ value of E. loricata collected across the Alaskan arctic shelf, from west to east, decreases from about -21.6 to -25.2, coincident with the isotopic change in

zooplankton (Chapter 7). The differences in the isotopic composition of the bryozoan species listed in Table 3 are noteworthy, as these animals do maintain some degree of trophic separation by possessing different mouth diameters that restrict the range of particles ingested (Winston, 1977). Therefore, differences in the isotopic composition of the various species (Table 2) likely reflect different phytoplankton food sources. Similarly, the mean $\delta^{13}\text{C}$ value of hydrozoans (-23.6 ‰) reflects its strictly carnivorous diet that consists primarily of small zooplankton and invertebrate larvae.

An interesting contrast to this high selectivity in diet is provided by ascidians. Since nearly all material pumped into the animal's branchial cavity is captured by mucous secretions and ultimately passed to the stomach, the food consists of both phytoplankton and detritus. This explains the distinct difference in $\delta^{13}\text{C}$ values recorded for a filter feeder collected in the Boulder Patch (-18.8%) where large amounts of kelp detritus are available, and outside of the Boulder Patch where phytoplankton (-25.5 ‰) are predominant (Table 4).

Sponges are also selective suspension feeders and appear to be mainly dependent upon particles much less than $50\ \mu\text{m}$ in size, particularly bacteria and unresolvable particulate organic matter (Reiswig, 1971). The mean $\delta^{13}\text{C}$ values of four species of sponges collected in the Boulder Patch ranged from -19.5 to -22.4 ‰ (Table 2), indicating a diet not based solely on the direct

consumption of phytoplankton. The difference in isotopic composition among the four species also suggests a possible diversity in feeding strategies and assimilation of isotopically heavier kelp carbon.

Still other evidence points to the assimilation of kelp detritus by suspension feeders in the Boulder Patch. I found that five organisms, including the mysid Mysis littoralis, were 1.4 to 2.0 ‰ heavier in April than in August (Table 3). The ^{13}C enrichment which occurs in M. littoralis between August and April coincides with the virtual absence of the isotopically lighter phytoplankton in the water column from November to April (Fig. 5). It also coincides with rapid linear growth and meiospore release in Laminaria solidungula between November and April (Dunton et al., 1982). M. littoralis derives a significant portion of its dietary carbon from phytoplankton (Barnes, 1980) and the $\delta^{13}\text{C}$ values of animals collected outside the Boulder Patch support this contention (Table 4). Mysids are also reported to feed on algal fragments drifting over the bottom from adjacent kelp beds in California (Clarke, 1971). In the Boulder Patch, the ^{13}C enrichment of mysids during the dark ice-covered period also suggests the usage of isotopically heavier kelp detritus. In areas of the Beaufort Sea where light is able to penetrate the ice canopy, mysids probably depend more heavily on ice algae and benthic diatoms, but the presence of a turbid ice canopy in the Boulder Patch in most years

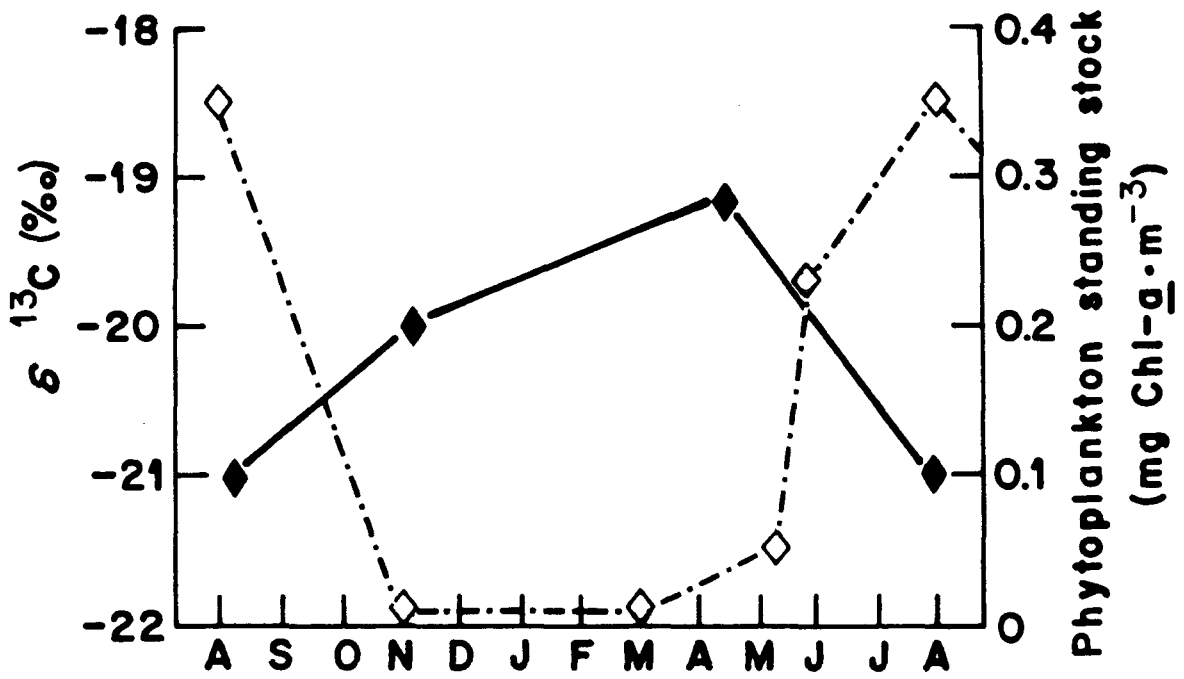


Figure 5. Seasonal variation in $\delta^{13}\text{C}$ of the mysid Mysis littoralis (closed triangles) relative to phytoplankton standing stock (from Schell et al., 1984) in the Boulder Patch. Data are from Table 3, all composite samples.

precludes any substantial inputs from these sources. Since turbid ice blocks light completely, ice algae is noticeably absent in the Boulder Patch (Schell et al., 1984) and productivity of both phytoplankton and benthic microalgae is negligible between October and June (Dunton, 1984). I suspect that the higher ^{13}C content in April of other organisms (Table 3) is related to increased dependence on kelp detritus in winter. The presence of higher April $^{13}\text{C}:^{12}\text{C}$ ratios in predators such as the scyphozoan Lucernaria infundibulum, which preys on small caprellid crustaceans, probably reflects a similar shift in the winter diet of caprellids.

Dependence of animals on kelp carbon

The $^{13}\text{C}:^{12}\text{C}$ measurements of plants and animals collected both within and outside of the Boulder Patch provide a means to obtain an estimate of the relative importance of kelp in the diets of the resident Boulder Patch fauna. To estimate the carbon contribution made by kelp to the Boulder Patch food web, I used the simple mixing equation employed by McConnaughey and McRoy (1979a) to interpret the $\delta^{13}\text{C}$ values of the fauna. Similar mixing models have been used by Hughes and Sherr (1983) and Haines (1976b), but do not account for isotope fractionation occurring in the food web. Such fractionation results from preferential respiration and metabolic processes of ^{12}C by the organism, resulting in a progressive enrichment of animal ^{13}C in the food chain. The extent of this

fractionation is not constant and appears to vary between 0.5 and 1.5 ‰ (see Fry and Sherr, 1984).

The mixing equation employed here accounts for post-photosynthetic isotope fractionation by using the $\delta^{13}\text{C}$ values of Boulder Patch organisms collected both within (site DS-11) and outside (sites BF-37 and PB) the Boulder Patch. The equation was based on proportional incorporation of Laminaria solidungula detritus carbon with an average $\delta^{13}\text{C}$ of -16.1 ‰ (-15.1 ‰ for macroalgal herbivores) and phytoplankton carbon with a $\delta^{13}\text{C}$ of -25.5 ‰ into animal tissue. In cases where I did not have individuals of the same species from both within and outside of the Boulder Patch (bryozoans, hydroids and a polychaete deposit feeder), I accounted for fractionation by assuming that the $\delta^{13}\text{C}$ value increases (becomes heavier) by 0.8 ‰ per trophic level (DeNiro and Epstein, 1978). I estimated an animal's trophic level from its feeding habit and from an isotope food web model constructed by McConnaughey and McRoy (1979b). Therefore, bryozoans (which feed on phytoplankton) had a trophic level of 1, hydroids (which feed on zooplankton) had a trophic level of 2, and a polychaete deposit feeder (which feeds on meiofauna) had a trophic level of 4.

The results of these analyses reveal that in addition to the macroalgal herbivores, various polychaetes, gastropods, sponges, crustaceans and an ascidian assimilated 30% or more of their body carbon from kelp (Fig. 6). The utilization of kelp detritus by

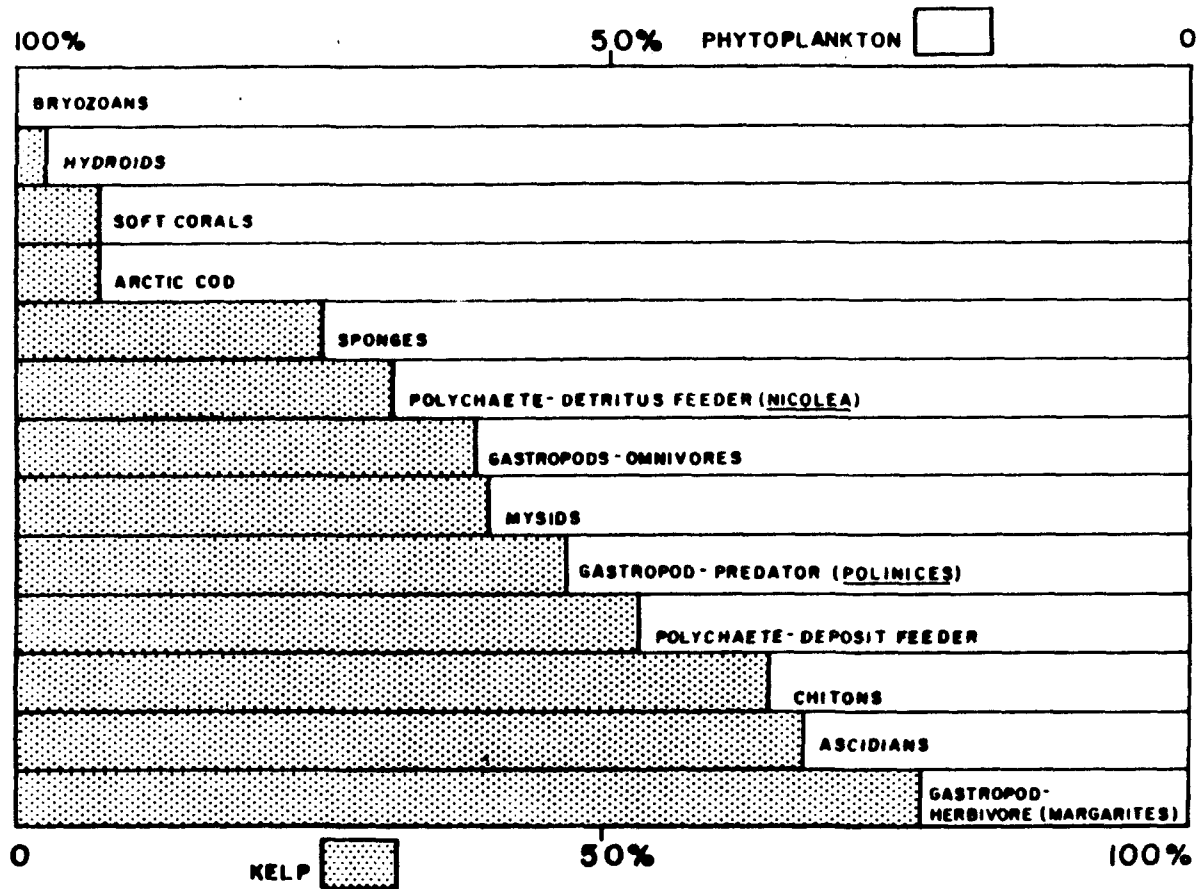


Figure 6. Proportion of body carbon derived from kelp (*Laminaria solidungula*) and phytoplankton for Boulder Patch fauna based on a simple mixing equation that accounts for post-photosynthetic fractionation.

