

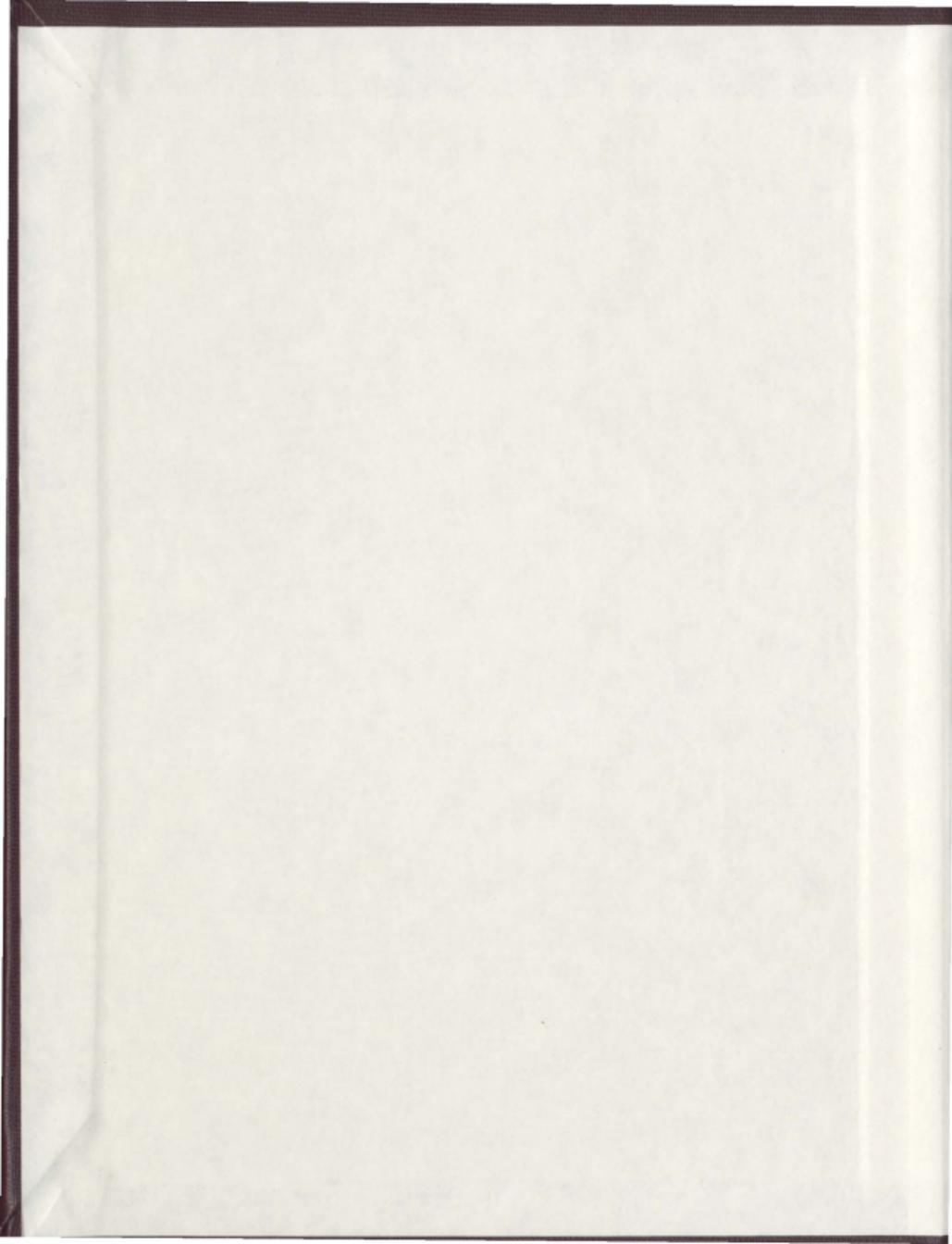
A COMPARATIVE STUDY OF THE PELAGIC FOOD
WEBS IN TWO NEWFOUNDLAND FJORDS USING
STABLE CARBON AND NITROGEN
ISOTOPE TRACERS

CENTRE FOR NEWFOUNDLAND STUDIES

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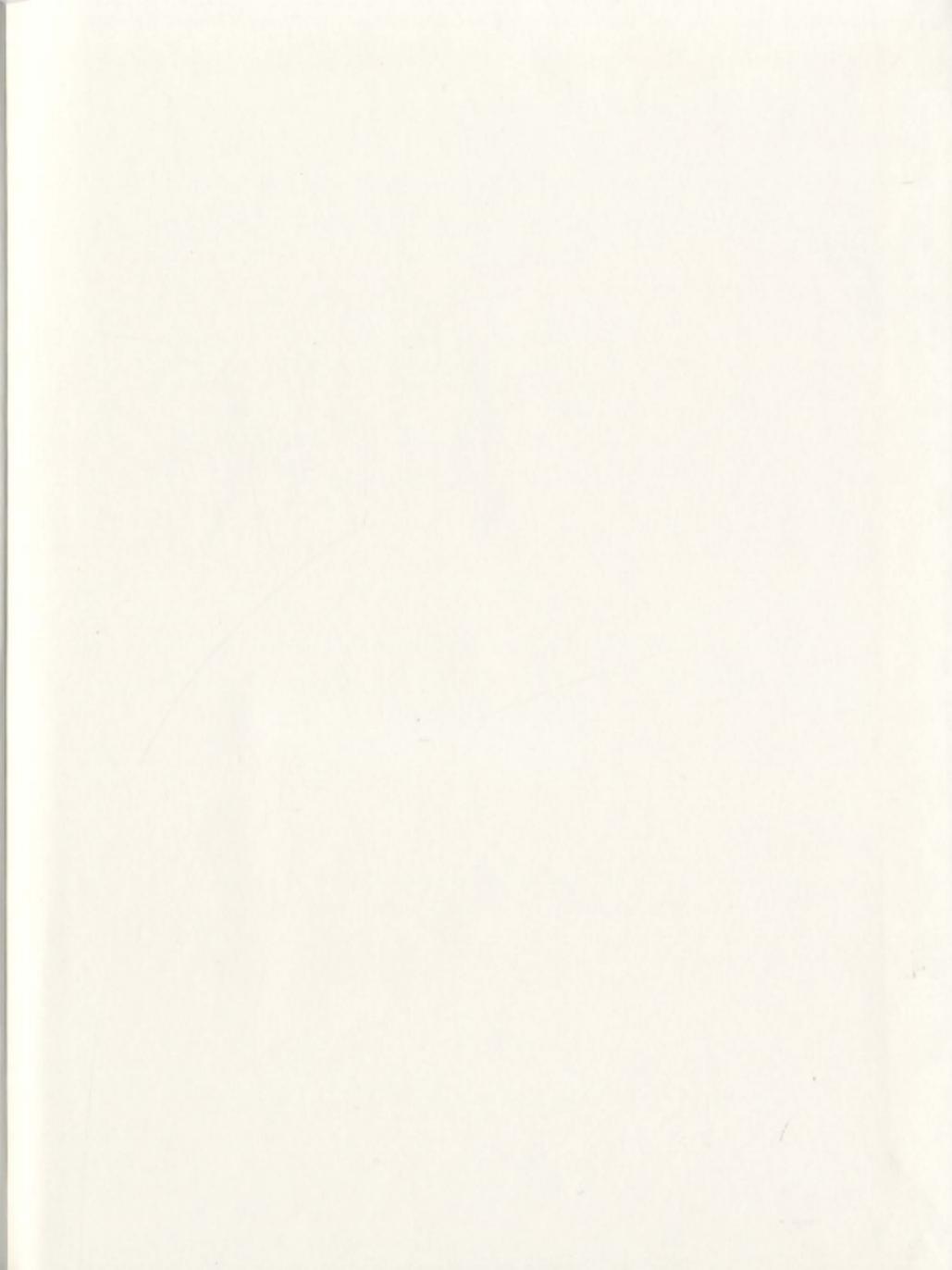
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MARY-LYNN DICKSON



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A COMPARATIVE STUDY OF THE PELAGIC FOOD WEBS IN TWO
NEWFOUNDLAND FJORDS USING STABLE CARBON AND NITROGEN
ISOTOPE TRACERS

BY

© MARY-LYNN DICKSON, B.Sc. (Honours)

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CANADA

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ABSTRACT

A comparative study was initiated to investigate the role of environmental variability on the trophic organization and structure of pelagic food chains in two fjords, Bay d'Espoir and Fortune Bay, along the south coast of Newfoundland, Canada. Although in close proximity, these fjords are biologically and physically distinct. On the basis of physical oceanographic studies, Bay d'Espoir was considered to be a relatively constant environment, while Fortune Bay had a dynamic water column, undergoing bi-annual deep-water renewal. Fauna, particulate organic matter (POM) and sediment were collected during summer and winter and analyzed for their stable carbon and nitrogen isotopic compositions.

This study entailed the elucidation of the trophic organization of the most complex ecosystems yet analyzed using dual stable isotope tracers. Stable carbon and nitrogen isotopes used in combination provided better resolution than either could have given singly. However, they only allowed the assignment of species to a trophic level and did not in themselves provide information on the linkages between and within levels.

The structure of the pelagic food webs and their principal food chains were determined for winter and summer. The trophic organization of the food webs was similar in both fjords within and between seasons; however, differences were observed in the food chains. With the exception of Bay d'Espoir in August, the top predators in both fjords occupied the fourth trophic level. The isotope data indicated which species were at intermediate trophic levels and the trophic position of the microzooplankton.

Three pelagic food chains were present in Bay d'Espoir during both seasons, while Fortune Bay had three in the winter and two in summer. On the basis of the carbon and nitrogen isotopic composition of the fauna and POM it is suggested these pelagic food chains are affiliated with specific water types. This study is the first to draw attention to a relationship between the isotopic composition of the fauna and POM deeper than the subsurface layer.

The trophic composition of the fauna differed between the two fjords; carnivores were dominant in Bay d'Espoir, while omnivores prevailed in Fortune Bay. A decrease in the proportion of omnivores in Fortune Bay was found between seasons, due to increased water column stability in the summer.

A progressive enrichment of ^{13}C and ^{15}N in the fauna was found with increasing trophic level. Trophic level enrichments calculated for each food web varied slightly between fjords and seasons. These values corresponded closely to those reported in the literature and suggest similar mechanisms are involved in the fractionation of stable isotopes in food chains, independent of geographic location. Although minor differences were noted in the food chains, the overall trophic organization of the two fjords was similar to the Bering Sea (McConnaughey 1978) and the Scotian Shelf (Mills and Fournier 1979, Mills *et al.* 1984) ecosystems. This confirms the claims of Dickie (1972) and Mills (1975) that coastal ecosystems in general are similarly structured.

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Many graduate students, too numerous to mention individually, assisted with the collection of samples. I thank them for their help and all the graduate students I have known in the Department of Biology for their friendship. Special thanks go to Jocelyn Richard for sharing her knowledge of the south coast fjords with me and confirming the identification of some macrozooplankton species and to David Methven for help in identifying some of the fish. I thank Peter Hurley of the Marine Fish Division, BIO, for the use of their Isaacs-Kidd Midwater Trawls.

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INTRODUCTION

1.1. Stable Isotopes

Traditional studies on the structure of food chains rely on the analysis of stomach contents data to deduce trophic relationships among species. The approach is time-consuming, tedious and subject to considerable error. In addition, it fails to provide any evidence on differential assimilation of ingested prey items. A new tool being applied to ecological studies to minimize these difficulties is stable isotope ratio mass spectrometry. This technique involves the measurement of stable isotope ratios in plant and animal tissues to determine feeding relationships. It has been applied to elucidate the trophic organization of estuarine and marine ecosystems (e.g. McConnaughey 1978, McConnaughey and McRoy 1979a,b, Hackney and Haines 1980, Fry *et al.* 1984, Mills *et al.* 1984, Harrigan 1986), and their components (e.g. Thayer *et al.* 1983, Nichols *et al.* 1985, Paull *et al.* 1985), and the diets of individual species (e.g. Fry *et al.* 1978, Haines and Montague 1979, Ince *et al.* 1982, Boutton *et al.* 1983, Macko *et al.* 1983, Gleason 1986).

Carbon and nitrogen each possess two stable isotopes that differ in their natural abundance. In the biosphere, the light isotopes of both elements predominate: $^{12}\text{C} \simeq 98.89\%$ versus $^{13}\text{C} \simeq 1.11\%$, and $^{14}\text{N} \simeq 99.64\%$ versus $^{15}\text{N} \simeq 0.36\%$ (Nier 1950). Stable carbon isotope ratio measurements are determined on carbon dioxide gas (CO_2) by comparing the amount of $^{13}\text{C}^{16}\text{O}^{16}\text{O}$ (atomic mass 45) and $^{12}\text{C}^{16}\text{O}^{16}\text{O}$ (atomic mass 44) in a sample with that of a carbon dioxide standard. A correction is made for $^{12}\text{C}^{17}\text{O}^{16}\text{O}$ which also has an atomic mass of 45 (Craig 1957). Stable nitrogen isotope analysis compares the ratio of $^{15}\text{N}^{14}\text{N}$ (atomic mass 29) to $^{14}\text{N}^{14}\text{N}$ (atomic mass 28) in a sample with that of atmospheric nitrogen (N_2). Differences in the composition of the material are

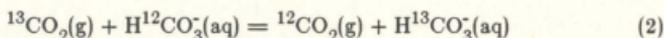
reported as delta (δ) values in units per mil (‰). Delta values are calculated using the following relationship between sample and standard isotope ratios:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where $X = {}^{13}\text{C}$ or ${}^{15}\text{N}$ and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$, respectively. Values greater than zero indicate samples that are enriched in the heavy isotope (i.e. ${}^{13}\text{C}$, ${}^{15}\text{N}$) relative to the standard; samples depleted in ${}^{13}\text{C}$ or ${}^{15}\text{N}$ have negative values.