these animals confirms their opportunistic feeding behavior as omnivorous scavengers. The fraction of kelp carbon in the polychaete Nicolea zostericola, which is often found in tubes attached to Laminaria solidungula, was 32%. Ingestion of L. saccharina detritus by the polychaete Platynereis dumerilii, also found attached to kelp blades, has been documented by Bedford and Moore (1985) off the coast of Scotland. The higher percentages of kelp carbon incorporated into the ascidian Mogula griffithsii (67%), the deposit feeding Orbiniid polychaete (53%) and the gastropod Neptunea borealis (47%), a scavenger (Pearce and Thorson, 1967), reflect the large amount of assimilable kelp detritus available relative to phytoplankton on and above the seabed. Similarly, a high incorporation of kelp (47%) was apparent in benthic predators, such as the boring gastropod Polinices pallidus. However, not all benthic animals exhibited a high fraction of kelp carbon in their tissues. Some omnivorous polychaetes and amphipods showed little dependence on kelp carbon as exemplified by Nereis zonata, Chaetozone setosa, Terebellides stroemi, Anonyx sarsi (nugax) and Atylus carinatus (Table 4).

A most significant finding of this study is the incorporation of significant amounts of kelp carbon in the tissues of two crustaceans, the mysid Mysis littoralis (40%), and the euphausiid Thysanoessa raschii (22%). These two species are the primary prey of fish, birds and marine mammals in the Beaufort Sea (Craig et al., 1984). Mysids are also abundant in temperate latitude kelp

communities and are important prey species for many common fishes inhabiting kelp beds (Clarke, 1971). In the Boulder Patch, the fraction of kelp carbon incorporated into a juvenile arctic cod was about 7%, which reflects its ingestion of crustaceans from both within and outside of the Boulder Patch. Thus, the importance of kelp as a carbon source may extend well into the pelagic food chain in temperate nearshore environments which are generally typified by much higher inputs of kelp carbon.

The results of this study support recent work that has documented the importance of benthic macroalgae and algal epiphytes as carbon sources for consumers (Fry, 1984b; Kitting et al., 1984). It also demonstrates that although most kelp carbon is channeled through the detrital food web, its abundance and high nutritional value insure its relatively efficient transfer throughout the benthic community. As a consequence, the Boulder Patch and temperate kelp beds support highly diverse and productive invertebrate populations that are important feeding grounds for birds, fish and marine mammals. In the next and final chapter, I will address the importance of isotopic gradients on an ecosystem level in the Beaufort Sea and their significance in understanding arctic food webs.

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CHAPTER 7. ZOOPLANKTON $^{13}\text{C}:^{12}\text{C}$ RATIOS IN THE WESTERN ARCTIC OCEAN:
A LONGITUDINAL GRADIENT

SUMMARY

Copepods (Calanus spp.) and chaetognaths (Sagitta elegans) collected along the Alaskan arctic coast, from the northeastern Chukchi Sea (158°W) to the U.S.-Canadian border (141°W) in the Beaufort Sea, exhibited a distinct gradient in their carbon isotopic composition. Zooplankters were isotopically lightest in the eastern Beaufort Sea, both nearshore and offshore. The net isotopic change from west to east was -1.9 ‰ for Calanus and -2.7 ‰ for Sagitta. The isotopic shift occurred in the absence of an observable change in phytoplankton species composition. Instead the ^{13}C depletion is related to the dilution of a warm water intrusion beneath and by cold arctic surface water, and an upwelling in the eastern Beaufort Sea. The presence of well-defined water masses and upwelling appear to account for depressed zooplankton $^{13}\text{C}:^{12}\text{C}$ ratios by cycling ^{13}C -depleted inorganic carbon into the euphotic zone.

INTRODUCTION

Previous studies on the distribution of stable carbon isotopes in marine plankton (Sackett et al., 1965; Degens et al., 1968a; Eadie, 1972; Eadie and Jeffrey, 1973; Fontugne and Duplessy, 1978, 1981) have not addressed high arctic ecosystems. To date, only two plankton samples have been analyzed for stable carbon isotopes from the High Arctic, and both were collected from the western Beaufort Sea on Alaska's north arctic coast (Rau et al., 1982). Rau used these samples to compare latitudinal trends in plankton $^{13}\text{C}:^{12}\text{C}$ ratios between northern and southern oceans. He found that, although the plankton in both hemispheres showed a depletion in ^{13}C with increasing latitude, the trends differed significantly. He attributed this difference to the presence of distinct hydro-geographical water masses possessing characteristic plankton isotopic signatures (Fontugne and Duplessy, 1978, 1981) that masked the relationship between sea surface temperature and plankton $\delta^{13}\text{C}$ values reported earlier by Sackett et al. (1965).

The $\delta^{13}\text{C}$ values reported by Rau et al. (1982), however, for Beaufort Sea plankton, -21.5 and -22.4 ‰, differed distinctly from our estimate of -24 to -26 ‰ (Dunton and Schell, 1982). Our estimate was based on the isotopic content of epilithic suspension feeders collected nearby in the central portion of the Alaskan Beaufort Sea. In addition, we noted that these species of epilithic invertebrates (e.g., Thuiaria sp., Gersemia rubiformis,

and Eucratea loricata) were 2 to 3.0 ‰ more depleted in ^{13}C than their counterparts on Alaska's northwest arctic coast in the Chukchi Sea (Dunton and Schell, 1984). The difference in the $^{13}\text{C}:^{12}\text{C}$ ratios of these epilithic invertebrates occurred in the absence of any significant change in latitude and is assumed to reflect similar shifts in plankton ^{13}C content.

To determine the location and magnitude of changes in plankton $\delta^{13}\text{C}$ values along Alaska's arctic coast, we measured the $^{13}\text{C}:^{12}\text{C}$ ratio of chaetognaths and copepods collected from the northeastern Chukchi Sea to the Alaskan-Canadian border in the Beaufort Sea. We also looked for evidence to explain the distinct longitudinal shift in isotopic composition that we observed.

MATERIALS AND METHODS

Plankton samples were collected by Horner (1980) during August and early September 1977 from the U.S. Coast Guard Cutter Glacier from 158° to 142° W longitude at an approximate latitude of 71° N (Fig. 1). Following capture in vertical net tows (bongo, 333 and 505 μ mesh), the plankton samples were stored in formalin. Animals were picked individually from these collections to represent two trophic levels: the copepod Calanus (including either C. hyperboreus or C. glacialis) a herbivore, and the chaetognath Sagitta elegans, a carnivore whose diet consists mainly of herbivorous crustaceans, including Calanus.

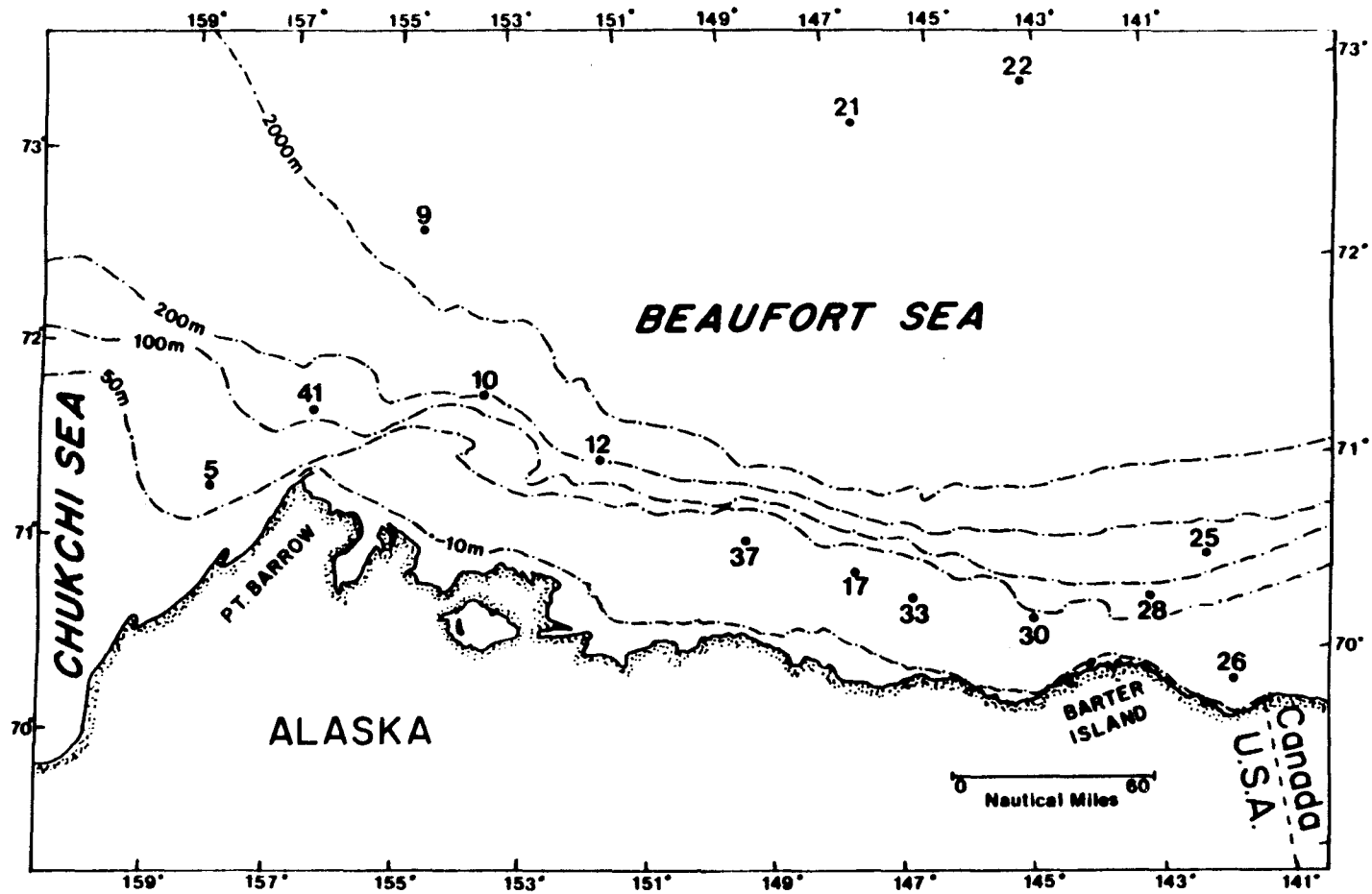


Figure 1. The location of numbered stations sampled along the Alaska arctic coast by Horner (1980) from the U.S. Coast Guard Cutter Glacier in 1977.