Stable isotopes of an element have the same number of protons but differ in the number of neutrons. Small variations in atomic mass result in differences in chemical and physical properties due to isotopic discrimination. Processes that incorporate or release one isotope preferentially are known as isotope fractionations. Fractionation is defined as the partitioning of isotopes between two substances with different ratios (Hoefs 1980) and occurs via either equilibrium or kinetic isotope effects.

Equilibrium isotope effects are rare in biological systems. Fractionations are produced by changing the isotopic distribution among different chemical substances, phases or individual molecules. Isotope equilibrium constants may be estimated using statistical mechanics (Bigeleisen and Mayer 1947). Stable carbon isotopes, for example, initially undergo fractionation during equilibrium exchange reactions between atmospheric carbon dioxide and oceanic bicarbonate. This may be the most important equilibrium effect in the carbon cycle (Parker and Calder 1970). The exchange reaction:



occurs during the hydration stage, not at the air-sea interface (Deuser and Degens 1967), and results in depletion of ${}^{13}\text{C}$ in atmospheric carbon dioxide ($\delta^{13}\text{C} = -7$ to -9 ‰) and an enrichment of ${}^{13}\text{C}$ in bicarbonate ($\delta^{13}\text{C} = 0$ ‰) (Craig 1953).

In biological systems, fractionations result from mechanism-dependent kinetic effects. Different rates of reaction normally cause depletion of the heavy isotope in the reaction products. Due to problems in characterizing the activated

species or transition states of biochemical reactions, the calculation of equilibrium constants associated with kinetic isotope effects is difficult (Bigeleisen and Mayer 1947, Kaplan 1975).

1.2. Kinetic Fractionations of Stable Isotopes by Plants and Animals

1.2.1. Carbon

Terrestrial plants fix carbon dioxide during photosynthesis by one of three pathways: (1) the Calvin cycle (C_3 metabolism), (2) the Hatch-Slack cycle (C_4 metabolism) or (3) crassulacean acid metabolism (CAM). Each pathway uses specific carboxylation enzymes which discriminate against ^{13}C to some extent; C_3 plants use ribulose-1,5-bisphosphate (RuBP) carboxylase (Park and Epstein 1960, 1961, Estep *et al.* 1978, Benedict *et al.* 1980), whereas C_4 plants use phosphoenolpyruvate (PEP) carboxylase (Whelan *et al.* 1973). A mixture of both enzyme systems is used by CAM plants, with the proportion determined by environmental conditions (O'Leary 1981).

Initial kinetic fractionations of the stable carbon isotopes, amounting to 7‰ relative to atmospheric CO_2 , take place in higher plants due to differences in the rates of CO_2 molecules encountering the leaves (Park and Epstein 1960). ^{12}C is slightly lighter and more abundant than ^{13}C , and strikes the leaves 1.1% more frequently than the heavier isotope (Degens 1969).

Park and Epstein (1960, 1961) concluded that the major step controlling the isotopic composition of plants depended on the initial carboxylation reaction and the magnitude of the fractionation associated with it. Subsequent studies (Whelan *et al.* 1973, Troughton *et al.* 1974, Estep *et al.* 1978) confirmed these findings. Depending on the enzymatic pathway followed, each plant group possesses a range of characteristic $\delta^{13}C$ values. These values range from -24 to -34‰ for C_3 plants and from -12 to -23‰ for C_4 plants (Benedict *et al.* 1980). Stable carbon isotope values of CAM plants span the known values for C_3 and C_4 plants, from -14 to -34‰ (Bender *et al.* 1973, Lerman *et al.* 1974).

Marine phytoplankton, like C_3 plants, catalyze the fixation of carbon dioxide with RuBP carboxylase but have $\delta^{13}C$ values that range from -18 to $-24^{\circ}/\text{oo}$ (Fry and Sherr 1984). Variations in sea surface temperatures have been implicated as the major factor causing changes in the isotopic composition of phytoplankton (Sackett *et al.* 1965, Wong and Sackett 1978, Fontugne and Duplessy 1981). Temperature coefficients ranging from $-0.13^{\circ}/\text{oo}$ per C° (Wong and Sackett 1978) to $+1.4^{\circ}/\text{oo}$ per C° (Christeller *et al.* 1976) have been calculated in a number of laboratories (Sackett *et al.* 1965, Degens *et al.* 1968, Libby 1972, Christeller *et al.* 1976, Wong and Sackett 1978). However, a strict temperature/ $\delta^{13}C$ relationship has not always been apparent (Fontugne and Duplessy 1978, Rau *et al.* 1982, Gearing *et al.* 1984). Alternative explanations have included different physico-chemical conditions and/or metabolic activities of phytoplankton species (Fontugne and Duplessy 1978), variations in cell density and growth rate (Pardue *et al.* 1976), the production of lipids by high latitude phytoplankton species (Smith and Morris 1980), changes in pH, and a temperature-associated carbon dioxide pool effect (Degens *et al.* 1968).

Parker (1964) was the first to note the similarity between $\delta^{13}C$ values of marine animals and their food. This and subsequent observations (e.g. Minson *et al.* 1975, DeNiro and Epstein 1978) have led to the generalization that large isotope fractionations are not associated with the incorporation of dietary carbon (^{13}C) into animal tissues (DeNiro 1977, DeNiro and Epstein 1978). Although secondary fractionation and turnover of stable isotopes in animals are poorly understood processes (Tieszen *et al.* 1983), isotopes are fractionated during respiration before being stored in various tissues (van der Merwe 1982). ^{12}C is selectively released, and ^{13}C is retained (DeNiro and Epstein 1978, McConnaughey and McRoy 1979a,b). ^{12}C can also be preferentially lost through assimilation and excretion (Fry *et al.* 1984) with the result that organisms on average are enriched in ^{13}C by approximately $1^{\circ}/\text{oo}$ relative to their diet (DeNiro and Epstein 1978). Laboratory studies of animals fed the same diet report a relatively small $\delta^{13}C$ variation of $1\text{-}2^{\circ}/\text{oo}$ among individuals (Fry 1977, DeNiro and Epstein 1978, Fry and Arnold 1982). Comparable intraspecific ranges have

also been shown in field studies (Fry *et al.* 1978, Haines and Montague 1979, Stephenson 1980, Stephenson and Lyon 1982). Fry and Parker (1979) reported a range in $\delta^{13}\text{C}$ values of 0.70‰ for 41 specimens of vermillion snapper (*Rhomboplites aurorubens*). However, some laboratory studies have found no ^{13}C -enrichment between animals and their diet (Teeri and Schoeller 1979, Macko *et al.* 1982b, Stephenson *et al.* 1986).

The relationship between the carbon isotope ratio of a tissue and the diet depends partially on the type of tissue and the nature of the diet. Different tissues in the same animal (e.g. muscle, fat, bone, hair) may have slightly different $\delta^{13}\text{C}$ values (van der Merwe 1982) due to variation in the isotopic ratios of the food components that contribute to the formation of the specific tissue types (DeNiro and Epstein 1978). Isotopic differences between tissues may reflect variation in their biochemical composition; a tissue containing a large proportion of lipid would have a more negative $\delta^{13}\text{C}$ value than one with a lower lipid content. Tieszen *et al.* (1983) attributed isotopic differences between various tissues in gerbils to differences in metabolic activity which affect the isotope turnover rate; higher turnover rates lead to tissues with more positive $\delta^{13}\text{C}$ values.

1.2.2. Nitrogen

Studies utilizing stable nitrogen isotopes are fewer than those based on carbon. However, this tracer has proven valuable in studies of the nitrogen cycle (Macko 1981, Saino and Hattori 1985, Sigleo and Macko 1985), oceanic particle dynamics (Wada and Hattori 1976, Mariotti *et al.* 1984, Altabet and Deuser 1985, Owens 1985, Altabet and McCarthy 1986, Altabet *et al.* 1986), and trophic organization (DeNiro and Epstein 1981, Rau 1981a,b; Minagawa and Wada 1984, Mullin *et al.* 1984, Paull *et al.* 1985).

Nitrogen enters the biosphere through fixation of molecular nitrogen by soil bacteria in terrestrial environments or by blue-green algae (cyanophytes) in aquatic systems. Fractionation during nitrogen fixation is small (Hoering and Ford 1960, Delwiche and Steyn 1970, Macko *et al.* 1982a); variations in $\delta^{15}\text{N}$ values are thought to be due to kinetic isotope fractionations during

denitrification, nitrification, ammonification and nitrate assimilation (Wada and Hattori 1976). The extent of the fractionations varies depending on the type, mode and mechanism of the reaction (Wada 1979).

In the oceanic environment, inorganic nitrogen occurs in the form of ammonia, molecular nitrogen, nitrate, nitrite and nitrous oxide. Wada and Hattori (1976) found oceanic nitrate $\delta^{15}\text{N}$ values depended on geographic location and depth within the water column. A relationship also exists between $\delta^{15}\text{N}$ values of marine phytoplankton and the nitrogenous compounds used for growth; the ^{15}N content of plankton samples is inversely correlated with ambient nitrate concentration (Wada and Hattori 1976). The degree of fractionation in organisms varies according to the growth rate, growth phase, light intensity, nitrogen source and species (Wada and Hattori 1978).

Variation in the natural abundance of ^{15}N in suspended particulate organic matter has been interpreted in terms of nitrogen cycle processes, depending on the input of nitrogen to the euphotic zone (Miyake and Wada 1967, Altabet and Deuser 1985, Saino and Hattori 1985). Wada and Hattori (1976) observed that plankton collected from nitrate-poor water, in which regenerated ammonia was the principal nitrogen source, had higher mean $\delta^{15}\text{N}$ values (+8.6‰) than organisms from tropical areas (+0.5‰) where the nitrogen-fixing cyanophyte *Trichodesmium* sp. dominated. Similar results have been reported by Macko *et al.* (1984) for the Gulf of Mexico and by Mullin *et al.* (1984) for the North Pacific Central Gyre and Southern California Bight.

The nitrogen isotopic composition of animals is a reflection of their diet and ultimately the nitrogen source (DeNiro and Epstein 1981, Macko 1981, Minagawa and Wada 1984). Animals incorporate dietary ^{15}N into their tissues preferentially (Steele and Daniel 1978, DeNiro and Epstein 1981), resulting in more positive $\delta^{15}\text{N}$ values of the animal relative to the diet. Minagawa and Wada (1984) have suggested that the enrichment in body $\delta^{15}\text{N}$ values may also be due to the type of excretory nitrogen formed and the excretion mechanism. As with carbon, the relationship between $\delta^{15}\text{N}$ values and the diet depends on both the type of tissue analyzed and the nature of the diet.

1.3. Food Chains and Stable Isotope Tracers

A major area of ecological research is concerned with establishing a relationship between ecosystem structure and function and uncovering the mechanism(s) involved in regulation. Food chains are representations of interspecific interactions in a community that trace the flow and cycling of energy and/or material in the system. Heterotrophic species consume organisms from the trophic level directly below them and are potential prey for those above. Food chains seldom contain more than five trophic levels and are classified as either grazing or detritus-based, depending on the source of organic matter (Odum 1971).

In the past, understanding of trophic organization was based primarily on data from stomach contents analyses. Such studies provide valuable information on species interactions but only represent a specific situation at one moment in time. They are hampered by their inability to identify the source of organic matter at the base of a food chain, 'invisible pathways' (Rounick and Winterbourn 1986), and possible differential assimilation of prey items by predators. The accuracy of the data also depends heavily on the observer's ability to recognize the remains of ingested food.

Stable isotope tracers provide a new approach to elucidating trophic organization. Unlike stomach contents analysis, this technique measures foods actually assimilated by an organism over time. As a result of ^{12}C being lost faster than ^{13}C , the ratio of ^{13}C to ^{12}C increases as carbon moves through a food chain (McConnaughey 1978). Thus the stable carbon isotope ratio of a top level consumer shows the greatest amount of enrichment relative to the base of the food chain (McConnaughey 1978). DeNiro and Epstein (1978) found an enrichment of 1 to 2‰ per trophic level for stable carbon isotopes in laboratory studies.

Likewise, the preferential retention of ^{15}N in an organism's tissues results in an enrichment in $\delta^{15}\text{N}$ values with increasing trophic level. Miyake and Wada (1967) found a stepwise enrichment in nitrogen of 3 to 4‰ per trophic level. Figure 1-1 illustrates the stable carbon and nitrogen isotope values encountered at

each trophic level in a hypothetical marine food chain. Note the enrichment in both isotopes with increasing trophic position or level. A trophic level has been defined as a position in a food chain determined by the number of energy-transfer steps to that level (Ricklefs 1979). Workers in the isotope field usually refer to trophic level, but the term more appropriately should be trophic continuum. In keeping with usage in the isotope literature, however, the term trophic level is used in the remainder of this thesis. In isotope studies trophic levels are defined according to enrichments of 1 to 2⁰/oo per trophic level for carbon and 3 to 4⁰/oo per trophic level for nitrogen, as was discussed above.