The samples were soaked in 1N HCl for 4-6 hours to remove carbonates, submerged in distilled water for 24 hours to leach remaining formalin from body tissues (Mullin et al., 1984), and then dried at 50°C for 1-2 days. Subsamples of 8-10 mg were then manually ground in the presence of copper oxide and individually combusted in evacuated sealed borosilicate glass tubes at 590°C for 2 hours. After combustion, the tube was placed on a vacuum line and cracked using a Cajon flexible stainless steel tube fitting (Des Marais et al., 1976). The carbon dioxide gas resulting from the combustion was then isolated and purified cryogenically. Isotope measurements were performed on a VG Isogas SIRA 9 triple collector isotope ratio mass spectrometer. By convention, the relative $^{13}\text{C}:^{12}\text{C}$ ratios are reported as $\delta^{13}\text{C}$, the relative parts-per-thousand (‰) difference between the isotopic ratio (R) of the sample and the PDB carbonate standard:

$$\delta^{13}\text{C} = \left[\frac{R_{\text{sample}}}{R_{\text{std}}} - 1 \right] \times 1000$$

My results were routinely reproducible to within ± 0.3 ‰.

Large amounts of phytoplankton, consisting mostly of diatoms, were present in three samples. These samples were prepared for isotopic analysis as already described. In addition, their individual C:N ratios were determined by measuring the amount of total tissue carbon and nitrogen on a Perkin-Elmer 240C elemental analyzer.

The $^{13}\text{C}:^{12}\text{C}$ ratio of lipid and nonlipid carbon was measured in the copepod Calanus hyperboreus and in the common diatom Thalassiosira collected from Station 28. For lipid extraction, I used the procedure outlined by Bligh and Dyer (1959). Wet samples were weighed and ground with a mortar and pestle. A 19-ml aliquot of chloroform-methanol (1:2 v/v) was added to each sample, and then each was homogenized. Homogenates were then centrifuged (1,000xg for 10 minutes) to remove proteinaceous residue. Supernatants were transferred to clean centrifuge tubes, and 6 ml of distilled water was added to each. After agitation on a test tube mixer, 6 ml of chloroform was added. The sample was then reagitated and recentrifuged. Lower layers containing total lipid were transferred by syringe to centrifuge tubes. Extracts were evaporated at 45°C under a stream of nitrogen and dispensed into clean scintillation vials for storage. Subsamples of lipids were combusted and prepared for mass spectrometry as described above.

RESULTS

Longitudinal gradient in zooplankton $\delta^{13}\text{C}$ values

The location of the samples and carbon isotopic composition of the zooplankton species, Sagitta elegans and Calanus spp., are shown in Table 1. The ^{13}C content of samples collected between 70

TABLE 1. Sample location and plankton carbon isotopic composition.

Station No.	Latitude (°N)	Longitude (°W)	$\delta^{13}\text{C}$ (‰)	
			<u>Sagitta elegans</u>	<u>Calanus spp.</u>
5	71°12'	158°22'	-20.9	-23.9 ^g
41	71°32'	156°30'	-21.0	-23.3 ^g
10	71°35'	153°29'	-21.0	-23.4 ^g
12	71°10'	151°30'	-20.8	-23.7 ^g
37	70°45'	149°03'	-21.4	-24.4 ^g
17	70°33'	147°24'	-21.5	-23.8 ^g
33	70°23'	146°26'	-21.6	-24.1 ^g
30	70°14'	144°28'	-22.6	-24.7 ^g
28	70°19'	142°32'	-23.1	-25.2 ^h
25	70°32'	141°32'	-23.5	-24.4 ^h
26	69°49'	141°31'	-23.6	-24.4 ^h
9	72°24'	154°37'	-20.9	-23.3 ^g
21	72°47'	146°34'	-24.0	-24.8 ^h
22	72°57'	143°20'	-24.6	-24.8 ^h

^h Calanus hyperboreus

^g Calanus glacialis

and 71°N latitude for both species remains nearly constant from the northeastern Chukchi Sea (158°W) to the central Alaskan Beaufort Sea (151°W), but then starts to steadily decrease across the eastern Alaskan Beaufort Sea coast to 141°W (Fig. 2). The net isotopic change from west to east was -1.9 ‰ for Calanus spp. and -2.7 ‰ for Sagitta elegans. Dunton and Schell (1984) noted a -2.0 to -2.5 ‰ difference in epilithic suspension feeders collected between the two areas in 1983. For both genera, longshore $\delta^{13}\text{C}$ values show the most rapid decrease in ^{13}C (about 1.5 ‰) between 149 and 143°W longitude and are isotopically lightest in the vicinity of Barter Island (-23.6 ‰ for Sagitta elegans, and -25.2 ‰ for Calanus hyperboreus).

The isotopically lightest chaetognath samples were collected at two stations 300 km offshore of Barter Island at about 73°N latitude. At these sites the measured $\delta^{13}\text{C}$ value for S. elegans was -24.6 and -24.0 ‰. Specimens of Calanus hyperboreus were also notably depleted in ^{13}C ($\delta^{13}\text{C} = -24.8$ ‰). However, at a station north of Pt. Barrow at latitude 72°20'N, the $\delta^{13}\text{C}$ values of chaetognaths and copepods were -20.9 and -23.3, respectively. This is similar to the nearshore $\delta^{13}\text{C}$ values for these two species.

$\delta^{13}\text{C}$ of lipid and nonlipid fractions in plankton

The isotopic composition of whole organism, and lipid and nonlipid carbon fractions in Calanus hyperboreus and the diatom Thalassiosira are

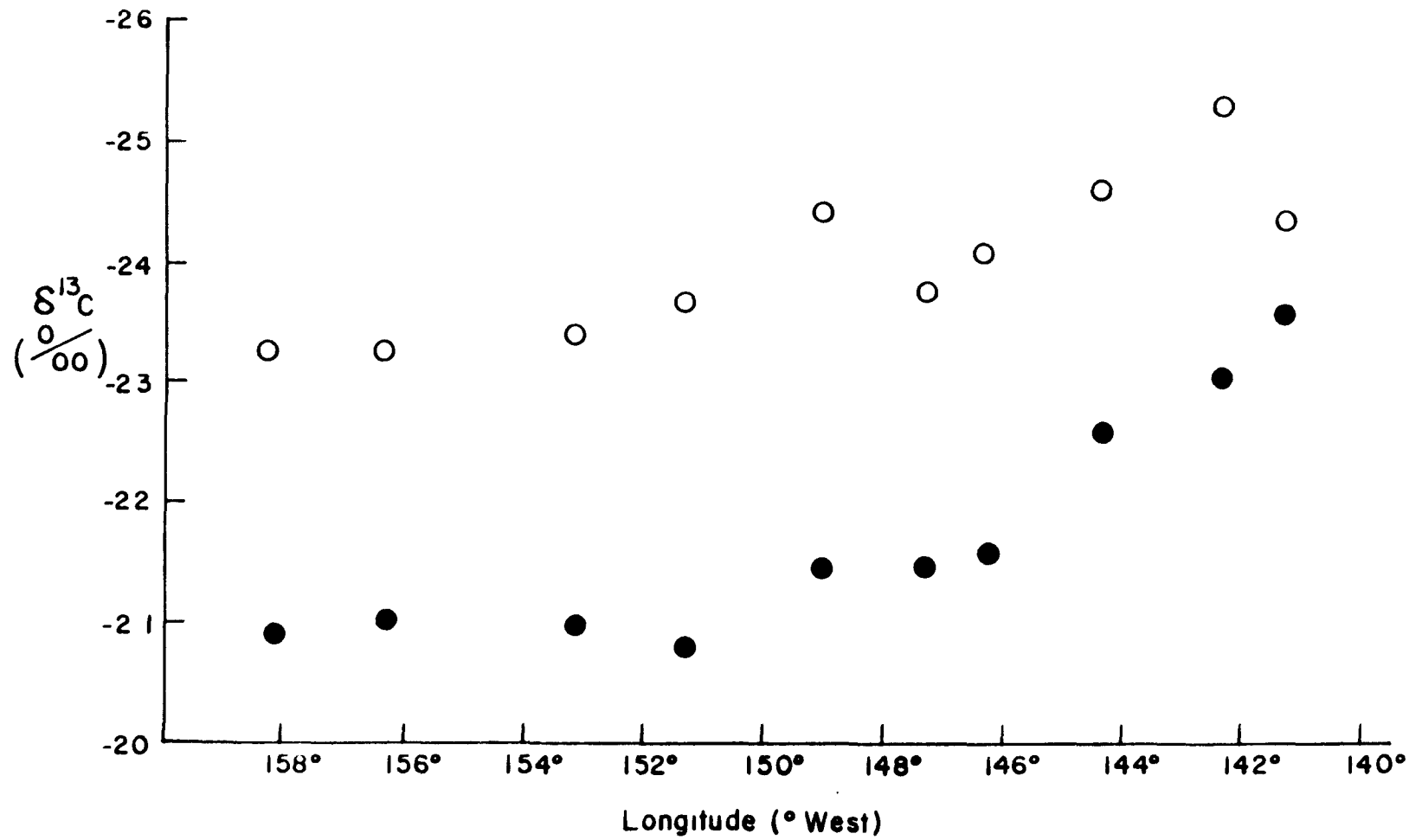


Figure 2. Chaetognath (solid circles) and copepod (open circles) $\delta^{13}\text{C}$ values versus longitude in samples collected between 70 and 71°N along the Alaskan arctic coast.

listed in Table 2. The difference between the $\delta^{13}\text{C}$ value of the whole organism and its lipid fraction was 1.4 ‰ for C. hyperboreus and 5.0 ‰ for Thalassiosira. These results generally agree with previous determinations reported on plankton lipid ^{12}C enrichment relative to total cell carbon (3-6 ‰) and reported lipid $\delta^{13}\text{C}$ values (about -30 ‰) in cold south polar seas (Sackett et al., 1965; Eadie, 1972).

Longitudinal variation in phytoplankton C:N ratios

The C:N ratios of phytoplankton collected at three locations along the Beaufort Sea coast are shown in Table 3. The ratios reflect the amount of lipid stored in the diatoms with higher C:N ratios indicating higher lipid content. C:N ratios ranged from a low of 4.8 in the central Alaskan Beaufort Sea to a high of 6.4 and 7.0 in the western and eastern portions, respectively. Comparison of the C:N ratios in both Thalassiosira and Chaetoceros spp. indicates that diatom lipid content in this region is not significantly different between genera.

DISCUSSION

Longitudinal trends in plankton $^{13}\text{C}:^{12}\text{C}$ ratios as shown in this study have not been observed before, although latitudinal

TABLE 2. $\delta^{13}\text{C}$ values (‰) of the lipid (benzene extractable) and nonlipid (benzene unextractable) carbon fraction in the copepod Calanus hyperboreus and the diatom Thalassiosira sp. collected from Station 28.

Species	Total	Lipid fraction	Nonlipid fraction
<u>Calanus hyperboreus</u>	-25.2	-26.6	-23.7
<u>Thalassiosira</u>	-25.3 ^c	-30.3	-23.1

^c Sample lost. Value calculated based on a lipid to nonlipid ratio of 0.43 for phytoplankton (Sackett et al., 1965).

TABLE 3. Phytoplankton C:N ratios at three locations along the Beaufort Sea coast.

Genus	Longitude (°W)	C:N ratio
<u>Chaetoceros</u> spp.	152°20'	6.4
<u>Chaetoceros</u> spp.	147°57'	4.8
<u>Thalassiosira</u>	142°32'	7.0

trends in plankton $^{13}\text{C}:^{12}\text{C}$ ratios are well documented (Sackett et al., 1965; Eadie, 1972; Fontugne and Duplessy, 1981; Rau et al., 1982). The cause of the latitudinal variation was largely explained by the differential effect of temperature on phytoplankton carbon fractionation (Degens et al., 1968a) during carbon fixation. In this case, the cause of isotopic variation is not as clear, since the change occurs over a relatively short distance at nearly constant latitude, depth and distance offshore. Mechanisms that may account for the observed variation are:

1. changes in phytoplankton species composition,
2. changes in the lipid content of the plankton,
3. differential isotopic fractionation caused by a longitudinal temperature gradient, and
4. variation in the isotopic composition of the inorganic carbon source.