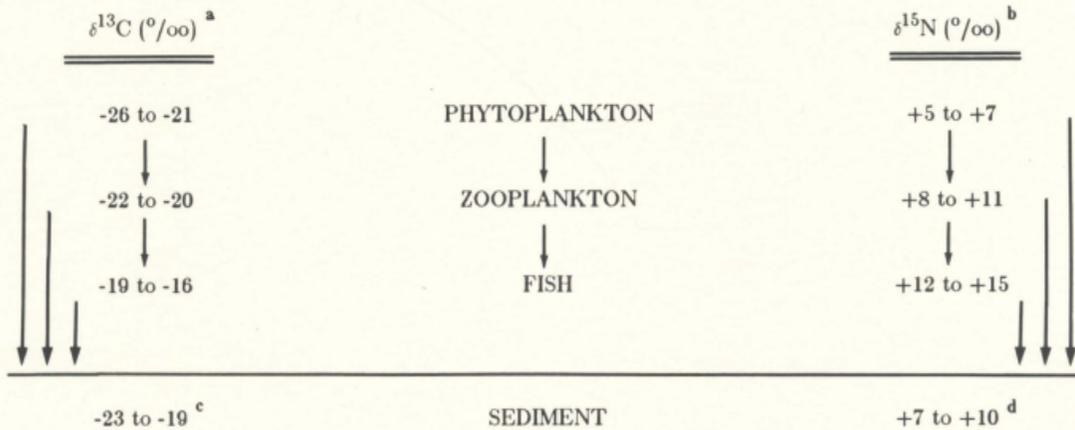
The majority of food chain studies utilizing stable isotope tracers have dealt primarily with delineation of the source(s) of organic matter. These studies are based on two important assumptions (McConnaughey 1978, Fry *et al.* 1982):

1. Sources of organic matter must be isotopically distinguishable.
2. Animal consumers reflect the isotopic composition of their diets.

A recent, comprehensive review by Fry and Sherr (1984) has dealt with the use of stable carbon isotopes as tracers of carbon flow in freshwater and marine ecosystems. A brief review of food chain studies utilizing stable carbon and/or nitrogen isotopes in marine ecosystems follows.

The study of food chains in coastal and marine ecosystems with stable isotope tracers has provided the best evidence for the existence of ¹³C- and ¹⁵N-enrichments with increasing trophic position in natural systems (McConnaughey 1978, McConnaughey and McRoy 1979b, Rau *et al.* 1983, Fry and Sherr 1984, Minagawa and Wada 1984, Harrigan 1986). Estuarine and coastal systems may have many sources of organic matter, whereas suspended particulate organic matter (POM) predominates in offshore environments. The preponderance of different types of primary producers in some coastal ecosystems has made the interpretation of data from studies using only carbon isotopes difficult due to overlapping values (Schwinghamer *et al.* 1983). As well, variability has been found by Stephenson *et al.* (1984) in the carbon isotopic

Figure 1-1: A hypothetical marine food chain illustrating the enrichment of stable carbon and nitrogen isotopes with increasing trophic level. Arrows on the far left and right indicate the eventual contribution of phytoplankton, zooplankton and fish to the sediment.



^a Table 3, Fry and Sherr 1984

^b Wada and Hattori 1976, Sweeney *et al.* 1978, Owens 1985, This Study

^c Hunt 1966

^d Ivany 1985

composition of macrophytes, which has important implications for food web studies of environments dominated by these plants. In nearshore environments, the incorporation of terrestrially-derived organic matter into food chains has been detected (Rau *et al.* 1981, Incze *et al.* 1982), although its affect dissipates quickly seaward (Thayer *et al.* 1983) and with depth (Fry *et al.* 1984). The use of allochthonous carbon sources has been found for an offshore benthic community (Spies and DesMarais 1983) and for stream invertebrates (Rounick *et al.* 1982).

Fry and Sherr (1984) suggest the major factors influencing the values of ^{13}C -enrichments in marine animals are diet and trophic position. Studies using stable carbon isotopes have attempted to calculate the amount of ^{13}C -enrichment per trophic level. A 1 to $1.5^{\circ}/\text{oo}$ per trophic level enrichment has been assumed based on laboratory investigations (DeNiro and Epstein 1978), and applied to field studies (McConnaughey 1978, McConnaughey and McRoy 1979b, Mills *et al.* 1984). However, trophic level enrichment values have been shown to vary from no enrichment between POM and zooplankton (Sackett *et al.* 1965, Degens *et al.* 1968, Deuser 1970, Tan and Strain 1983) to $0.5 - 2.2^{\circ}/\text{oo}$ per trophic level (Thayer *et al.* 1983, Gearing *et al.* 1984).

Rau *et al.* (1983) found that the amount of enrichment per trophic level in pelagic food chains differed between coastal and open ocean sites. Food chains in the coastal waters off southern California had an enrichment of $1.38^{\circ}/\text{oo}$ per trophic level compared to $0.73^{\circ}/\text{oo}$ per trophic level in the eastern tropical Pacific Ocean. Each food chain had 5 trophic levels. In a study of a benthic community at a natural petroleum seepage, a difference of $1.32^{\circ}/\text{oo}$ was found between the petroleum carbon being utilized and the fauna (Spies and DesMarais 1983). A study of the planktonic food chain in the northern Gulf of Mexico (Thayer *et al.* 1983) found trophic enrichment did not exceed $\pm 1.8^{\circ}/\text{oo}$ per level. McConnaughey (1978) and McConnaughey and McRoy (1979b) have suggested that the food chain of the Bering Sea ecosystem consists of 5 to 6 trophic levels by assuming an enrichment of $1.5^{\circ}/\text{oo}$ per trophic level. Mills *et al.* (1984) found the food chain from phytoplankton to benthic fishes on the Scotian Shelf also had 5 to 6 trophic levels and concluded that the trophic organization was similar to that of

the Bering Sea. However, their study assumed a trophic level enrichment of 1⁰/oo instead of the 1.5⁰/oo used by McConnaughey (1978) and McConnaughey and McRoy (1979b).

The largest ¹³C-enrichments, on the order of 7 to 9⁰/oo (Fry and Sherr 1984), have been observed in benthic consumers (McConnaughey 1978, McConnaughey and McRoy 1979b, Dunton and Schell 1984, Gearing *et al.* 1984, Mills *et al.* 1984). This may be due to reworking of the carbon in sediments by microbes or meiofauna (McConnaughey and McRoy 1979b), and implies that, due to benthic-pelagic coupling, food chains of continental shelf ecosystems may have more trophic levels than is normally assumed (Fry and Sherr 1984).

Stable carbon and nitrogen isotopes have been used to confirm chemosynthetic nutrition in an abyssal seep (Paull *et al.* 1985), shallow-water benthic (Spiro *et al.* 1986) and hydrothermal vent communities (Rau 1981a,b). Hydrothermal vent studies have suggested that neither a photosynthetic pathway nor the transfer of matter via pelagic coupling is employed. In addition to elucidating a chemosynthetic pathway, differences in carbon isotope values between worm and bivalve tissues suggest the presence of two unique food sources (Rau 1981a). Stable nitrogen isotope data indicate that animals at vents are not dependent on a photosynthetic pathway, and low values may be associated with nitrogen fixation (Rau 1981b). Rau (1981b) has speculated that nitrogen fixation precedes the synthesis of nutritional organic nitrogen. Similar results have been reported by Paull *et al.* (1985) for an abyssal seep community in the Gulf of Mexico.

1.4. Rationale and Research Objectives of the Present Study

Explanations for the existence and maintenance of food chains in nature with no more than five or six trophic levels have been attempted by a number of authors (Elton 1927, Lindeman 1942, Pimm and Lawton 1977, DeAngelis *et al.* 1978, Lawton and Pimm 1978, Saunders 1978, Hastings and Conrad 1979, Pimm 1980, 1982, DeAngelis *et al.* 1983, May 1983, Yodzis 1984 and Pimm 1985, among others), but without a consensus. Briand (1983b) has speculated that

environmental variability imposes constraints on the types of viable trophic patterns. Analysis of 40 food webs showed that fluctuating environments had a significantly different food web structure than more constant systems. Those from fluctuating environments were dominated by species that optimized feeding due to the amplitude of the changes, not their degree of predictability (May 1981), and had significantly lower connectance than webs from constant environments (Briand 1983b). Similar results have been found by Briand (1983a) and Cohen and Briand (1984). The authors suggest the results are a reflection of greater constraints on the trophic structure of food webs in fluctuating environments.

Empirical studies on the trophic organization of plankton (Timonin 1971), macrophyte (Littler and Littler 1981), seabird (Springer *et al.* 1984), and rocky intertidal communities (McQuaid and Branch 1985) have found that environmental variability affected trophic organization via either dynamic (Elton 1927, Pimm and Lawton 1977, Lawton and Pimm 1978, Saunders 1978, Pimm 1982) or energetic (Lindeman 1942, DeAngelis *et al.* 1978, Yodzis 1984) constraints. Trophic organization tends to be more similar within than between ecosystem types (e.g. estuarine, forest, intertidal, pelagic, terrestrial) and as a result, environmental variability probably exerts a greater influence on trophic structure than has been thought previously (Briand 1983a,b). Constant systems should be characterized by herbivores and carnivores and a food chain with many trophic levels (Briand 1983a,b). Fluctuating environments should experience a greater loss of material to the sediments as a result of inefficient use by omnivorous and opportunistic species. Given comparable communities, Pimm (1982, 1985) suggests that food chains in variable environments should have fewer trophic levels than those in constant systems. Although hypothesis testing in natural ecosystems is uncommon and difficult, some evidence supports Pimm's claim (Kitching 1981).

The present project was initiated to examine the structure of pelagic food chains in two fjords, along the south coast of the island of Newfoundland, differing with respect to their degree of environmental fluctuation. Biological (Richard 1986, Richard and Haedrich, in press) and physical oceanographic

studies (de Young 1983, Richard and Hay 1984) have shown that although the fjords are in close proximity, they are biologically and physically distinct. One appears to be a relatively stable system; it is warm, undergoes only partial deep-water renewal and maintains a diverse community of pelagic animals. The other system is quite dynamic; it is characterized by cold water, is subject to bi-annual renewal of the water column and has a fauna dominated by a few highly abundant species. Differences between the two fjords in their fish fauna and the processes regulating the populations (*in situ* biological versus physical) have been attributed to contrasting water column stabilities (Richard and Haedrich, in press).

Based on the empirical and theoretical studies already cited, the food web in the constant or stable ecosystem was predicted to have many trophic levels and to be efficient in its cycling of organic matter, whereas the food web in the fluctuating or dynamic system was predicted to have fewer trophic levels and a lesser efficiency. This lesser efficiency would manifest itself by a greater accumulation of organic matter in the sediments. Table 1-1 summarizes some of the important physical and biological characteristics of the two fjords along with predictions on the trophic organization of each.

To assess these predictions, a dual stable isotope approach employing carbon and nitrogen tracers was used to provide integrated dietary information on resident organisms of the fjords. This technique is especially useful on species of small body size and on midwater organisms, which often either egest their stomach contents or feed while in the net. The ability to resolve food chains is increased and the source(s) of organic matter more easily identified when a number of isotopes are used in combination instead of singly (Fry and Sherr 1984, Peterson *et al.* 1985).

Table 1-1. A summary of some of the important biological and physical characteristics of Bay d'Espoir and Fortune Bay and predictions on the trophic organization.

KNOWN:

PREDICTED:

Fjord	Maximum Depth (m)	Deep-Water Renewal	Water Types	Type of Environment	Fauna	Processes Regulating Populations	Dominant Feeding Type	Food Web Structure	Cycling of Organic Matter
Bay d'Espoir	745	Annual (partial)	3 Summer 3 Winter	Constant	Diverse	<i>in situ</i> Biological	Carnivores	Long, Thin Many Trophic Levels	Efficient
Fortune Bay	398	Bi-annual (dynamic)	2 Summer 3 Winter	Fluctuating	Depauperate	Physical	Omnivores	Short, Fat Few Trophic Levels	Inefficient

MATERIALS AND METHODS

2.1. Study Site Description

Bay d'Espoir and Fortune Bay, two fjords along the south coast of Newfoundland, Canada (Figures 2-1 and 2-2), were chosen as study sites. Although in close proximity (40 km), their physical characteristics differ markedly.

Bay d'Espoir is a narrow fjord consisting of a deep outer basin (798 m depth) connected to two principal arms leading inland (Figure 2-2a). It has one outer sill separating it from Hermitage Channel, and nine inner sills (Richard and Hay 1984, Richard 1986). The water column of the outer basin is stratified year round and during the summer consists of three layers: a near-surface layer, an intermediate depth cold-water layer and a deep warm-water layer (Richard and Hay 1984). The near-surface layer is approximately 20 m deep and is dissipated during winter mixing. The intermediate depth, cold-water layer (temperature: -1 to -0.5°C, salinity: 33.0‰) extends from about 20 to 150 m and originates from Labrador Current Water (LCW) and winter-cooled surface water (Richard and Hay 1984). The water below 150 m is Modified Slope Water (MSW), formed from water at intermediate depths along the continental slope and modified by mixing while moving through the Laurentian and Hermitage Channels. This water type is warm (4 to 6°C), saline (34.5‰) and is considered to be a permanent feature of the outer basin (Richard and Hay 1984). Deep-water renewal in the outer basin occurs annually in the spring, although it may only be partial (Richard and Hay 1984), and involves only MSW. It has been correlated with strong north-northeasterly winds along the south coast in winter (Richard 1986). On the basis of this physical information, Bay d'Espoir is considered to be a relatively constant or stable ecosystem compared to Fortune Bay.