Differences in assemblages of phytoplankton species are probably responsible for the distinct plankton isotopic signatures characteristic of different water masses (Fontugne and Duplessy, 1978). The isotopic differences appear due to the presence of different metabolic pathways used for the uptake and fixation of

inorganic carbon (Wong and Sackett, 1978). The species composition of phytoplankton collected by Horner (1980) at various stations in 1977 is shown in Table 4. At nearly all stations, the diatom Chaetoceros dominates the algal assemblage. It is therefore unlikely that the observed isotopic gradient is caused by a difference in the phytoplankton species present.

Since the $\delta^{13}\text{C}$ of the lipid fraction in the diatom Thalassiosira sp. is 7 ‰ more negative than the $\delta^{13}\text{C}$ value of the entire organism (Table 2), higher lipid contents in the eastern Alaskan Beaufort Sea phytoplankton would result in a lower $\delta^{13}\text{C}$ value of phytoplankton from this region. However, C:N ratios were not observed to increase along the Beaufort Sea coast to account for the isotopic decrease (Table 3). Similarly, excess lipid could not entirely explain the ^{13}C depletion observed in high-latitude plankton from the southern hemisphere (Sackett et al., 1965) or the differences in the $^{13}\text{C}:^{12}\text{C}$ ratios of phytoplankton grown under identical laboratory conditions (Wong and Sackett, 1978). The differences in amount of photosynthate incorporated into lipids in diatoms examined from north and south polar seas have also been attributed to differences in species composition (Li and Platt, 1982). Since the isotopic variation observed in this study occurs in the absence of a change in species composition, the effects of lipid synthesis or metabolism are also probably negligible.

TABLE 4. Frequency of occurrence (%) of phytoplankton species at various stations and depths between Pt. Barrow and the Canadian border in 1977 (from Horner, 1980).

Station depth	<u>Chaetoceros</u> spp.	All other diatoms	Flagellates	Dinoflagellates
5-45	88	8	4	<1
6-100	82	13	5	1
7-45	83	12	5	-
8-45	68	1	30	<1
9-20	29	6	65	-
10-20	81	3	16	-
11-20	73	19	7	<1
12-10	61	33	6	<1
13-10	73	17	9	1
14-10	65	33	2	<1
15-06	69	28	2	<1
17-15	69	30	1	<1
18-20	90	9	1	<1
26-06	84	11	5	<1
27-00	57	33	9	1
29-25	97	2	1	<1

Isotopic fractionation resulting from temperature differences

The correlation between low water temperatures and decreased plankton $\delta^{13}\text{C}$ values has been demonstrated in field (Sackett et al., 1965) and laboratory studies (Degens et al., 1968a). Temperature coefficients ranging from 0.23 ‰ per °C (Sackett et al., 1965) to 0.35 ‰ per °C (Degens et al., 1968a; Fontugne and Duplessy, 1981) have been reported. The $\delta^{13}\text{C}/T$ relationship is not always linear, however, and may be masked by differences in plankton metabolism (Fontugne and Duplessy, 1978; Rau et al., 1982).

A major feature of the distribution of temperature in the near-surface waters of the Alaskan Beaufort Sea is the presence of a relatively warm water mass that results from the intrusion of eastward flowing water from the Bering and Chukchi seas (Mountain, 1974). The horizontal distribution of this warm water intrusion can be traced as far east as about 144°W (near Barter Island), with a maximum corresponding temperature differential (between Barter Island and Pt. Barrow at 156°W) of about 5°C (Hufford et al., 1974). The warm water mass appears to extend from the 25 m contour to at least 71°40'N at depths of about 20 to 75 m.

Mountain (1974), however, showed that this intrusion was composed of two water masses, called Alaskan coastal water and Bering Sea water. He noted that the former mixed rapidly with ambient surface water as it moved eastward and was not clearly identifiable east of about 147-148°W. On the other hand, he traced Bering Sea water, which

possesses a much deeper temperature maximum (50-75 m) as far as Barter Island, at 143°W. It is noteworthy that the rapid decrease in zooplankton $\delta^{13}\text{C}$ values begin at about 147-148°W (Figure 2), the most easterly extent of Alaskan coastal water. Using an average $\delta^{13}\text{C}/T$ coefficient of 0.30 ‰ and given a maximum 5°C temperature difference (most of which appears to occur between Pt. Barrow and about 147°W), temperature may account for as much as 1.5 ‰ of the mean 2.3 ‰ difference in zooplankton $^{13}\text{C}:^{12}\text{C}$ ratio observed between Pt. Barrow and Barter Island.

Variation in the isotopic composition of the DIC

Since the dissolved inorganic carbon (DIC) pool is the source, through photosynthesis, of marine organic carbon -- changes in the $\delta^{13}\text{C}$ value of the inorganic carbon pool would be reflected in a plant's $^{13}\text{C}:^{12}\text{C}$ ratio. The importance of this relationship has been demonstrated previously in aquatic plants (Osmond et al., 1981; McMillan and Smith, 1982), and in identifying the importance of river water DIC ($\delta^{13}\text{C} = -5$ to -10 ‰) and ocean water DIC ($\delta^{13}\text{C} = +2$ ‰) in estuarine regions (Sherr, 1982; Tan and Strain, 1983).

In the open ocean, the $\delta^{13}\text{C}$ content of the DIC pool decreases with depth (Fig. 3; Kroopnick et al., 1977) as ^{13}C -depleted CO_2 is added to the DIC pool through the oxidation of isotopically light organic matter. Eadie (1972) observed that the minimum $\delta^{13}\text{C}$ value of the DIC pool usually coincided with the depth of the O_2 minimum layer.

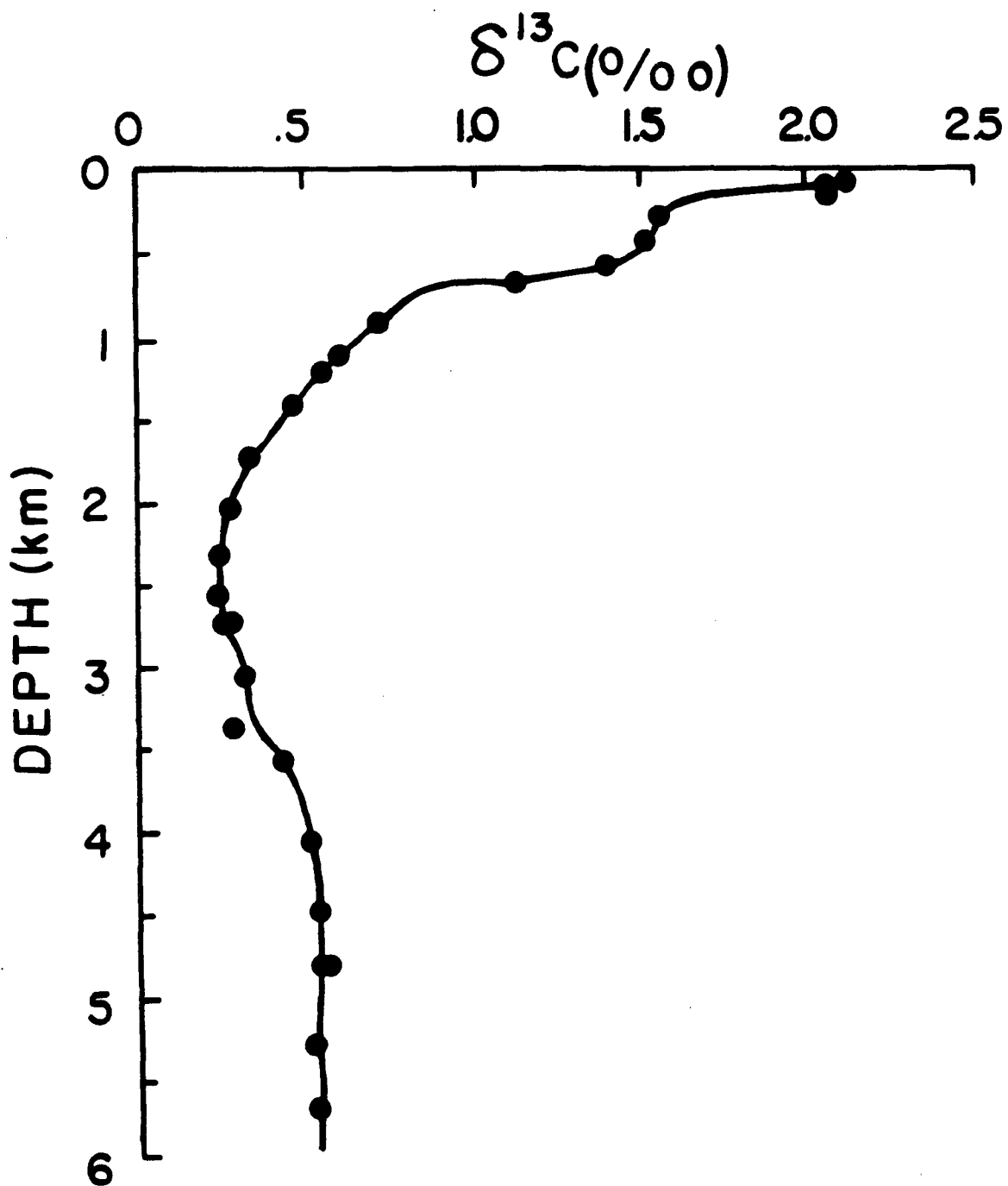


Figure 3. Vertical profile of $\delta^{13}\text{C}$ values of DIC at a typical midlatitude Pacific Ocean site (from Kroopnick et al, 1977).

He also demonstrated how differences in the $\delta^{13}\text{C}$ value of this pool in surface waters can be used to identify upwelling events, since water transported from depth is depleted in ^{13}C compared to the surface water mass.

It is noteworthy, then, that the distinct drop in plankton $^{13}\text{C}:^{12}\text{C}$ ratios at Barter Island coincides with upwelling identified by Hufford (1974) and subsequently by Mountain (1974). Both found evidence for upwelling in different years from about the 125 m level offshore in the vicinity of Barter Island (Fig. 4). Easterly winds present throughout the summer created an offshore Ekman transport in the surface layers, which led to the upwelling of deeper offshore water onto the shelf (Hufford, 1974). No other nearshore upwelling has been reported along the nearshore Alaskan Beaufort Sea coast, although Aagard (1981) has observed upwelling offshore at depths of 200 m or more, but of limited (50 m) vertical extent above the bottom.

Unfortunately, no $\delta^{13}\text{C}$ values of the DIC pool at this site are available, but a first approximation on the effect of this upwelling on the isotopic composition of the plankton can be calculated based on the dissolved oxygen data. Good correlations between the $\delta^{13}\text{C}$ value of the DIC pool and oxygen concentration have been demonstrated in upwelling areas (Deuser and Hunt, 1969; Craig and Weiss, 1970; Eadie, 1972). Eadie (1972) noted a drop of about 0.7 ‰ in the $\delta^{13}\text{C}$ value of DIC pool between the O_2 minimum layer and the surface at an upwelling site. Kroopnick (1985) also

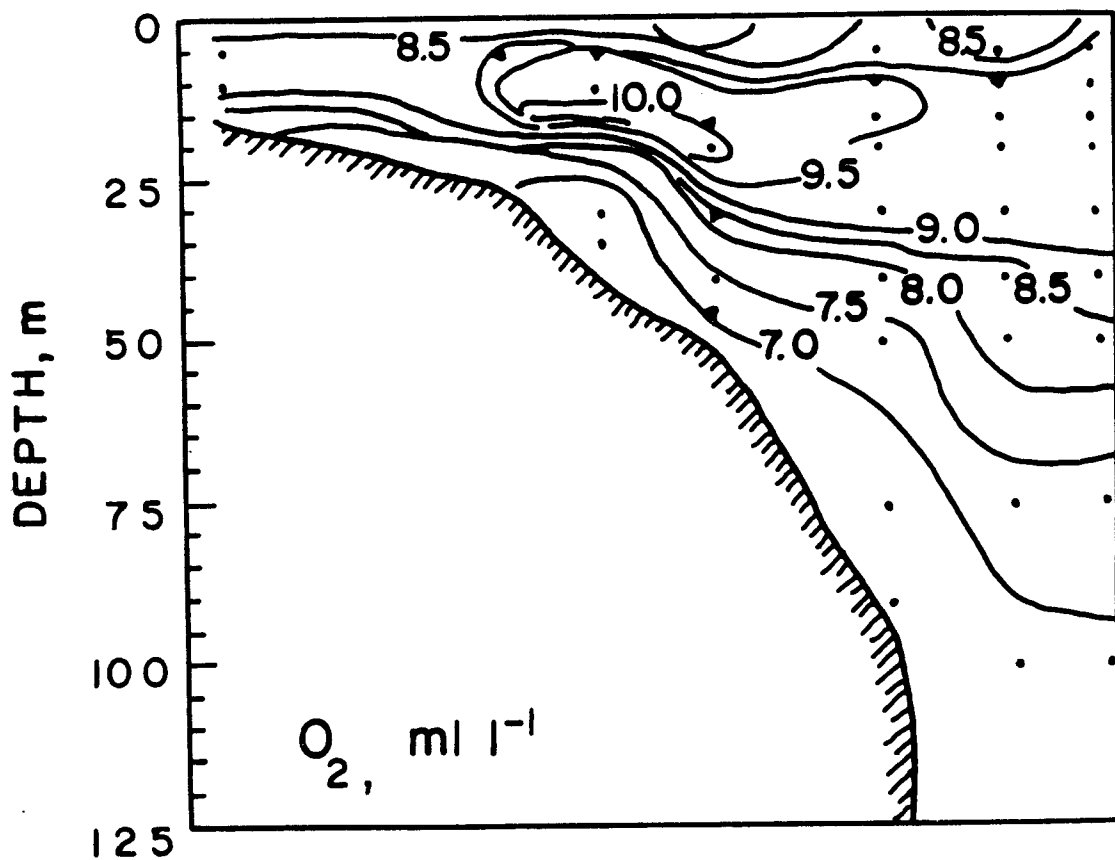


Figure 4. Vertical profile of dissolved oxygen (ml l^{-1}) in early August 1972 near Barter Island (from Hufford, 1974).

found an excellent correlation between $\delta^{13}\text{C}$ values and apparent oxygen utilization (AOU) in midoceanic waters. He expressed the relationship by the regression equation: $\delta^{13}\text{C} = 1.5 - 0.0075(\text{AOU})$.

Assuming a $\delta^{13}\text{C}$ value of -25 ‰ for organic carbon in this region, a $\delta^{13}\text{C}$ value of 1.5 ‰ for surface polar DIC (Kroopnick et al., 1977) and an average seawater alkalinity of 2.3 m moles l^{-1} (Broecker, 1974), I computed the $\delta^{13}\text{C}$ values of the DIC pool upwelled from depth into the euphotic zone as

$$\delta^{13}\text{C}_{\text{DIC}} = \frac{(2.3 \times 1.5 \text{ ‰}) + K(-25 \text{ ‰})}{2.3 + K}$$

where K equals the moles of CO_2 released into seawater through oxidation of organic matter. To calculate K, I used the salinity and temperature data from Hufford (1974) to obtain a saturation value of 8.6 ml l^{-1} for oxygen (0.38 m moles at STP), an O_2 minimum layer at 75% saturation at a depth of 150-200 m at Barter Island (Hufford et al., 1974), and a respiratory quotient of 0.77 (Broecker and Peng, 1982). Therefore,

$$K = [0.38 - 0.38(0.75)] \times 0.77$$

Solving,

$$\delta^{13}\text{C}_{\text{DIC}} = 0.7 \text{ ‰}.$$

A similar result ($\delta^{13}\text{C} = 0.8 \text{ ‰}$) is obtained using Kroopnick's (1985) regression equation. These calculations assume, however, that the surface water is nearly 100% oxygen saturated before significant phytoplankton production begins in early July. The difficulty of sampling during breakup has prevented us from making the necessary oxygen measurements, so this assumption is difficult to test. Hufford et al. (1974) noted a positive correlation between high salinities and oxygen supersaturation in near-freezing waters. This is caused by freeze concentration of solutes including oxygen during winter. We also suspect that sufficient exchange occurs between the ocean and atmosphere during breakup to allow conditions near equilibrium to develop.

Late summer dissolved oxygen measurements near Barter Island and elsewhere in the Beaufort Sea indicate that oxygen saturation in offshore surface waters may approach 120% (Figure 4; Hufford, 1974). This is attributed to photosynthesis beneath an ice cover that prevents air-sea exchange and retards establishment of equilibrium oxygen conditions. In this case, the net change in % O_2 saturation is nearly 45% (as opposed to 25%) and the $\delta^{13}\text{C}$ value of the DIC pool would approach 0 ‰ (Fig. 5). Thus, the $\delta^{13}\text{C}$ value of the upwelled DIC pool may range from 0.7 to 1.5 ‰ lighter than the DIC pool of typical arctic surface waters. Upwelling provides the mechanism to transport or cycle the ^{13}C -depleted DIC into the euphotic zone. Future studies in this

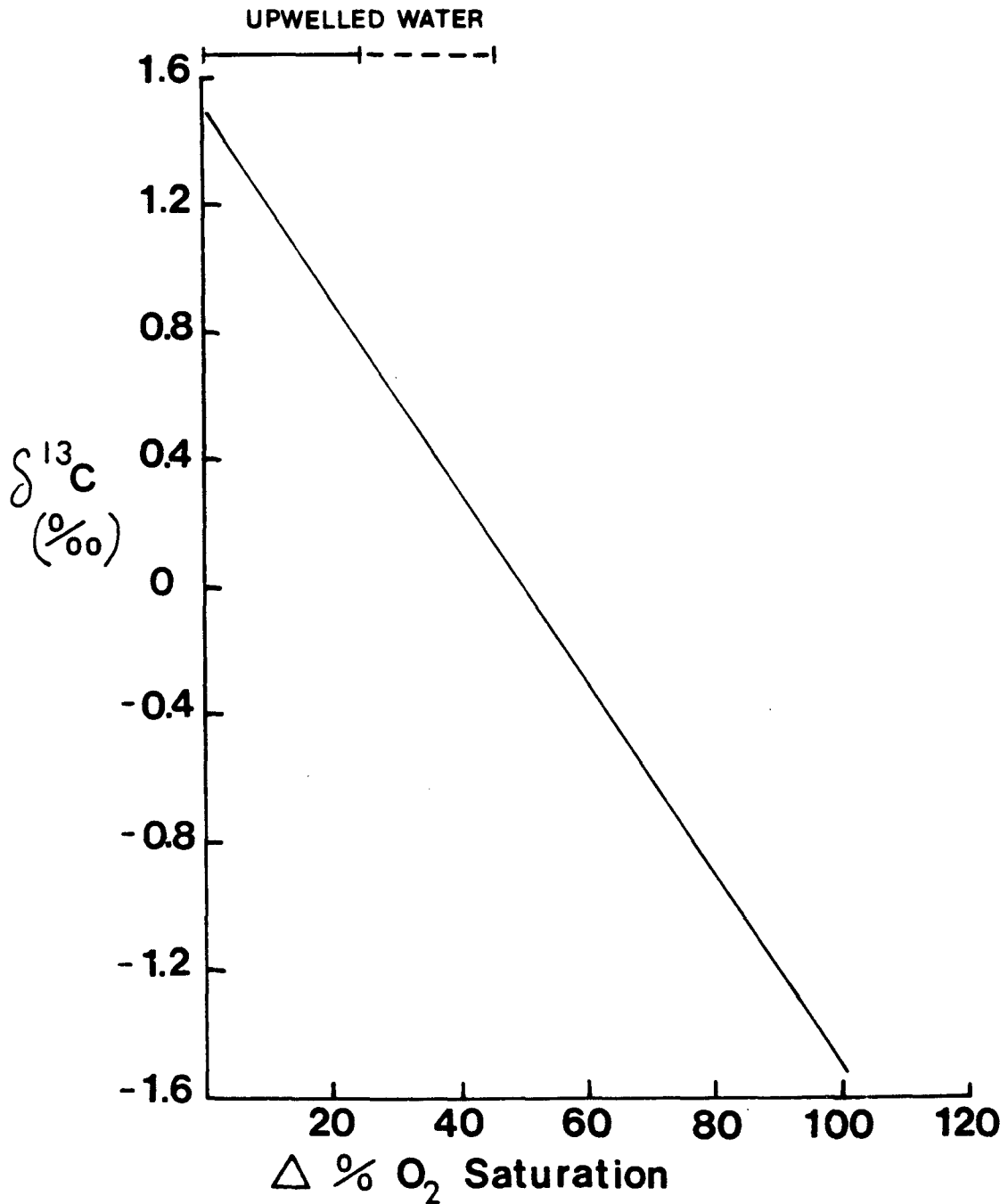


Figure 5. The effect of biogenic CO_2 produced from the oxidation of organic matter (based on the net change in $\% \text{O}_2$ saturation between the surface and the O_2 minimum layer) on the $\delta^{13}\text{C}$ value of the DIC pool.

area will focus on the collection of water samples for $\delta^{13}\text{C}$ analysis of the DIC pool to resolve this question.

Ecological significance of zooplankton $^{13}\text{C}:^{12}\text{C}$ ratios on the Beaufort Sea shelf

The distinct trend in zooplankton $\delta^{13}\text{C}$ across the Alaskan Beaufort Sea shelf appears to be due to the intrusion of water masses having distinct physical or chemical characteristics. From Pt. Barrow (158°W) to longitude 147°W (the most easterly extent of the warm Alaskan coastal water), the zooplankton $\delta^{13}\text{C}$ value drops about 1 ‰, coincident with the dilution of the warm coastal water with ambient surface water. From 147°W to Barter Island (143°W), the $\delta^{13}\text{C}$ values of both copepods and chaetognaths drop sharply by 1 to 2 ‰. This rapid change in $^{13}\text{C}:^{12}\text{C}$ ratios coincides with the upwelling at Barter Island. The upwelled water is characterized by a DIC pool that may be 0.7 to 1.5 ‰ lighter than surface DIC, according to our calculations.