Figure 2-1: The location of Bay d'Espoir and Fortune Bay along the south coast of Newfoundland, Canada.

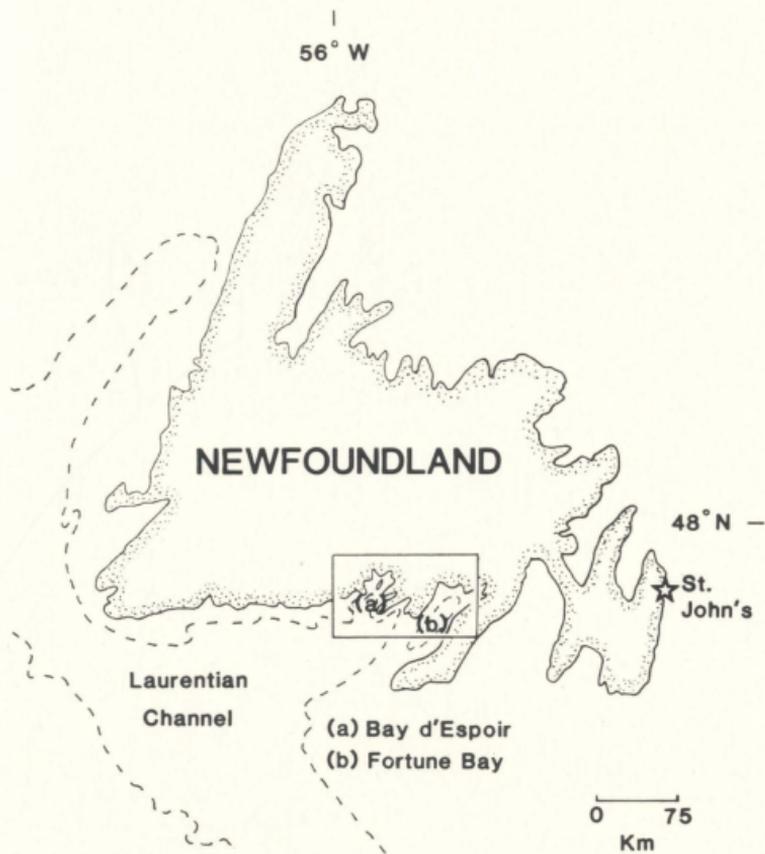
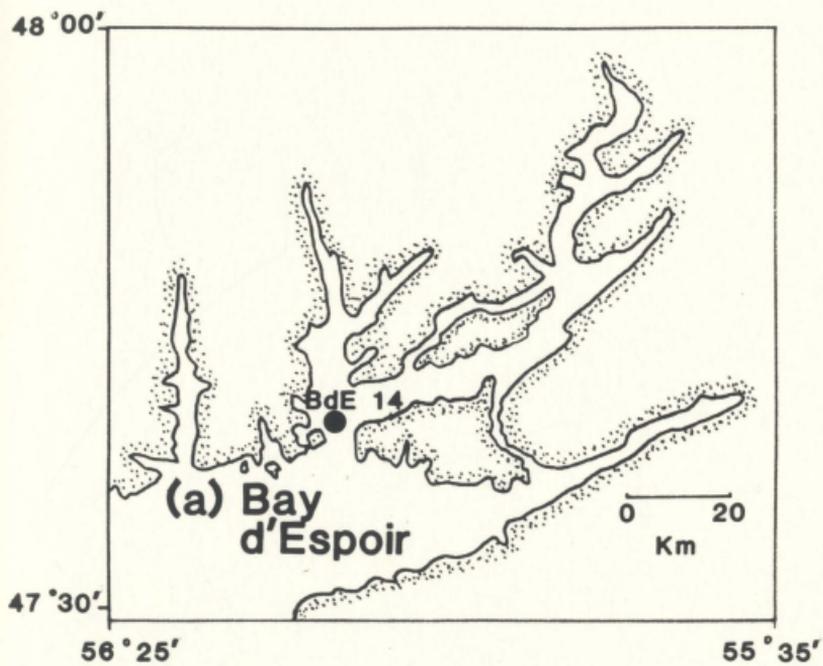
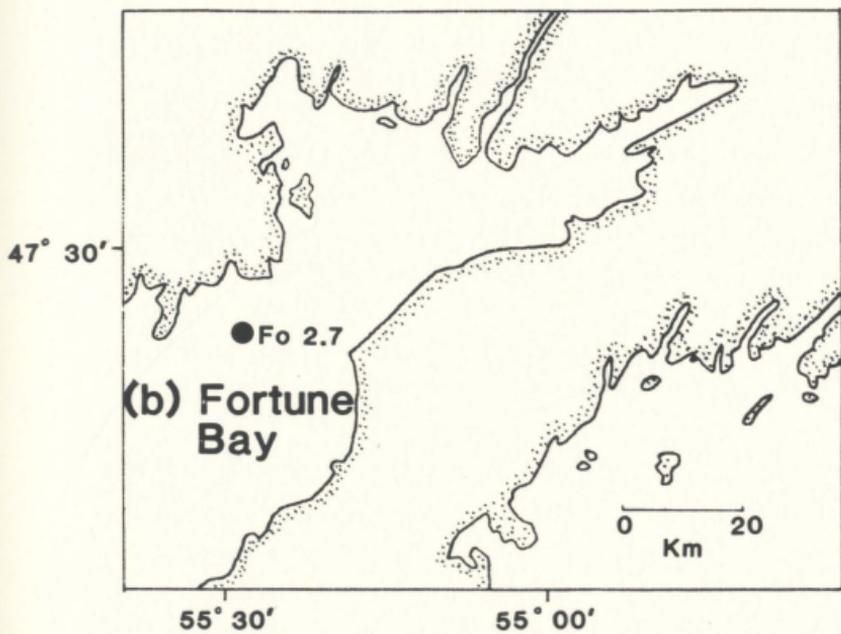


Figure 2-2: Sampling site locations in the main outer basin of (a) Bay d'Espoir and (b) Fortune Bay.





Fortune Bay is a large, broad fjord (Figure 2-2b) with three outer sills and one inner sill. The outer basin has a maximum depth of 400 m. This fjord has two sources of deep-water: Modified Slope Water (MSW), which moves from the west via Hermitage Channel, and Labrador Current Water (LCW) from the east following the Avalon and St. Pierre Channels. MSW is warm and saline (4 to 6°C, 34.5‰), while LCW is cold and less saline (-1 to -0.5°C, 33.0‰; de Young 1983, Richard 1986).

Deep-water renewal occurs bi-annually (summer and winter) and is accompanied by intense vertical mixing (Richard and Hay 1984). In summer, this exchange involves LCW and results in water temperatures near 0°C throughout the water column of the outer basin. During the winter months, MSW flows over the outer sills and sinks to the bottom of the basin, raising deep-water temperatures to between 2.0 and 2.5°C (de Young 1983, Richard and Hay 1984). Stratification may occur in the deeper water, but it is weaker than that in Bay d'Espoir (Richard 1986). Due to the unpredictable nature of its water column structure, Fortune Bay is considered to be a fluctuating, dynamic and highly variable environment.

2.2. Collection of Samples

Sampling was conducted from the CSS *Dawson* in December 1984 and August 1985 at two permanent hydrographic stations in the main outer basins of Bay d'Espoir and Fortune Bay (Figures 2-2a and 2-2b). The sampling site in Bay d'Espoir, station BdE 14, was located at 47°40.1'N, 56°08.0'W, with a depth of approximately 798 meters. The station sampled in Fortune Bay, Fo 2.7, was located at 47°23.3'N, 55°29.4'W and was 400 meters deep.

Suspended particulate organic matter (POM) was collected from the mixed layer by filtering water pumped from the ship's seawater intake located 5 meters below the surface. During the August cruise, Labrador Current Water (LCW) from 80 m and Modified Slope Water (MSW) from near the bottom (745 m) of Bay d'Espoir, and LCW from near the bottom (378 m) of Fortune Bay, was collected in 1.7 l Niskin bottles attached to a rosette sampler. The POM was

collected on pre-ashed (500°C, 1h), 47 mm Whatman GF/C glass fiber filters; once clogged, the filters were frozen. Conductance and temperature profiles for each station were recorded with a CTD probe (Neil Brown Instrument Systems Inc.) attached to the rosette.

Small zooplankton, primarily copepods, were collected with a 333 μ m mesh ring net in vertical hauls from approximately 10 m off the bottom to the surface. Samples and labels were placed in plastic bags and frozen.

Macroinvertebrates and fishes were caught with a 1.8 m Isaacs-Kidd Midwater Trawl in December and with a 3 m trawl in August. The outer mesh of the net was 3 x 3 cm, with an inner liner of 7 x 7 mm mesh. Trawls consisted of an oblique tow from 50-100 m off the bottom to the surface in stepped increments of 100 m. Fishing began once the net reached depth, with total fishing time lasting from 30 minutes to 1 h. Once on deck, the catch was partially sorted, packed in plastic bags, labeled and frozen. A representative sample of fish caught during the the summer cruise was fixed in seawater containing 5% (v/v) buffered formalin for stomach content analysis.

Sediment was collected with a 0.25 m² van Veen grab. Undisturbed surficial portions were subsampled, placed in plastic bags, labeled and frozen.

Samples remained frozen during and after transportation to the laboratory and were only thawed prior to sorting and identification in preparation for isotopic analysis.

All material was collected either several hours after sunset or before sunrise to ensure sufficient numbers of animals. The only exception was at station Fo 2.7 in August, when the ship schedule dictated that fishing could only be done at 0800 hrs.

2.3. Stable Isotope Ratio Mass Spectrometry

2.3.1. Sample Preparation

The filters on which POM was collected were thawed and examined with a stereomicroscope for zooplankton which were removed. The filters were then acidified¹. Once dry, the top layers of two filters were scraped and the scrapings placed in a 30 cm length of 10 mm outer diameter (o.d.) quartz tube with an excess of fired (900°C, 1h) cupric oxide (CuO) in alternate layers. A layer of granular copper metal (Cu) was placed on top. Approximately 5 g of CuO and 1 g of Cu were used per sample. Prior to use, the quartz tubes were pre-combusted in a muffle furnace for 1 h at 500°C to remove contaminants.

Frozen samples of animals were thawed, rinsed in distilled water, sorted and identified to species level wherever possible. Taxonomic keys used included: Dunbar (1963) for amphipods; Fraser (1957) for chaetognaths; Sars (1903), Wilson (1972) and Harding (unpublished manuscript) for copepods; Allen (1967), Rice (1967) and Smaldon (1979) for decapod shrimp; Einnarsson (1945) and Mauchline (1971) for euphausiids; Leim and Scott (1966) and Fahay (1983) for fishes; Tattersall (1951), Tattersall and Tattersall (1951) and Brunel (1960) for mysids; Muus (1953) for pelagic polychaetes and Morton (1957) for pteropods.

Whole adult animals were used for analysis; those animals with exoskeletons were acidified, the acid decanted off and the animals dried. Animals with soft bodies were not acidified, but were placed immediately in the drying oven. Larger zooplankton (i.e. euphausiids, some mysids and shrimp) and fish had muscle tissue dissected out and dried for separate analysis. Once dry, the samples were ground into a powder in a glass mortar with a pestle. Approximately 10 mg of sample was weighed to ± 0.1 mg and placed in a 30 cm length of 6 mm o.d. quartz tube with 1.5 g of CuO and 0.5 g of Cu.

Sediment samples were thawed, acidified and dried. The dried samples were

¹Samples requiring acidification, such as animals with exoskeletons, POM collected on filters, and sediment, were placed in an excess of 20% HCl until bubbling ceased and dried. All samples were dried at 40°C for 48 h.

ground into powder and a 200 mg subsample taken. This was placed in a 30 cm length of 10 mm o.d. quartz tube with approximately 5 g of CuO and 1 g of Cu.

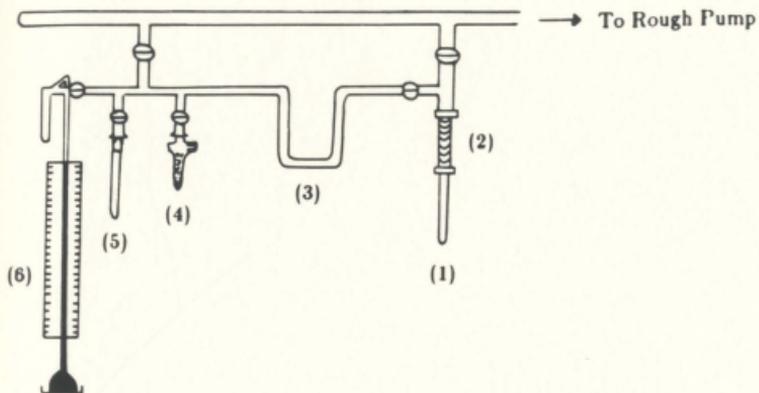
All sample tubes were sealed under a high vacuum and the contents thoroughly mixed to allow intimate contact between sample and oxidant. A modified Dumas combustion was carried out in which the tubes were heated in a muffle furnace to 850°C for 1 h and then allowed to cool at 750°C, 650°C and 550°C for 1 h each (Macko 1981).

2.3.2. Collection and Analysis of CO₂ and N₂ Gases

The vacuum line used for the collection of carbon dioxide and nitrogen gases is illustrated in Figure 2-3. Numbers in parentheses in the following text refer to labels on the diagram. Sample tubes (1) were scribed with a glass cutter and placed in a flexible Cajon joint (2) attached to the vacuum line (DesMarais and Hayes 1976). The line was evacuated and tested for air leaks. If no leaks were found, the sample tube was cooled with liquid nitrogen and then broken. A hot air gun was used to heat the sample tube, expanding the gases into the line. Prior to collection of gases a U-trap (3) in the line was cooled with liquid nitrogen for 6 minutes. Nitrogen was collected first to avoid contamination with carbon monoxide present, as both molecules have ions with an atomic mass of 28. A second Dewar flask of liquid nitrogen was placed under a collection tube containing a molecular sieve (4) and nitrogen gas was collected for six minutes, after which the tube was closed and the liquid nitrogen removed. The collection tube was placed in the sample inlet of the mass spectrometer and heated for five minutes at $\approx 150^\circ\text{C}$. The gas was then introduced into the instrument for analysis.

Carbon dioxide was collected from the same sample by replacing the Dewar flask of liquid nitrogen under the U-trap (3) with another flask containing a methanol-dry ice slush. This allowed the previously frozen CO₂ to thaw and expand into the vacuum line. A Dewar flask of liquid nitrogen was placed under a pyrex tube (5) and the CO₂ allowed to collect in it for four minutes. The tube was then sealed and the carbon dioxide samples were analyzed later on the mass spectrometer.

Figure 2-3: The vacuum line used in the collection of carbon dioxide and nitrogen gases.

**Legend**

1=Sample Tube

2=Cajon Joint

3=U-Trap

4=Molecular Sieve

5=Pyrex Tube

6=Calibrated Manometer

The amounts of CO_2 and N_2 present in sediment samples were recorded to calculate the percentage of carbon, nitrogen and an atomic C:N ratio. The absolute amount of carbon dioxide gas was measured on a calibrated manometer (6) attached to the vacuum line. Nitrogen gas was measured directly as the ion intensity in a calibrated volume of the mass spectrometer. Atomic C:N ratios were calculated using the formula:

$$\text{C:N} = (\text{C/N}) \times (14/12) \quad (3)$$

where C and N were the amounts (milligrams) of carbon and nitrogen in a sample and 12 and 14 the atomic mass of carbon and nitrogen, respectively.

Samples were analyzed for their stable carbon and nitrogen isotopic compositions using a Micromass 903E mass spectrometer with a triple collector (V.G. Ltd., Middlewich, Cheshire, England). A minimum of six comparisons was made between the sample and reference materials. Stable isotope compositions are reported relative to the carbonate standard PDB (^{13}C) or atmospheric nitrogen (^{15}N).

Delta (δ) values for stable carbon and nitrogen isotopes were calculated using equation 1 (page 2). Stable carbon isotope measurements were corrected for ^{17}O using factors reported by Craig (1957). Instrument precision for carbon and nitrogen measurements was better than $\pm 0.05\text{‰}$.

2.4. Reconstruction of the Pelagic Food Webs and Chains

Trophic level enrichments (EN) for the carbon and nitrogen isotopes were calculated for Bay d'Espoir and Fortune Bay during winter and summer relative to the carbon and nitrogen isotopic composition of the top predator *M. atlanticum* in Bay d'Espoir and *A. malmgreni* in Fortune Bay. This is represented by the equation:

$$\text{EN} = (\text{R}_{\text{predator}} - \text{R}_{\text{POM}})/\text{TL} \quad (4)$$

where $\text{R}_{\text{predator}}$ was the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value of the top predator in each fjord and

R_{POM} was the carbon or nitrogen isotopic composition of the subsurface POM. The trophic level occupied (TL) by *M. atlanticum* or *A. malmgreni* was calculated by applying trophic level enrichments of $1.0^{\circ}/\text{oo}$ per trophic level for carbon (DeNiro and Epstein 1978) and $3.0^{\circ}/\text{oo}$ per trophic level (Miyake and Wada 1967) to the calculated difference between the isotopic composition of the predator and the POM. The calculations showed both top predators were on the fourth trophic level; three levels above the POM.

The pelagic food webs and chains in Bay d'Espoir and Fortune Bay were reconstructed from the stable carbon and nitrogen isotope data. A scaled trophic level occupied by each species was determined by calculating $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for each species (data in Appendix E through K) and evaluating them relative to calculated trophic level enrichments. The $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for each species was calculated using the equation:

$$\Delta X = (X_{\text{Animal}} - X_{\text{POM}}) \quad (5)$$

where X_{Animal} is the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ composition of a species and X_{POM} is the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ composition of the POM. For example, if the trophic level enrichments for carbon and nitrogen were $1.0^{\circ}/\text{oo}$ and $3.0^{\circ}/\text{oo}$, respectively, a species with a $\Delta\delta^{13}\text{C}$ value of $1.0^{\circ}/\text{oo}$ and $\Delta\delta^{15}\text{N}$ value of $3.0^{\circ}/\text{oo}$ would be on the second trophic level, directly above the POM. Likewise, a species with $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values of $2.0^{\circ}/\text{oo}$ and $6.0^{\circ}/\text{oo}$, respectively, would be placed on the third trophic level and so on.

The trophic composition of each fjord by season was determined by classifying each species into a broad trophic category (carnivore, herbivore and omnivore) based on information from the literature. The percentage of each feeding type was calculated for the fauna in Bay d'Espoir and Fortune Bay by season.

2.5. Stomach Contents Analysis

Stomach contents analyses were done on *Melanostigma atlanticum* caught in Bay d'Espoir in August 1985. This species was the most abundant fish taken there. Samples initially preserved at sea in 5% (v/v) buffered formalin were transferred to 70% ethanol in the lab. Total lengths were measured to ± 0.02 mm with dial calipers and wet weights were measured to ± 0.01 g.

The mouths of the fish were examined for prey items, as indicative of feeding or regurgitation in the net. Individuals found with prey items in their mouths were not used in the analysis. Following this, the stomachs were dissected from the fish and the contents examined with a stereomicroscope and identified to species wherever possible. The number of prey items and the presence/absence of unidentifiable material was noted.

The percentage of various prey species ingested by each size class of fish, and the isotopic composition of the prey species, were used to predict stable carbon and nitrogen isotope values of the fish and to compare them to actual measurements. The calculations were based on a relationship that assumes total body isotope values are a function of the amount of a specific food consumed and its isotopic composition. This is expressed as:

$$X_{\text{predator}} = (\%_{\text{prey } 1}) \times (R_{\text{prey } 1}) + (\%_{\text{prey } 2}) \times (R_{\text{prey } 2}) + \dots + \text{EN} \quad (6)$$

where X_{predator} is the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value of the predator, $\%_{\text{prey}}$ was the percentage of a prey species consumed and R_{prey} was the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ value of the prey species. Trophic level enrichments (EN) of 1.0 and 2.9‰ calculated for *M. atlanticum* in August (using equation 4) were applied to the predicted carbon and nitrogen values, respectively, to account for trophic position.

2.6. Statistical Analysis

All analyses were done using statistical and plotting packages available in SPSS-X (SPSS Inc. 1983). Two-tailed t-tests (Sokal and Rohlf 1981) were done to test for significant differences in mean carbon and nitrogen isotope values between and within seasons and fjords. The mean stable carbon and nitrogen isotopic compositions of the fauna were tested statistically to look for differences among species within the fjords seasonally and between the fjords within a season. Significant differences in the isotopic composition of a species indicate either changes in the dietary sources of carbon and/or nitrogen, or in the proportions of various biochemical constituents (e.g. lipids) in the tissues. The species level was chosen to test for differences instead of grouping the data into large taxonomic aggregations (e.g. amphipods, copepods, fishes), as this latter classification scheme would have meant lumping together animals with diverse feeding strategies (herbivores, omnivores and carnivores).

RESULTS

3.1. Faunal Composition

The species composition of the midwater fauna differed between fjords in the same season and seasonally within a fjord (Table 3-1). Of the 40 species caught, nine were found in both fjords during both seasons. Eighteen species were common in both winter and summer in Bay d'Espoir and seventeen in Fortune Bay. There were no shared fish or mysid species between fjords, and ostracods were collected only in Bay d'Espoir. Thirty percent of the species were common to both fjords in December and 33% in August.

3.2. Physical Oceanography

The water column was stratified during winter and summer in Bay d'Espoir (Figures 3-1a,b), although stratification was weaker in December. In winter (Figure 3-1a), three water types were present and included a mixed layer of subsurface water and MSW, a mixed intermediate-depth layer of LCW and MSW (referred to as LCW type), and a warm layer of MSW which extended to the bottom of the basin. The water column also consisted of three layers in the summer (Figure 3-1b), although each water type was more clearly defined in the summer than the winter. The near-surface layer consisted of a shallow, warm lens which overlaid a thicker layer of cold LCW. The water below the LCW type consisted entirely of warm MSW.

The winter profile (Figure 3-1c) of Fortune Bay showed the presence of a mixed subsurface layer of MSW, an intermediate-depth layer of LCW which extended from 126 to 252 meters and a mixed bottom layer of LCW and MSW. This latter water type will be referred to as MSW. Although the water column was stratified at the time of sampling, the hydrography of the outer basin changes

Table 3-1. A species list for collections made in Bay d'Espoir and Fortune Bay in December 1984 and August 1985. Presence is indicated by a plus (+) symbol and absence by a minus (-) symbol.

Taxonomic Group	Species	Bay d'Espoir		Fortune Bay	
		Dec.	Aug.	Dec.	Aug.
AMPHIPODS	<i>Acanthostephia malmgreni</i>	-	-	+	+
	<i>Halirages fulvocinctus</i>	-	+	+	+
	<i>Hyperia medusarum</i>	-	-	+	-
	<i>Parathemisto abyssorum</i>	+	-	+	+
	<i>P. gaudichaudii</i>	+	-	+	+
CHAETOGNATHS	<i>Eukrohnia hamata</i>	+	+	+	+
	<i>Sagitta elegans</i>	+	+	+	+
	<i>S. maxima</i>	+	+	-	+
COPEPODS	<i>Calanus hyperboreus</i>	+	+	+	+
	<i>Centropages hamatus</i>	+	-	-	+
	<i>Euchaeta norvegica</i>	+	+	-	+
	<i>Gaidius tenuispinus</i>	+	+	-	-
	<i>Metridia longa</i>	+	+	+	+
	<i>Pseudocalanus elongatus</i>	+	-	-	-
	<i>Temora longicornis</i>	+	-	+	-
DECAPODS	<i>Pandalus borealis</i>	-	-	+	+
	<i>P. propinquis</i>	-	-	+	-
	<i>Pasiphaea multidentata</i>	+	+	+	+
	<i>Sergestes arcticus</i>	+	+	-	-
EUPHAUSIIDS	<i>Meganyctiphanes norvegica</i>	+	+	+	+
	<i>Thysanoessa inermis</i>	+	+	+	+
	<i>T. longicaudata</i>	-	-	+	+
	<i>T. raschii</i>	+	+	+	+

Table 3-1. Continued.

Taxonomic Group	Species	Bay d'Espoir		Fortune Bay	
		Dec.	Aug.	Dec.	Aug.
FISHES	<i>Benthoosema glaciale</i>	+	+	-	-
	<i>Clupea harengus</i>	+	-	-	-
	<i>Cyclothone microdon</i>	-	+	-	-
	<i>Glyptocephalus cynoglossus</i>	+	-	-	-
	<i>Mallotus villosus</i>	-	-	+	-
	<i>Melanostigma atlanticum</i>	+	+	-	-
	<i>Sebastes</i> sp.	-	+	-	-
MYSIDS	<i>Boreomysis arctica</i>	+	+	-	-
	<i>B. nobilis</i>	-	-	+	+
	<i>Meterythrops robusta</i>	-	-	+	-
	<i>Mysis mixta</i>	-	-	+	+
	<i>Pseudomma truncatum</i>	-	-	+	-
OSTRACODS	Ostracod spp.	+	+	-	-
POLYCHAETES	<i>Tomopteris helgolandica</i>	+	-	+	-
PTEROPODS	<i>Clione limacina</i>	+	+	-	+
GELATINOUS ZOOPLANKTON	<i>Aurelia</i> sp.	-	+	-	-
	Ctenophores	+	+	+	+

unpredictably during the winter months (J. Richard, personal communication). In summer (Figure 3-1d), the physical structure of the water column changed with the introduction of a considerable amount of LCW. The water was uniformly cold (-0.30°C) except in the surface-warmed layer. Thus Fortune Bay is occupied by different water types seasonally, whereas this was not the case in Bay d'Espoir.

3.3. Stable Carbon and Nitrogen Isotopic Compositions

A total of 355 pairs of stable carbon and nitrogen isotope measurements were made on the fauna, particulate organic matter and sediment. All isotope data generated in the course of this research are given in Appendix A through D.