The upwelling identified at Barter Island is also accompanied by the highest primary production rates ($>50 \text{ g C m}^{-2}\text{yr}^{-1}$) on the Alaskan Beaufort Sea coast (Schell et al., 1982), and by the feeding activity of bowhead whales (Lowry and Frost, 1984). Thus, given otherwise identical physical and chemical oceanographic conditions, isotopic changes in zooplankton $^{13}\text{C}:^{12}\text{C}$ ratios may be a valuable tool for locating areas of potential ecological

significance. In addition, the low $\delta^{13}\text{C}$ values (-24 to -25 ‰) of eastern Beaufort Sea zooplankton collected far offshore, where an ice cover is usually present year-round, reflect the high water stability that cycles biogenic CO_2 in the arctic surface layer (0-200 m). This situation may be analogous to the depletion of plankton ^{13}C caused by refixation of biogenic CO_2 in a subalpine lake (Rau, 1978). In the western Alaskan Beaufort Sea, the $\delta^{13}\text{C}$ values of offshore zooplankton (station 9) are isotopically heavier and reflect the influence of the Bering Sea water flowing northward into the Arctic Polar Basin (Coachman and Barnes, 1961).

Comparison of the isotopic composition of the two calanoid species with the chaetognath Sagitta elegans in the Beaufort also provides a measure of the ^{13}C enrichment between trophic levels on a geographical basis. Adults of C. glacialis are small (2-3 mm) and occupy the western Alaskan Beaufort Sea, while C. hyperboreus are large (6-7 mm) and occupy the eastern Beaufort Sea (Table 1), with little overlap between the two species. The $\delta^{13}\text{C}$ value of S. elegans averaged 1.0 ‰ heavier than C. hyperboreus (range 0.2 to 2.1 ‰), and 2.5 ‰ heavier than C. glacialis (range 2.1 to 3.0 ‰). The isotopic difference between phytoplankton and C. hyperboreus near Barter Island was only 0.1 ‰ (Table 2). Previous estimates of the ^{13}C enrichment per trophic level have ranged from 0.7 to 1.5 ‰ (McConnaughey and McRoy, 1979a; Rau et al., 1982).

The large isotopic difference between C. glacialis and S. elegans in the western Alaskan Beaufort Sea may be explained by the addition of zooplankton omnivores in the diet of S. elegans. Such omnivores include nonselective suspension feeders such as invertebrate larvae and small amphipods (e.g., Apherusa glacialis), which would be isotopically heavier than the calanoid herbivores and would represent an intermediate trophic level between chaetognaths and copepods. In the eastern Beaufort Sea, S. elegans may derive nearly all of its carbon by preying exclusively on the larger C. hyperboreus.

The $^{13}\text{C}:^{12}\text{C}$ ratios of plankton analyzed from the eastern Beaufort Sea nearly approximate plankton $\delta^{13}\text{C}$ values of south polar seas. Near Barter Island, copepod and phytoplankton $\delta^{13}\text{C}$ values ranged from -25.2 to -26 ‰, compared to -26 to -30 ‰ for south polar seas (Sackett et al., 1965; Eadie and Jeffrey, 1973). Using plankton isotopic data obtained from the western Beaufort, Rau et al. (1982) reached a different conclusion, but for reasons that can be explained on the basis of the data presented here. The trends in plankton $\delta^{13}\text{C}$ values illustrated in our study lend further support to the importance of different water types in modifying carbon isotope abundances in marine plankton. But in this case, we attribute the isotope changes to temperature and DIC effects, and not to differences in phytoplankton biosynthesis and metabolism associated with changes in species composition.

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APPENDICES

APPENDIX A

Summary of average photosynthetic and dark fixation rates (means \pm 95% confidence limits) in different regions of the frond of Laminaria solidungula based on uptake of $^{14}\text{CO}_2$ in plants incubated at 6.5 m.

Incubation No.	Measurement date	Hours of incubation	Net Photosynthesis (mg C x 10 ⁻⁴ mg ⁻¹ hr ⁻¹)			Dark Carbon Fixation		
			Meristem	Basal Blade	Blade 2	Meristem	Basal Blade	Blade 2
1	29-30 July	18	1.33 \pm 0.48	1.86 \pm 0.26	1.16 \pm 0.47	---	---	---
2	1-2 August	24.5	1.09 \pm 0.30	0.98 \pm 0.22	0.70 \pm 0.21	0.22 \pm 0.07	0.20 \pm 0.07	0.15 \pm 0.09
3	2-3 August	27	0.85 \pm 0.24	1.17 \pm 0.18	0.47 \pm 0.06	0.07 \pm 0.04	0.09 \pm 0.02	0.04 \pm 0.01
4	2-3 August	24.5	0.77 \pm 0.21	1.14 \pm 0.20	0.77 \pm 0.23	0.17 \pm 0.09	0.15 \pm 0.07	0.11 (N=1)

APPENDIX B

Percent carbon, nitrogen and C:N ratios for Laminaria solidungula stipes collected seasonally from November 1979 to November 1980.

Month (gwyr 1980)	Cat #	% C	% N	C:N
November	119-S-1	36.9	1.5	24.6
	119-S-17	33.8	1.6	21.1
February	20-S-1	35.1	1.6	21.9
	20-S-2	31.0	2.0	15.5
April	40-S-27	32.0	1.6	20.0
	40-S-31	34.8	1.2	29.0
August	80-S-24	36.5	1.9	19.2
	80-S-31	35.6	2.8	12.7
November	110-S-30	36.4	1.4	26.0

APPENDIX C

Annual weight gain of entire plants compared to the weight gain in the basal blade for plants incubated in situ at DS-11 in gwyr 1981.

Plant No.	Plant initial wet weight (g) Nov. 80	Plant final wet weight (g) Nov. 81	Plant wet weight increase (g)	Weight of first blade (g)	% difference between columns 2 and 3
1	10.2	15.0	4.8	4.2	-14.3
4	12.5	17.6	5.1	5.6	+8.9
5	14.6	21.9	7.3	6.9	-5.8
7	20.2	27.8	7.6	7.8	+2.6
8	10.1	14.2	4.1	4.4	+6.8
10	11.6	16.6	5.0	4.2	-19.0
11	16.2	27.9	11.7	11.9	+1.7
12	14.9	21.7	6.8	7.6	+10.5
13	12.2	18.9	6.7	6.3	-6.3
16	24.2	36.5	12.3	13.2	+6.8
18	14.3	21.4	7.1	7.1	0
20	10.4	15.2	4.8	4.6	-4.3
22	16.6	24.5	7.9	8.4	+5.9
Mean % change:					-0.5

APPENDIX D

$\delta^{13}\text{C}$ values ($^{\circ}/\text{oo}$) of kelp tissue discs punched along the frond of two Laminaria solidungula plants collected in April and November at DS-11

Date	First blade meristem	First blade top	Second blade middle	Distal blade
April 1980	-15.8	-15.7	-15.7	-18.2
November 1981	-16.3	-17.1	-15.8	ND

ND: no data

APPENDIX E. Summary of $\delta^{13}\text{C}$ values (‰) of biota collected in the Beaufort Sea.

Sample Number	Description	$\delta^{13}\text{C}_{\text{CSL}}$	$\delta^{13}\text{C}_{\text{SIRA}}$
BOULDER PATCH			
PORIFERA			
41-4	<u>Choanites lutkenii</u>	-20.0	
70-28	<u>Choanites lutkenii</u>		-18.7
111-14	<u>Choanites lutkenii</u>		-19.9
41-18	<u>Haliclona gracilis</u>		-21.8/-21.1
70-47	<u>Haliclona gracilis</u>		-23.4
41-9	<u>Halichondria panicea</u>		-20.6
41-14	<u>Halichondria panicea</u>		-21.6
41-2	<u>Phakettia cribrosa</u>	-18.6	
41-16	<u>Phakettia cribrosa</u>		-20.4
70-32	<u>Phakettia cribrosa</u>		-22.1
CNIDARIA			
Hydrozoa			
41-58,12	Unknown hydroid(?)		-22.7
41-59	<u>Sertularia cupressoides</u>	-23.5	
70-60	<u>Sertularia cupressoides</u>		-23.9
71-1	<u>Sertularia cupressoides</u>		-23.7
70-59	<u>Thuiaria sp.</u>	-23.2	-23.3
Anthozoa			
41-20	<u>Gersemia rubiformis</u>	-22.0	
70-49(1)	<u>Gersemia rubiformis</u>		-22.6
70-49(2)	<u>Gersemia rubiformis</u>		-23.0
70-49(3)	<u>Gersemia rubiformis</u>		-23.1
111-6(1)	<u>Gersemia rubiformis</u>		-22.6
111-6(2)	<u>Gersemia rubiformis</u>		-22.1
51-BF37-1	<u>Gersemia rubiformis</u>		-23.3
Scyphozoa			
70-19	<u>Lucernaria infundibulum</u>	-20.3	

APPENDIX E. (Continued)

41-56	<u>Lucernaria infundibulum</u>	-18.2
41-31	<u>Lucernaria infundibulum</u>	-19.4
NEMERTEA		
41-36	<u>Cerebratulus</u> sp.	-18.5
81-DS30-9	<u>Cerebratulus</u> sp.	-20.6
51-BF37-10	<u>Cerebratulus</u> sp.	-19.4
70-10F	<u>Cerebratulus</u> sp.	-20.0
ANNELIDA		
Polychaeta		
81-DS30-10	<u>Anaitides groenlandica</u>	-20.6
41-6	<u>Antinoella sarsi</u>	-20.8
70-101	<u>Brada sachalina</u> (composite)	-19.5
119-4F	<u>Chaetozone setosa</u> (composite)	-21.6
111-7	<u>Cirratulus cirratus</u> (composite)	-22.2
41-33	<u>Cirratulus cirratus</u> (composite)	-20.9
41-26	<u>Flabelligera affinis</u> (composite)	-18.8
70-50	<u>Flabelligera affinis</u> (composite)	-20.6
110-7F	<u>Haploscoloplos elongata</u> (composite)	-19.9
59-5F	<u>Haploscoloplos elongata</u> (composite)	-20.2
70-6F	<u>Haploscoloplos elongata</u> (composite)	-19.3
70-67	<u>Harmothoe imbricata</u>	-19.5
41-49	<u>Harmothoe imbricata</u>	-21.7
71-55	<u>Nereis zonata</u>	-23.4
71-3	<u>Nereis zonata</u>	-19.2
71-4	<u>Nereis zonata</u>	-25.0
83-BF37-3	<u>Nereis zonata</u>	-24.4
111-4	<u>Nereis zonata</u>	-22.3
70-54, 55	<u>Nereis zonata</u>	-21.7
70-56	<u>Nereis zonata</u>	-24.9
83-BF37-4	<u>Nicolea zostericola</u> (composite)	-21.8
83-1	<u>Nicolea zostericola</u> (composite)	-18.8

APPENDIX E. (Continued)