3.3.1. Particulate Organic Matter

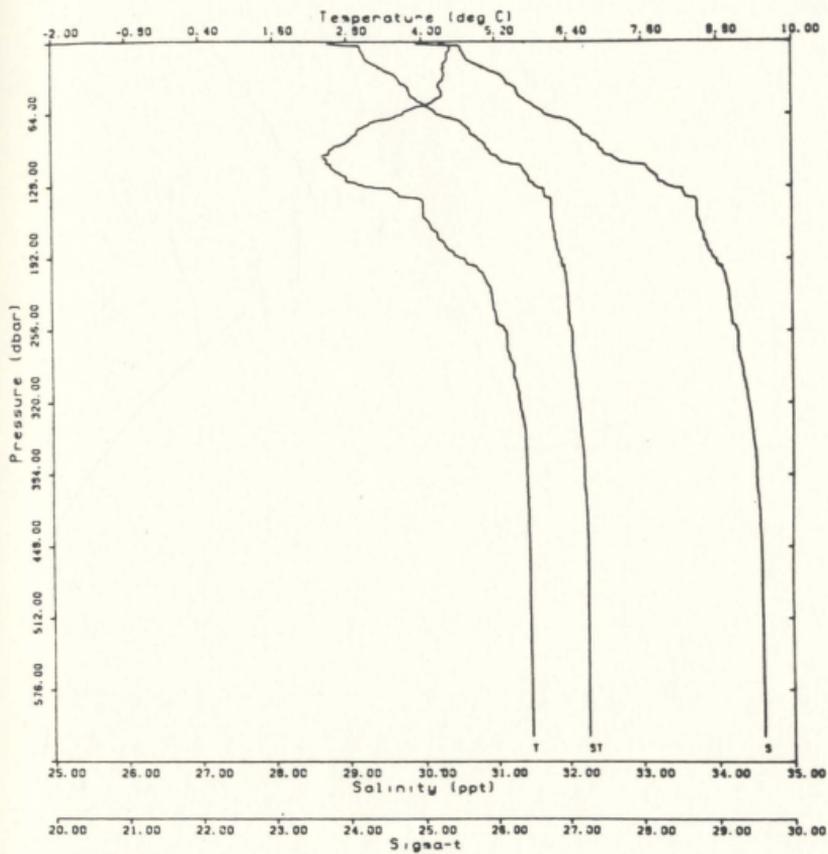
The stable carbon and nitrogen isotopic compositions of particulate organic matter (POM) are presented in Table 3-2. The stable carbon and nitrogen isotope values of the subsurface POM could not be tested statistically for seasonal differences within and between fjords due to the small number of measurements made. The carbon isotopic composition of the subsurface POM in each fjord was similar within a season (Table 3-2), although $\delta^{13}\text{C}$ values were different between seasons in Bay d'Espoir. This was not the case in Fortune Bay.

Particulates collected in Bay d'Espoir in August from the near-surface mixed layer, intermediate-depth layer (LCW), and bottom water (MSW) showed a progressive shift to more positive $\delta^{13}\text{C}$ values with depth (Table 3-2). A similar positive shift in POM $\delta^{13}\text{C}$ values between the subsurface layer and bottom water (LCW) was also apparent in Fortune Bay in August (Table 3-2). The amount of ^{13}C -enrichment between the subsurface layer and bottom water POM in Bay d'Espoir was approximately double that of Fortune Bay, $0.9^{\circ}/\text{oo}$ versus $0.5^{\circ}/\text{oo}$ (Table 3-2).

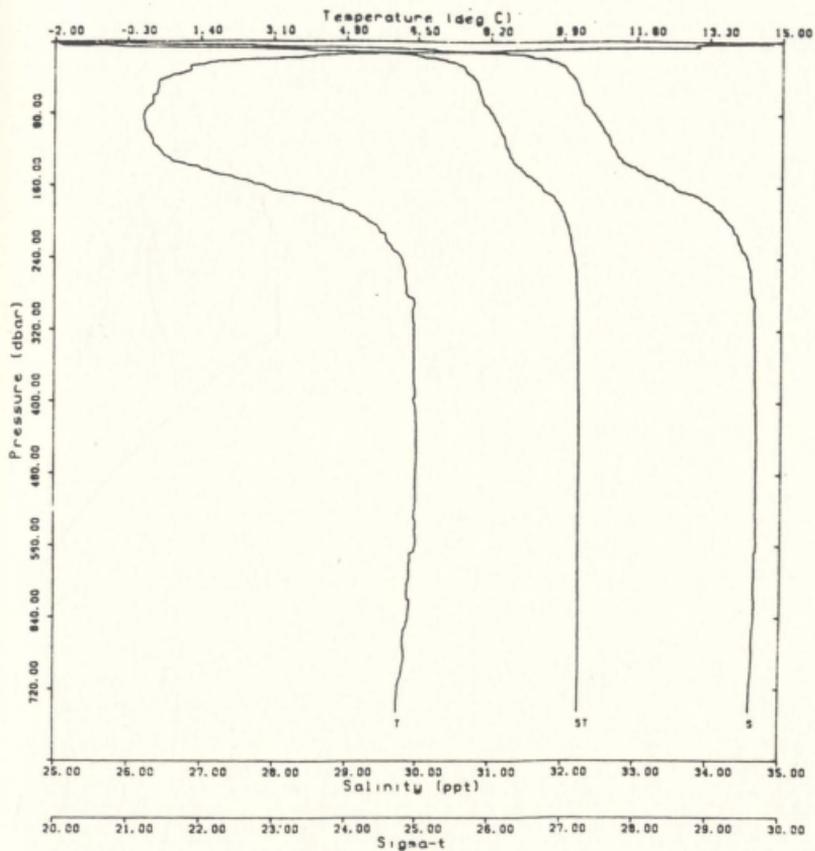
Mean stable nitrogen isotope values of subsurface POM ranged from $+4.9$ to $+5.0^{\circ}/\text{oo}$ between the fjords in December and from $+4.6$ to $+5.0^{\circ}/\text{oo}$ in August (Table 3-2). Stable nitrogen isotope values in Bay d'Espoir in August increased by $5.5^{\circ}/\text{oo}$ from the subsurface layer ($\delta^{15}\text{N} = +5.0^{\circ}/\text{oo}$) to the intermediate-depth

Figure 3-1: Conductance and temperature profiles of the main outer basins in Bay d'Espoir in winter (a) and summer (b) and in Fortune Bay in winter (c) and summer (d).

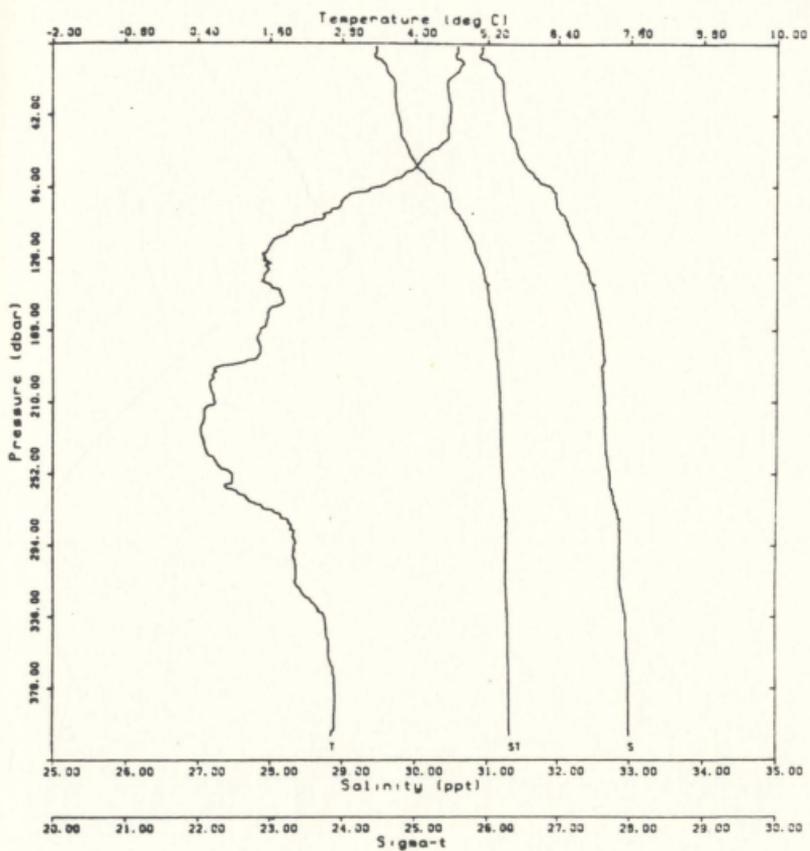
(a). Bay d'Espoir - December 1984



(b). Bay d'Espoir - August 1985



(c). Fortune Bay - December 1984



(d). Fortune Bay - August 1985

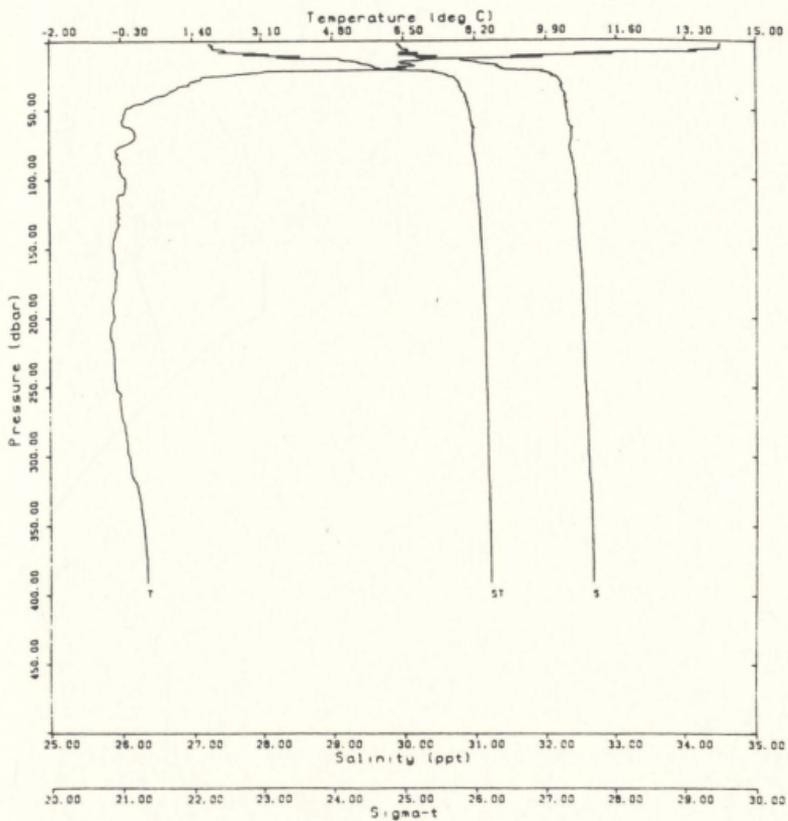


Table 3-2. Stable carbon and nitrogen isotope measurements of particulate organic matter and sediment collected in Bay d'Espoir and Fortune Bay in December 1984 and August 1985. The categories for the POM refer to the depths sampled. Intermediate refers to LCW at 80 m in Bay d'Espoir, while the bottom water was collected from MSW at 745 m in Bay d'Espoir and from LCW at 378 m in Fortune Bay.

Organic Matter	Bay d'Espoir - December		Bay d'Espoir - August		Fortune Bay - December		Fortune Bay - August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)						
Particulates:								
subsurface	-25.1,-24.9	+4.9	-24.0,-23.8	+4.6,+5.1	-25.3,-24.1	+4.7,+5.2	-24.5	+4.6
intermediate			-23.5	+10.5				
bottom			-23.1,-22.9	+7.9,+8.6			-24.0,-23.9	+8.9
Sediments:	-23.1,-23.0	+7.5,+7.7	-21.8	+7.6	-23.0,-23.0	+7.3,+7.4	-22.0,-21.8	+7.5,+7.7

layer (LCW) ($\delta^{15}\text{N}=+10.5\text{‰}$) and then decreased by 2.2‰ in the bottom water (MSW) ($\delta^{15}\text{N}=+8.3\text{‰}$; Table 3-2). In Fortune Bay the POM $\delta^{15}\text{N}$ values increased from $+4.6$ to $+8.9\text{‰}$ between the subsurface and bottom water (LCW). Mean bottom water POM $\delta^{15}\text{N}$ values were similar between Bay d'Espoir ($+8.3\text{‰}$) and Fortune Bay ($+8.9\text{‰}$).

3.3.2. Sediment

Sediment $\delta^{13}\text{C}$ values were more positive in Bay d'Espoir and Fortune Bay in August than December (Table 3-2). The seasonal difference in the carbon isotopic composition of the sediment was nearly identical in magnitude for both fjords (1.3‰ in Bay d'Espoir versus 1.1‰ in Fortune Bay) and was in the same direction as the seasonal change in subsurface POM $\delta^{13}\text{C}$ values.

Stable nitrogen isotope values of the sediment were similar in both fjords regardless of the season (Table 3-2). The sediments consistently had a mean $\delta^{15}\text{N}$ value of $+7.6\text{‰}$, with the exception of the December sample from Fortune Bay (Table 3-2).

Fortune Bay sediments contained more organic carbon and nitrogen than those in Bay d'Espoir (Table 3-3). Mean C:N ratios were consistently higher in Bay d'Espoir (December=9.2 and August=8.3) than Fortune Bay (December=8.2 and August=7.5).

3.3.3. Fauna

3.3.3.1. Bay d'Espoir

Seasonal stable carbon and nitrogen isotope values of the fauna (whole bodies) from Bay d'Espoir are given in Table 3-4. The majority of species had more positive mean $\delta^{13}\text{C}$ values than the subsurface POM during both seasons. This finding is in keeping with other food chain studies (e.g. McConnaughey 1978, McConnaughey and McRoy 1979a,b, Mills *et al.* 1984) that have shown that species are generally enriched in ^{13}C relative to the primary producers. Exceptions were the mysid *Boreomysis arctica* in December and the amphipod

Table 3-3. The mean percentage of carbon, nitrogen and C:N ratios of sediments collected in Bay d'Espoir and Fortune Bay in December 1984 and August 1985.