70-58	Orbiniidae (composite)		-17.3
41-52	<u>Spinther alaskensis</u>	-21.8	
70-2	<u>Spinther alaskensis</u>	-21.5	-22.1
70-3	<u>Spinther alaskensis</u>		-22.2
41-48	Terebellidae (composite)		-20.1
119-1F	<u>Terebellides stroemi</u> (composite)		-21.6
79-3F	<u>Terebellides stroemi</u> (composite)		-21.7
MOLLUSCA			
Gastropoda			
51-BF37-2	<u>Buccinum angulosum</u>		-19.7
71-DS30-17	<u>Buccinum angulosum</u>		-17.9
70-18	<u>Eubranchus</u> sp. (Eolid Nudibranch)		-18.3
41-69	<u>Eubranchus</u> sp. (Eolid Nudibranch)		-21.7
41-29	<u>Eubranchus</u> sp. (Eolid Nudibranch)		-20.7
70-6	<u>Margarites vorticifera</u>		-16.4
70-27	<u>Margarites vorticifera</u>		-15.3
81-DS30-1	<u>Margarites vorticifera</u>		-17.0
111-3(1)	<u>Margarites vorticifera</u>		-18.1
41-10(2)	<u>Margarites vorticifera</u>		-16.4
81-DS30-2	<u>Margarites vorticifera</u>		-16.5
41-10(1)	<u>Margarites vorticifera</u>		-17.1
51-BF37-8	<u>Natica clausa</u>		-22.2
51-BF37-15	<u>Neptunea heros</u>		-22.1
70-17	<u>Neptunea borealis</u>		-18.4
70-62	<u>Oenopota</u> sp.		-20.2
111-5	<u>Plicifusus kroyeri</u>		-20.0
70-103	<u>Plicifusus kroyeri</u>		-19.7
41-63	<u>Plicifusus kroyeri</u>		-19.2
41-11	<u>Polinices</u> spp. (several)	-17.0	
81-DS30-15	<u>Polinices pallidus</u>		-22.2/-22.4
70-63(2)	<u>Polinices pallidus</u>		-17.1
70-63(1)	<u>Polinices pallidus</u>		-18.6
41-13(2)	<u>Polinices pallidus</u>		-17.2

APPENDIX E. (Continued)

41-13(1)	<u>Polinices pallidus</u>		-17.2
71-2	<u>Velutina undata</u>		-22.4
Polyplacophora			
70-20	<u>Amicula vestita</u>	-17.8	
70-43A	<u>Amicula vestita</u>		-18.9
70-43B	<u>Amicula vestita</u>		-19.0
70-44	<u>Amicula vestita</u>		-19.2
70-45	<u>Amicula vestita</u>		-18.9
70-8	<u>Amicula vestita</u>		-19.2
70-102	<u>Amicula vestita</u>		-17.4
41-3	<u>Amicula vestita</u>	-17.5	-17.6
41-72(1)	<u>Amicula vestita</u>		-18.0
41-72(2)	<u>Amicula vestita</u>		-18.5
111-1(1)	<u>Amicula vestita</u>		-17.5
111-1(2)	<u>Amicula vestita</u>		-18.4
70-16	<u>Ischnochiton albus</u>		-17.8
41-28(1)	<u>Ischnochiton albus</u>		-17.4
41-28(2)	<u>Ischnochiton albus</u>		-17.5
41-74	<u>Ischnochiton albus</u>		-18.5
111-2(1)	<u>Ischnochiton albus</u>		-16.4
111-2(2)	<u>Ischnochiton albus</u>		-18.6
110-3	<u>Ischnochiton albus</u>		-17.2
Bivalvia			
81-DS30-21	<u>Musculus discors</u>		-21.6
ARTHROPODA			
Pycnogonida			
81-DS30-3(2)	<u>Nymphon grossipes</u>		-21.0
81-DS30-3(1)	<u>Nymphon grossipes</u>		-22.0
Crustacea			
41-73	<u>Hyas coarctatus alutaceus</u>		-20.4
70-40	<u>Hyas coarctatus alutaceus</u>		-20.5
70-65	<u>Hyas coarctatus alutaceus</u>		-19.7
41-44(1)	<u>Mysis litoralis</u> (3 ind.)	-19.4	

APPENDIX E. (Continued)

41-44(2)	<u>Mysis litoralis</u> (3 ind.)	-18.9	
111-1(11-81-01)	<u>Mysis litoralis</u> (4 ind.)	-20.0	
41-43J	<u>Mysis litoralis</u> (8, ind. all juveniles)	-20.9	
81-DS30-8(8)	<u>Mysis litoralis</u> (8 ind.)		-20.8
81-DS30-8(2)	<u>Mysis litoralis</u> (8 ind.)		-21.1
81-DS30-8(1)	<u>Mysis litoralis</u> (8 ind.)		-20.6
81-2(8-81-02)	<u>Mysis litoralis</u> (3 ind.)	-21.2	
81-DS30-11	<u>Pagarus trigonocheirus</u>		-18.4
81-DS30-19	<u>Pagarus trigonocheirus</u>		-19.5
81-DS30-20	<u>Pagarus trigonocheirus</u>		-19.0
70-25	<u>Saduria entomon</u>	-21.5	
30-9F	<u>Thysanoessa raschii</u> (composite)		-20.2
119-8F	<u>Thysanoessa raschii</u> (composite)		-21.6
Amphipods			
41-40(1)	<u>Anonyx sarsi/nugax</u>		-20.1
41-40(2)	<u>Anonyx sarsi/nugax</u>		-19.9
70-26	<u>Anonyx sarsi/nugax</u>	-21.7	-22.2
41-1(1)	<u>Atylus carinatus</u>	-19.5	
41-1(2)	<u>Atylus carinatus</u>	-22.3	
41-1(3)	<u>Atylus carinatus</u>		-19.9
83-BF37-2	<u>Atylus carinatus</u>		-19.8
51-BF37-4	<u>Atylus carinatus</u>		-20.3
83-BF37-1	<u>Atylus carinatus</u>	-19.7	
41-42	<u>Gammaracanthus loricatus</u>	-20.2	
51-BF37-12	<u>Gammaracanthus loricatus</u>		-20.5
41-77	<u>Gammarus setosus</u>	-20.5	
51-BF37-9	<u>Paramphithoe polyacantha</u> <u>bruggeni</u>		-22.9
41-76	<u>Weyprechtia heuglini</u>	-21.0	
BRYOZOA			
41-37	<u>Alycondium</u> sp.		-23.5
41-35	<u>Alycondium gelatinosum</u>		-21.8

APPENDIX E. (Continued)

70-48	<u>Eucratea loricata</u>	-25.9	
70-48A	<u>Eucratea loricata</u>	-25.4	
41-70	<u>Eucratea loricata</u>		-23.3
70-46	<u>Flustra carbacea</u>	-23.8	-24.0
51-BF37-14	<u>Flustra securifrons</u>	-22.6	
41-60	<u>Flustrella</u> sp.		-22.5
111-8	<u>Flustrella</u> sp.		-23.6
ECHINODERMATA			
41-7	<u>Leptasterias groenlandica</u>	-21.7	
70-39	<u>Leptasterias groenlandica</u>	-20.8	
70-1	<u>Leptasterias polaris</u> (juvenile)		-23.1
UROCHORDATA			
41-34	<u>Mogula griffithsii</u>	-18.8	
81-DS30-14	Burrowing ascidian		-21.2
CHORDATA			
41-21	<u>Boreogadus saida</u> (4.0 cm)	-21.2	
110-1(1)	<u>Boreogadus saida</u> (1.5 cm)		-22.5
110-1(2)	<u>Boreogadus saida</u> (1.5 cm)		-22.7
110-1(3,4)	<u>Boreogadus saida</u> (1.5 cm)		-22.7
81-DS30-18	<u>Boreogadus saida</u> (13.0 cm)		-19.1
51-BF37-13	<u>Boreogadus saida</u> (4.5 cm)		-21.9
81-PB-2	<u>Boreogadus saida</u> (7 cm)		-18.6
81-PB-3	<u>Boreogadus saida</u> (7 cm)		-20.4
81-PB-4	<u>Boreogadus saida</u> (9 cm)		-18.8
41-25	<u>Gymnelis viridis</u>		-19.8
110-2(1)	<u>Liparis herschelinius</u>		-21.4
110-2(2)	<u>Liparis herschelinius</u>		-21.6
41-38(1)	<u>Liparis herschelinius</u>	-21.3	
41-38(2)	<u>Liparis herschelinius</u>	-20.1	
41-75	<u>Myoxocephalus quadricornis</u>	-18.8	
70-38	<u>Myoxocephalus quadricornis</u>	-19.4	-19.9

APPENDIX E. (Continued)

ALGAE

41-26B2	<u>Laminaria solidungula</u>	-14.6
Unknown (6 Feb 1982)	<u>Laminaria solidungula</u>	-14.7
41-68	<u>Neodilsea integra</u>	-18.8

EASTERN BEAUFORT SEA

83-BIS-4	<u>Haliclona gracilis</u>	-22.5
81-SC-1(1) (8-81-SC1)	<u>Calanus hyperboreus</u> (12 ind.)	-24.6
81-SC-1(2) (8-81-SC2)	<u>Calanus hyperboreus</u> (14 ind.)	-23.2
81-SC-13	<u>Thuiaria</u> sp.	-26.3
81-BDR-1(8-81-BDR)	<u>Mysis litoralis</u> (3 ind.)	-21.0
83-BIS-3	<u>Mysis litoralis</u> (3 ind.)	-22.0
81-SC-3(8-81-SC3)	<u>Mysis litoralis</u> (composite)	-20.8
83-BIS-6	<u>Saduria entomon</u>	-20.8
83-BIS-7	<u>Acanthostephia behregensis</u>	-18.7
83-BIS-8	<u>Acanthostephia behregensis</u>	-19.2
81-BL-6(2)	<u>Acanthostephia behregensis</u>	-20.9
83-BIS-10	<u>Atylus carinatus</u>	-19.6
83-BIS-9	<u>Atylus carinatus</u>	-20.5
81-BDR-3(1)	<u>Atylus carinatus</u>	-19.5
81-DB-1	<u>Atylus carinatus</u>	-19.6
82-CB-2	<u>Gammaracanthus loricatus</u>	-20.7
82-CB-7	<u>Gammarus setosus</u>	-20.0
82-CB-4(1)	<u>Onisimus litoralis</u>	-22.0
83-BIS-1	<u>Eucratea loricata</u>	-25.2
81-SC-11	<u>Flustrella</u> sp.	-22.8
81-SC-12	<u>Flustrella</u> sp.	-21.2
81-BL-4(1)	<u>Rhizomogula globularis</u>	-26.1
82-CB-1(1)	<u>Rhizomogula globularis</u>	-25.3
82-CB-1(2)	<u>Rhizomogula globularis</u>	-24.9
81-BL-10(1)	<u>Myoxocephalus quadricornis</u>	-19.5

APPENDIX E. (Continued)

81-BL-10(2)	<u>Myoxocephalus quadricornis</u>	-19.3
81-BL-7(1)	<u>Myoxocephalus quadricornis</u>	-19.2
81-BL0-2	<u>Myoxocephalus quadricornis</u>	-20.2
81-SC-10(1)	<u>Mallatus villosus</u>	-20.2
81-SC-10(2)	<u>Mallatus villosus</u>	-20.8
81-BL-5	<u>Liopsetta glacialis</u>	-19.5
83-BL-2	<u>Coregonus autumnalis</u>	-21.2
83-BL-3	<u>Coregonus autumnalis</u>	-23.0

PRUDHOE BAY

PBT2-T7-1	<u>Calanus glacialis</u> (composite)	-22.3
PBT2-T7-2	<u>Calanus glacialis</u> (composite)	-22.4
92-PB-4(1)	<u>Mysis litoralis</u> (composite)	-23.3
92-PB-4(2)	<u>Mysis litoralis</u> (composite)	-24.4
81-PB-1	<u>Mysis relicta</u> (3 ind.)	-22.0
92-PB-2(1)	<u>Anonyx sarsi/nugax</u>	-21.4
92-PB-2(2)	<u>Anonyx sarsi/nugax</u>	-23.9
92-PB-1	<u>Gammaracanthus loricatus</u>	-21.4
92-PB-7(1)	<u>Saduria entomon</u>	-22.5
44-PB-1	<u>Cerebratulus</u> sp.*	-20.9
79-II-1	<u>Terebellides stroemi</u> * (composite)	-21.7
79-II-2	<u>Terebellides stroemi</u> * (composite)	-21.5
119-II-3	<u>Chaetozone setosa</u> * (composite)	-21.3
81-DS21-1	<u>Priapulus caudatus</u>	-19.1
81-DS21-3	<u>Eucratea loricata</u>	-21.8
81-DS21-2	<u>Flustrella</u> sp.	-24.7

* Previously in formalin and red dye, extracted.

WESTERN BEAUFORT SEA

NTA-1	Ice Algae	-19.7
NT3B	Ice Algae	-18.5

APPENDIX E. (Continued)

PBT2-T7-1	<u>Calanus glacialis</u> (composite)	-22.3	
23-CH-1(1)	<u>Balanus crenatus</u> (composite)	-19.5	
23-CH-1(2)	<u>Balanus crenatus</u> (composite)	-19.4	
23-CH-2	<u>Eucratea loricata</u>	-19.7	
23-CH-6	<u>Eucratea loricata</u>		21.1
23-CH-3	<u>Saduria entomon</u>	-19.0	
23-CH-3A	<u>Saduria entomon</u>	-19.2	
23-CH-4	<u>Buccinum polare</u>	-17.5	
23-CH-5	Hermit crab		-18.5

CHUKCHI SEA

93-IE2A-D(A)	Phytoplankton (<u>Chaetoceros</u>)	-22.2	
93-IE2A-D(B)	Phytoplankton (<u>Chaetoceros</u>)		-22.6
93-CK7-2	<u>Phakettia cribrosa</u>	-18.9	
93-CK40-8	<u>Thuiaria</u> sp.	-19.3	
93-CK15-2(B)	<u>Gersemia rubiformis</u>	-20.1	
93-CK15-1	<u>Gersemia rubiformis</u>		-20.8
93-CK15-1A	<u>Gersemia rubiformis</u>		-21.0
93-CK11-3	<u>Lumbrineris</u> sp.		-19.4
93-CK7-3	<u>Antinoella sarsi</u>		-20.3
60-PST55-1(1)	<u>Axiothella catenata</u>		-17.6
60-PST55-2	<u>Scalibregma inflatum</u>		-17.4
93-CK4-8	<u>Natica clausa</u>		-17.4
93-CK4-2(1)	<u>Natica clausa</u>		-18.1
93-CK4-2(2)	<u>Natica clausa</u>		-17.6
93-CK11-1	<u>Buccinum angulosum</u>		-17.5
93-CK9-4	<u>Buccinum angulosum</u>		-17.9
93-CK4-9	<u>Margarites obvaceous marginatus</u>		-16.8
93-CK4-5	<u>Margarites costalis</u>		-16.7
93-CK4-6	<u>Margarites costalis</u>		-17.0
93-CK4-7	<u>Polinices pallidus</u>		-18.0
93-CK4-3	<u>Neptunea borealis</u>		-16.3
93-CK4-4	<u>Velutina undata</u>		-20.8

APPENDIX E. (Continued)

CK-36-3D (93-CK36-3)	<u>Amicula vestita</u>	-16.0	
93-CK15-4	<u>Eucretea loricata</u>		-20.9
93-CK15-4B	<u>Eucretea loricata</u>		-21.7
93-CK36-2	<u>Flustra carbacea</u>	-18.7	
CK-38-3D (93-CK38-3)	<u>Flustra securifrons</u>	-18.6	
93-CK39-43	<u>Chelyosoma macleayanum</u>	-19.7	
CK-36-9D (93-CK36-9)	<u>Boreogadus saida</u>	-19.0	

STANDARDS

KS (82-13-69, Ziemann)	<u>Laminaria solidungula</u>	-16.8	
KS-A (7-26-83)	<u>Laminaria solidungula</u>	-14.4	
KS-B (10-10-83)	<u>Laminaria solidungula</u>	-14.8	
KS-FE	<u>Laminaria solidungula</u>	-15.4	
K-1	<u>Laminaria solidungula</u>		-15.0
K-2	<u>Laminaria solidungula</u>		-15.1
28 Oct 1982	Sucrose (9.8, 9.9, and 9.7)	- 9.8	
Sucrose-2	Sucrose (23 Dec 1983)	-10.0	
30 Sept 1982	Brine shrimp (as CO ₂ gas)	-18.3	
Ziemann's sample	Brine shrimp	-18.9	
BS-SF-1	Brine shrimp (San Francisco)		-18.9
BS-OD-1	Brine shrimp (Oregon Desert)		-19.8
BS-OD-4	Brine shrimp (Oregon Desert)		-20.1
BS-OD-5	Brine shrimp (Oregon Desert)		-20.1
Gollub Standard	(23 Dec 1983, CSL)	-13.0	(¹⁸ O = -28.7)
Gollub Standard	(NASA-AMES)	-12.64	(¹⁸ O = 11.31)
Sucrose (ANU)			-10.2

EXTRACTIONS

40-K-FA	<u>Laminaria solidungula</u> (scrape)	-19.4	
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APPENDIX E. (Continued)

40-K-FA-E	<u>Laminaria solidungula</u> (scrape)	-18.9
23-CH-A (2-3)	<u>Balanus crenatus</u>	-18.6
23-CH-A-E (2-4)	<u>Balanus crenatus</u>	-18.6
23-CH-D (1-1)	<u>Saduria entomon</u>	-19.5
23-CH-F (1-2)	<u>Saduria entomon</u>	-20.6
23-CH-FE (1-4)	<u>Saduria entomon</u>	-21.6
G77-28-P(1)	Oil from <u>Thalassiosira</u>	-30.3
G77-28-P(2)	Oil from <u>Thalassiosira</u>	-30.3
G77-28-C(1)	Oil from <u>Calanus hyperboreus</u>	-26.2
G77-28-C(2)	Oil from <u>Calanus hyperboreus</u>	-26.9
G77-28-PP(A)	Nonlipid - <u>Thalassiosira</u>	-23.1
G77-28-PP(B)	Nonlipid - <u>Thalassiosira</u>	-23.2
G77-28-CP(A)	Nonlipid - <u>Calanus hyperboreus</u>	-23.7
G77-28-CP(B)	Nonlipid - <u>Calanus hyperboreus</u>	-23.7
Cu0-1	0.2 mg C	-16.6
Cu0-2	0.1 mg C	-16.3

SUMMARY OF CARBON ISOTOPE RATIOS OF ZOOPLANKTON -
CGS GLACIER (1977)

Station	Chaetognath		Copepod		Other	
	<u>Sagitta</u> Cat #	<u>elegans</u> $\delta^{13}\text{C}$	<u>Calanus</u> Cat #	sp. $\delta^{13}\text{C}$	Cat #	$\delta^{13}\text{C}$
G77-26	4	-23.6	1	-24.4 ⁺	2	-22.7/-22.1/ -23.7/-24.3 ^e
G77-30	3	-22.6	1A	-24.8*	2	-23.1/-24.4/ -23.2/-23.3 ^e
			1B	-24.6*		
G77-17	3	-21.5	1	-23.8*	2	-20.4 ^c
G77-41	3	-21.0	1	-23.3*		
G77-5	3	-20.9	2B	-23.3*	2A	-22.5 ^a
G77-12	3	-20.8	1	-23.7*		
G77-22	3	-24.6	1	-24.8 ⁺		
G77-28	3	-23.1	1	-25.2 ⁺	2	-23.0 ^e
G77-9	3	-20.9	1	-23.3*		
G77-37	3	-21.4	1	-24.5*/-24.4*		
G77-33	3	-21.6	1	-24.1*	2	-22.9 ^e
G77-25	3	-23.5	1	-24.4 ⁺		
G77-21	3	-24.0	1(2)	-25.0 ⁺ /-24.7 ⁺		
G77-10	3	-21.0	1	-23.4*		

- * Calanus glacialis
⁺ Calanus hyperboreus
^e Thysanoessa raschii
^c Cragonidae
^a Apherusa glacialis

NOTE: all samples are composites of at least six individuals.

SUMMARY OF CARBON ISOTOPE RATIOS IN LAMINARIA SOLIDUNGULA

Seasonal Variations

Month (gwy 1980)	Blade 1		Blade 2		ROP	
	Cat #	$\delta^{13}\text{C}$	Cat #	$\delta^{13}\text{C}$	Cat #	$\delta^{13}\text{C}$
November	119-B1-4	-14.8				
	119-B1-11	-15.3	119-B2-5	-14.4	119-ROP-9	-16.5
	119-B1-7	-14.8	119-B2-10	-14.7	119-ROP-1	-15.4
February	20-B1-7	-15.4	20-B2-28	-15.2	20-ROP-30	-16.0
	20-B1-28	-15.2	20-B2-7	-14.3	20-ROP-28	-15.6
April	40-B1-32	-16.4	40-B2-31	-15.3	40-ROP-33	-16.8
	40-B1-23	-16.2	40-B2-32	-15.7	40-ROP-19	-15.8
August	80-B1-8	-15.3	80-B2-18	-16.2	80-ROP-19	-13.9
	80-B1-12	-15.0	80-B2-7	-14.5	80-ROP-10	-16.1
November	110-B1-22	-13.4	110-B2-16	-14.8	110-ROP-32	-14.7
	110-B1-1	-13.5	110-B2-18	-15.5	110-ROP-28	-15.9

FROND VARIATIONS
(Same plant)

Date	Meristem(B1)	Blade 1(T1)	Blade 2(M2)	Distal End (DE)
April 1980	-15.8	-15.7	-15.7	-18.2
November 1982	-16.3	-17.1	-15.8	--

CSL: Coastal Science Laboratories, Austin, Texas.

SIRA: SIRA 9 mass spectrometer, University of Alaska, Fairbanks.

APPENDIX F. Mass spectrometric methods

The standards used in cross-calibration checks of our working CO₂ (Gollub) gas included NBS-22 ($\delta^{13}\text{C} = -29.8 \text{ ‰}$) and ANU sucrose ($\delta^{13}\text{C} = -10.15\%$). Our Gollub CO₂ working standard ($\delta^{13}\text{C} = 12.64 \text{ ‰}$; $\delta^{18}\text{O} = 11.31 \text{ ‰}$) was analyzed by D. Des Marais at NASA-Ames in Mountain View, California. Optimum sample size for analysis on our SIRA 9 mass spectrometer was 5 mg carbon (0.4 m moles or 9 cc CO₂). However, the automated coldfinger on the machine is capable of measuring quantities down to 2 μ mol CO₂.

The calculations used to determine $\delta^{13}\text{C}$ values from $^{13}\text{C}:^{12}\text{C}$ ratios of the samples are from Craig (1957). The raw $\delta^{13}\text{C}$ value is obtained by comparing the $^{13}\text{C}:^{12}\text{C}$ ratios of the standard and sample in the equation $\delta^{13}\text{C}_u = [^{13}\text{C}:^{12}\text{C}_{\text{sample}} / ^{13}\text{C}:^{12}\text{C}_{\text{standard}} - 1] \times 1000$ (where $\delta^{13}\text{C}_u$ is the uncorrected $\delta^{13}\text{C}$ value). Two corrections are then made. Their order is extremely important and must not be reversed. The Craig corrections for carbon and oxygen are made first. These corrections account for the ^{17}O contribution to mass-45 (which is about 6.5% of the total mass-45 beam). Secondly, since all analyses are measured against a standard other than PDB, the isotopic analyses must be converted to δ values relative to PDB. In the original SIRA 9 computer program, the order of these two calculations was reversed, resulting in erroneous $\delta^{13}\text{C}$ values. The problem has since been

corrected. Other information on mass spectrometric techniques and sample preparation is provided in Chapters 6 and 7.

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