Sedimentary Organic Matter	Bay d'Espoir		Fortune Bay	
	December	August	December	August
% carbon	2.7	3.1	3.9	3.3
% nitrogen	0.34	0.43	0.55	0.51
C/N	9.2	8.3	8.2	7.5

Halirages fulvocinctus and the chaetognath *Sagitta elegans* in August. Bamstedt (1978) found the main biochemical component of *B. arctica* during the winter was lipid. High lipid levels in the body of this species may account for the very negative carbon isotope value observed, as lipids are depleted in ^{13}C (DeNiro and Epstein 1977). All species had mean $\delta^{15}\text{N}$ values more positive than that of the subsurface POM during both seasons.

Copepods and ostracods generally had the most negative mean $\delta^{13}\text{C}$ values, relative to the rest of the fauna, indicating their low trophic position as herbivores or omnivores. Of five species that could be tested for seasonal differences in body $\delta^{13}\text{C}$ values, only *Calanus hyperboreus* and *Metridia longa* proved to be statistically different ($p < 0.05$) (Table 3-5). The majority of species were enriched in ^{15}N in August compared to the December samples, although this was only statistically significant ($p < 0.05$) for the ostracods and *T. raschii* (Table 3-5). Animals depleted in ^{15}N between seasons were ctenophores, *C. limacina*, *M. atlanticum* and *S. maxima* (Table 3-4).

None of the other species tested for seasonal differences in their whole body $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were significantly different (Table 3-5). In many cases the carbon isotope values became more negative from winter to summer (Table 3-4).

Muscle tissue from decapods, euphausiids, fishes and mysids was also analyzed for its stable carbon and nitrogen isotopic composition (Table 3-6). This tissue was enriched in ^{13}C and ^{15}N relative to whole body samples (Table 3-4). Notable exceptions were found in the nitrogen isotopic composition of *S. arcticus* and *B. glaciale* collected in August. In all cases muscle $\delta^{13}\text{C}$ values were more positive in winter than summer but this pattern was not evident with nitrogen; $\delta^{15}\text{N}$ values either remained the same, increased or decreased depending on the species. Significant seasonal differences ($p < 0.05$) occurred in the $\delta^{13}\text{C}$ values of muscle tissue of *B. glaciale*, *M. norvegica*, *P. multidentata* and *T. inermis* (Table 3-7). Only *M. norvegica* exhibited a significant change in its mean nitrogen isotope ratio between seasons (Table 3-7).

Table 3-4. The stable carbon and nitrogen isotopic composition (mean±s.d.) of fauna (whole bodies) collected in Bay d'Espoir in December 1984 and August 1985. Sample sizes are in parentheses.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>C. hyperboreus</i>	-22.1±0.4 (2)	+9.4±0.1 (2)	-22.6±0.3 (3)	+9.5±0.2 (3)
<i>C. hamatus</i>	-21.8±0.4 (2)	+8.8±0.1 (2)		
<i>E. norvegica</i>	-22.7±0.2 (4)	+11.8±0.8 (4)	-23.5±0.9 (4)	+12.3±0.8 (4)
<i>G. tenuispinus</i>	-23.2±0.1 (3)	+10.5±0.8 (3)	-23.3±0.6 (3)	+10.8±0.6 (3)
<i>M. longa</i>	-22.6±0.4 (5)	+10.0±0.8 (5)	-23.9±0.2 (3)	+10.1±0.6 (3)
Mixed copepods			-21.8±0.9 (2)	+9.3±0.4 (2)

Table 3-4. Continued.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>P. elongatus</i>	-21.9 (1)			
<i>T. longicornis</i>	-21.4±0.6 (3)	+7.7±0.8 (3)		
Ostracod spp.	-22.8±0.1 (2)	+10.0±0.0 (2)	-22.7±0.6 (2)	+10.9±0.1 (2)
<i>H. fulvocinctus</i>			-24.1 (1)	+9.5 (1)
<i>P. abyssorum</i>	-21.9 (1)	+11.3 (1)		
<i>P. gaudichaudii</i>	-22.2±0.5 (5)	+10.7±0.3 (5)		
<i>M. norvegica</i>			-21.4 (1)	+10.1 (1)
<i>T. inermis</i>	-21.7±0.9 (3)	+11.1±0.4 (3)	-22.4±1.0 (2)	+11.2±0.5 (2)
<i>T. raschii</i>	-22.3±0.3 (3)	+10.6±0.1 (3)	-21.4±0.6 (2)	+10.8±0.0 (2)

Table 3-4. Continued.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>P. multidentata</i>			-20.7 (1)	+12.1 (1)
<i>S. arcticus</i>			-20.6 (1)	+12.6 (1)
<i>B. arctica</i>	-25.2 (1)	+10.8 (1)		
<i>E. hamata</i>	-22.1±0.7 (5)	+12.1±0.4 (5)	-22.4±0.3 (3)	+12.5±0.4 (3)
<i>S. elegans</i>	-20.3±0.4 (2)	+11.8±1.9 (3)	-24.2±2.5 (2)	+12.7±0.8 (2)
<i>S. mazima</i>	-21.2 (1)	+14.1 (1)	-22.6 (1)	+11.1 (1)
<i>T. helgolandica</i>	-21.1±0.8 (2)	+10.9±0.6 (2)		
<i>B. glaciale</i>			-20.6 (1)	+14.0 (1)
<i>C. harengus</i>	-20.9 (1)	+11.6 (1)		

Table 3-4. Continued.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>C. microdon</i>			-22.5 (1)	+12.1 (1)
<i>G. cynoglossus</i>	-23.4±0.1 (2)	+10.5±0.4 (2)		
<i>M. atlanticum</i>	-21.2±0.8 (10)	+14.3±0.4 (10)	-21.0±0.8 (2)	+13.8±0.1 (2)
<i>C. limacina</i>	-21.3 (1)	+10.9 (1)	-23.7 (1)	+9.7 (1)
Ctenophores	-20.1±1.7 (3)	+11.3±0.3 (3)	-20.3±0.2 (2)	+10.8±0.3 (2)
<i>Aurelia</i> sp.			-21.9 (1)	+8.3 (1)

Table 3-5. Results of two-tailed t-tests on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ whole body values of fauna collected in winter compared to summer in Bay d'Espoir. Sample sizes are in parentheses.

Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>C. hyperboreus</i>	$p=0.01$ (9)	$p=0.49$ (9)
<i>E. hamata</i>	$p=0.52$ (8)	$p=0.22$ (8)
<i>E. norvegica</i>	$p=0.11$ (8)	$p=0.46$ (8)
<i>G. tenuispinus</i>	$p=0.65$ (6)	$p=0.67$ (6)
Ctenophores	$p=0.89$ (5)	$p=0.19$ (5)
<i>M. atlanticum</i>	$p=0.69$ (12)	$p=0.11$ (12)
<i>M. longa</i>	$p<0.00$ (8)	$p=0.87$ (8)
Ostracod spp.	$p=0.91$ (4)	$p=0.01$ (4)
<i>S. elegans</i>	$p=0.16$ (4)	$p=0.61$ (5)
<i>T. inermis</i>	$p=0.50$ (5)	$p=0.91$ (5)
<i>T. raschii</i>	$p=0.10$ (5)	$p=0.03$ (5)

Table 3-6. The stable carbon and nitrogen isotopic composition (mean±s.d.) of fauna (muscle) collected in Bay d'Espoir in December 1984 and August 1985. Sample sizes are in parentheses.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>P. multidentata</i>	-20.8±0.4 (6)	+12.4±0.5 (6)	-19.0±0.5 (3)	+12.3±0.8 (3)
<i>S. arcticus</i>	-20.3±0.7 (3)	+12.6±0.5 (3)	-19.6±0.3 (3)	+11.7±0.7 (3)
Shrimp sp.			-18.6±0.3 (2)	+13.6±1.0 (2)
<i>M. norvegica</i>	-20.8±0.5 (5)	+9.4±0.3 (5)	-19.7±0.1 (3)	+10.0±0.3 (3)
<i>T. inermis</i>	-21.5±0.5 (3)	+12.2±0.2 (3)	-20.4±0.1 (3)	+12.4±0.2 (3)
<i>T. raschii</i>	-21.6±0.2 (3)	+11.3±0.2 (3)	-20.6±0.6 (3)	+11.2±0.2 (3)

Table 3-6. Continued

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>B. arctica</i>	-19.3 (1)	+11.7 (1)	-19.2±0.3 (3)	+11.5±0.4 (3)
<i>B. glaciale</i>	-21.6±0.1 (4)	+13.0±0.5 (4)	-20.6±0.2 (3)	+13.4±0.1 (3)
<i>M. atlanticum</i>	-20.1±1.3 (2)	+14.6±0.5 (2)	-19.6±0.9 (3)	+13.9±0.6 (3)
<i>Sebastes</i> sp.			-18.6 (1)	+14.2 (1)

Table 3-7. Results of two-tailed t-tests on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ muscle values of fauna collected in winter compared to summer in Bay d'Espoir. Sample sizes are in parentheses.

Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>B. arctica</i>	$p=0.88$ (4)	$p=0.68$ (4)
<i>B. glaciale</i>	$p<0.00$ (7)	$p=0.27$ (7)
<i>M. norvegica</i>	$p=0.01$ (8)	$p=0.03$ (8)
<i>M. atlanticum</i>	$p=0.70$ (5)	$p=0.29$ (5)
<i>P. multidentata</i>	$p<0.00$ (9)	$p=0.78$ (9)
<i>S. arcticus</i>	$p=0.20$ (6)	$p=0.15$ (6)
<i>T. inermis</i>	$p=0.02$ (6)	$p=0.35$ (6)
<i>T. raschii</i>	$p=0.06$ (6)	$p=0.52$ (6)

3.3.3.2. Fortune Bay

All species in Fortune Bay had $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values greater than those of the subsurface POM during both summer and winter (Table 3-8). The copepod fauna of the main outer basin of Fortune Bay in December was dominated by one species, *M. longa*, which, of the three copepod species collected, had the most negative $\delta^{13}\text{C}$ value ($-23.3 \pm 0.2\text{‰}$). Neither *C. hyperboreus* or *M. longa* had carbon values that differed significantly between seasons (Table 3-9). However, samples of *C. hyperboreus* were significantly different ($p < 0.05$) in their stable nitrogen isotopic composition between seasons (Table 3-9), indicating a possible change in diet.

The only species found to have significantly different ($p < 0.05$) $\delta^{13}\text{C}$ values between seasons was the carnivorous amphipod *P. gaudichaudii* (Table 3-9). No clear trend of more negative carbon isotope values in summer than winter was apparent. Some species had the same $\delta^{13}\text{C}$ value in winter as summer (e.g. *M. longa*), while others became slightly more negative or positive (e.g. *T. raschii* and *M. mixta*, respectively). The copepod *C. hyperboreus* and the amphipods *H. fulvocinctus* and *P. gaudichaudii* had significant differences ($p < 0.05$) in their stable nitrogen isotopic composition between winter and summer (Table 3-9).

Carbon and nitrogen isotope values from muscle tissues were enriched in the heavy isotopes relative to whole body values (Tables 3-8 and 3-10). Significant seasonal differences ($p < 0.05$) in the stable carbon isotopic composition of muscle tissue were found for *M. norvegica* and *T. raschii* (Table 3-11). Only *M. norvegica* had a significant difference in its nitrogen composition with season.

3.3.3.3. Seasonal Comparison of the Fjords

This section compares the isotopic composition of the fauna common to Bay d'Espoir and Fortune Bay during winter (December) and summer (August). Differences in the isotopic composition of a species found in both fjords within a season might indicate changes in diet or biochemical composition. Mean carbon and nitrogen isotopic values for animals from Bay d'Espoir are in Table 3-4, and Table 3-8 contains the Fortune Bay values. Results of the statistical analysis are given in Table 3-12.

Table 3-8. The stable carbon and nitrogen isotopic composition (mean±s.d.) of fauna (whole bodies) collected in Fortune Bay in December 1984 and August 1985. Sample sizes are in parentheses.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>C. hyperboreus</i>	-21.8 (1)	+10.6 (1)	-21.7±0.3 (4)	+9.9±0.1 (4)
<i>C. hamatus</i>			-23.7 (1)	+9.7 (1)
<i>E. norvegica</i>			-23.6±0.3 (3)	+12.7±1.1 (3)
<i>M. longa</i>	-23.3±0.2 (5)	+10.9±0.5 (5)	-23.3±0.3 (5)	+10.6±0.6 (5)
<i>T. longicornis</i>	-20.8 (1)	+8.0 (1)		
<i>A. malmgreni</i>	-21.7±0.6 (3)	+13.8±0.8 (3)	-21.1±0.6 (3)	+14.4±0.7 (3)

Table 3-8. Continued.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>H. fulvocinctus</i>	-23.4 \pm 1.0 (6)	+10.9 \pm 0.3 (6)	-23.7 \pm 0.5 (3)	+9.7 \pm 0.6 (4)
<i>H. medusarum</i>	-22.9 \pm 0.1 (2)	+11.4 \pm 0.4 (2)		
<i>P. gaudichaudii</i>	-22.3 \pm 0.3 (5)	+10.2 \pm 0.3 (4)	-23.3 \pm 0.3 (4)	+11.1 \pm 0.4 (4)
<i>T. inermis</i>	-22.4 \pm 0.4 (4)	+11.3 \pm 0.4 (4)		
<i>T. longicaudata</i>	-23.0 \pm 0.9 (3)	+10.5 \pm 0.8 (3)	-22.1 \pm 0.6 (2)	+11.5 \pm 0.6 (2)
<i>T. raschii</i>	-21.4 \pm 0.5 (3)	+10.7 \pm 0.3 (3)	-21.7 \pm 0.3 (2)	+10.6 \pm 0.1 (2)
<i>B. nobilis</i>			-22.3 (1)	+12.6 (1)
<i>M. mixta</i>	-22.5 \pm 0.8 (4)	+11.0 \pm 0.4 (4)	-21.8 (1)	+10.4 (1)
<i>M. robusta</i>	-22.6 (1)	+10.6 (1)		

Table 3-8. Continued.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>P. truncatum</i>	-22.3 (1)	+12.7 (1)		
<i>E. hamata</i>	-23.4 (1)	+11.9 (1)	-22.4 (1)	+12.2 (1)
<i>S. elegans</i>	-22.2±0.9 (5)	+12.9±0.4 (5)	-21.8±0.3 (5)	+12.9±0.6 (5)
<i>S. mazima</i>			-21.4 (1)	+14.6 (1)
<i>T. helgolandica</i>	-22.2 (1)	+11.2 (1)		
<i>M. villosus</i>	-22.5±1.4 (3)	+11.7±0.2 (3)		
<i>C. limacina</i>			-21.1 (1)	+10.1 (1)
Ctenophores	-22.0±1.1 (5)	+11.1±1.5 (5)		

Table 3-9. Results of two-tailed t-tests on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ whole body values of fauna collected in winter compared to summer in Fortune Bay. Sample sizes are in parentheses.

Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>A. malmgreni</i>	$p=0.24$ (6)	$p=0.40$ (6)
<i>C. hyperboreus</i>	$p=0.76$ (5)	$p=0.01$ (5)
<i>H. fulvocinctus</i>	$p=0.73$ (9)	$p<0.00$ (9)
<i>M. longa</i>	$p=0.83$ (11)	$p=0.36$ (10)
<i>M. mixta</i>	$p=0.47$ (5)	$p=0.29$ (5)
<i>P. gaudichaudii</i>	$p<0.00$ (9)	$p=0.02$ (8)
<i>S. elegans</i>	$p=0.32$ (10)	$p=0.91$ (10)
<i>T. longicaudata</i>	$p=0.30$ (5)	$p=0.20$ (5)
<i>T. raschii</i>	$p=0.51$ (5)	$p=0.70$ (5)

Table 3-10. The stable carbon and nitrogen isotopic composition (mean±s.d.) of fauna (muscle) collected in Fortune Bay in December 1984 and August 1985. Sample sizes are in parentheses.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>P. borealis</i>	-20.5±0.8 (6)	+13.3±1.0 (6)	-18.4 (1)	+12.9 (1)
<i>P. multidentata</i>	-20.4±0.2 (2)	+13.2±0.1 (2)	-20.5 (1)	+13.2 (1)
<i>P. propinquis</i>	-21.2 (1)	+12.7 (1)		
<i>M. norvegica</i>	-21.3±0.8 (10)	+9.4±0.4 (10)	-20.0±0.2 (3)	+10.3±0.3 (3)
<i>T. inermis</i>	-21.8±0.8 (12)	+12.2±0.4 (12)	-21.3 (1)	+12.6 (1)
<i>T. raschii</i>	-21.3±0.3 (9)	+11.6±0.2 (9)	-20.8±0.1 (3)	+11.2±0.7 (3)

Table 3-10. Continued.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>B. nobilis</i>	-20.7±0.2 (3)	+13.6±0.5 (3)		
<i>M. mixta</i>	-21.6 (1)	+11.4 (1)		
<i>M. villosus</i>	-21.5±0.9 (4)	+13.1±0.4 (4)		

Table 3-11. Results of two-tailed t-tests on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ muscle values of fauna collected in winter compared to summer in Fortune Bay. Sample sizes are in parentheses.

Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>M. norvegica</i>	$p=0.03$ (13)	$p<0.00$ (13)
<i>T. inermis</i>	$p=0.59$ (13)	$p=0.31$ (13)
<i>T. raschii</i>	$p=0.01$ (12)	$p=0.13$ (12)

The distribution of the stable carbon and nitrogen isotope values of the fauna in each fjord are shown in Figure 3-2. Carbon and nitrogen values of the fauna (muscle and whole body tissues) from Bay d'Espoir ranged from -25.9 to -18.4‰ and +7.0 to +15.2‰ versus -24.8 to -20.2‰ and +8.0 to +14.6‰ in Fortune Bay.

None of the species of amphipods, euphausiids, pteropods or ctenophores common to both fjords were significantly different in their carbon and nitrogen isotopic compositions in either the summer or winter.

In the majority of cases, species collected from Fortune Bay in December had more negative mean whole body $\delta^{13}\text{C}$ values than their counterparts in Bay d'Espoir. These included *E. hamata*, *M. longa*, *S. elegans*, *T. inermis*, *T. helgolandica* and ctenophores. However, only *M. longa* and *S. elegans* proved to be significantly different ($p < 0.05$). Conversely, animals from Bay d'Espoir in August tended to have more negative $\delta^{13}\text{C}$ values than the same species in Fortune Bay. Significant differences ($p < 0.05$) were only found in *C. hyperboreus* and *M. longa*.

Copepods from Fortune Bay were usually more enriched in ^{15}N than their counterparts from Bay d'Espoir during winter and summer. A significant difference ($p < 0.05$) in the mean whole body $\delta^{15}\text{N}$ values between the fjords was found for *C. hyperboreus* during both seasons and for *M. longa* in winter.

Statistical analysis was also done on the stable carbon and nitrogen values of muscle tissue from the decapod *P. multidentata* and the euphausiids *M. norvegica*, *T. inermis* and *T. raschii*. No significant differences were found in $\delta^{13}\text{C}$ values between fjords in December (Table 3-13). In August, samples of *M. norvegica* and *T. inermis* were significantly different ($p < 0.05$) between the fjords.

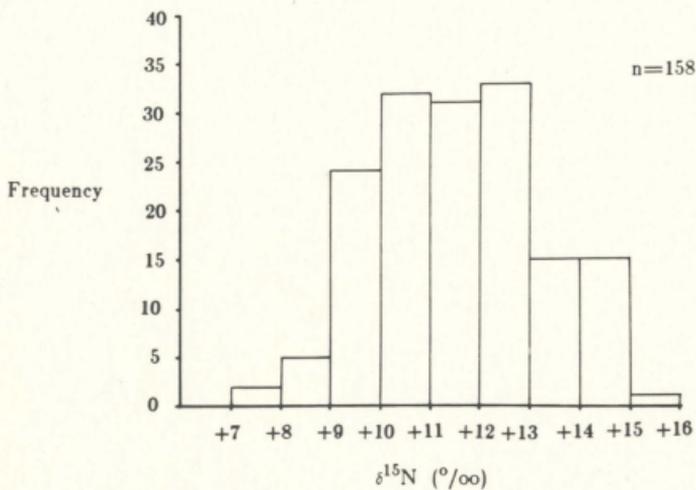
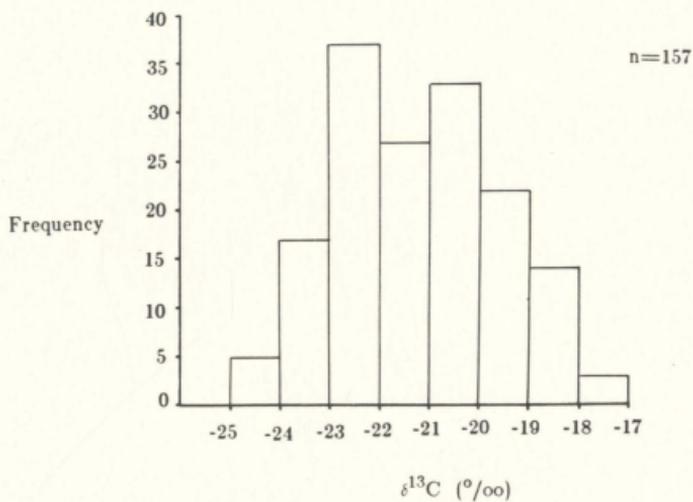
Stable nitrogen isotope values were only significantly different between fjords for *T. raschii* in December (Table 3-13). No differences were found in the $\delta^{15}\text{N}$ values of animals in Bay d'Espoir and Fortune Bay in August.

Table 3-12. Results of two-tailed t-tests on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ whole body values of fauna collected in winter and summer in Bay d'Espoir compared to Fortune Bay. Sample sizes are in parentheses.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>C. hyperboreus</i>	p=0.25(7)	p=0.01 (7)	p=0.01 (7)	p=0.01 (7)
<i>E. norvegica</i>			p=0.85 (7)	p=0.58 (7)
<i>M. longa</i>	p=0.02 (10)	p=0.05 (10)	p=0.02 (9)	p=0.26 (8)
<i>T. longicornis</i>	p=0.49 (4)	p=0.78 (4)		
<i>H. fulvocinctus</i>			p=0.53 (4)	p=0.82 (5)
<i>P. gaudichaudii</i>	p=0.75 (10)	p=0.06 (9)		
<i>T. inermis</i>	p=0.26 (7)	p=0.50 (7)		
<i>T. raschii</i>	p=0.06 (6)	p=0.73 (6)	p=0.57 (4)	p=0.18 (4)
<i>E. hamata</i>	p=0.17 (6)	p=0.64 (6)	p=0.94 (4)	p=0.60 (4)
<i>S. elegans</i>	p=0.04 (7)	p=0.23 (7)	p=0.06 (7)	p=0.67 (7)
Ctenophores	p=0.09 (8)	p=0.85 (8)		

Figure 3-2: Frequency histograms of the stable carbon and nitrogen isotopic composition of the fauna in Bay d'Espoir (a) and Fortune Bay (b).

(a). Bay d'Espoir



(b). Fortune Bay

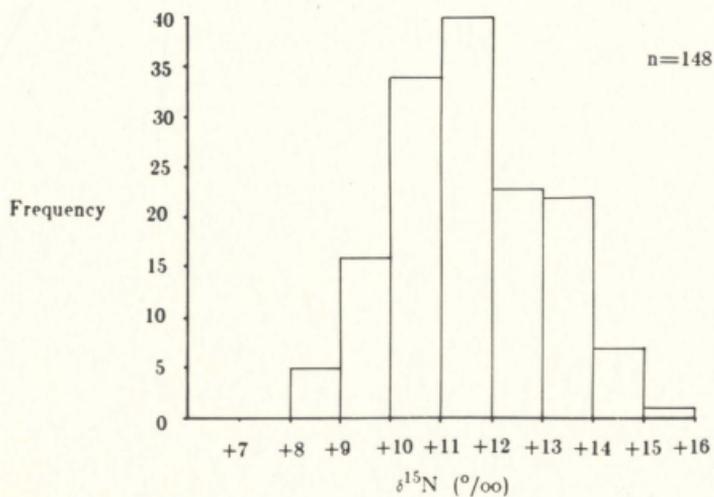
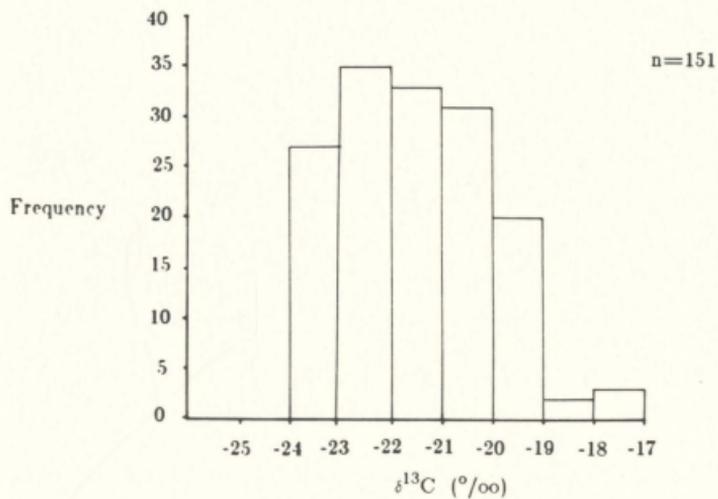


Table 3-13. Results of two-tailed t-tests on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ muscle values of fauna collected in winter and summer in Bay d'Espoir compared to Fortune Bay. Sample sizes are in parentheses.

Species	December		August	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>M. norvegica</i>	p=0.28 (15)	p>1.00 (15)	p=0.03 (6)	p=0.25 (6)
<i>P. multidentata</i>	p=0.17 (8)	p=0.07 (8)	p=0.12 (4)	p=0.41 (4)
<i>T. inermis</i>	p=0.56 (15)	p>1.00 (15)	p=0.02 (4)	p=0.43 (4)
<i>T. raschii</i>	p=0.15 (12)	p=0.04 (12)	p=0.67 (6)	p=0.94 (6)

3.4. Pelagic Food Chains and Water Types

The existence of a relationship between individual food chains and specific water types was suggested from plots (Figures 3-3a,b,c and d) of the distribution of the carbon and nitrogen isotope values of the fauna relative to the isotopic composition of the POM. The starting point of each line on the plots represents the carbon and nitrogen isotopic composition of the POM from that water type. Only subsurface water was sampled in either fjord in winter, therefore the position of the lines representing the other water types (in winter) was based on the isotopic compositions of the near-surface layer POM in winter and summer, the isotopic compositions of LCW and MSW types in summer and from known water type affiliations of various species (Richard 1986). The slope of each line, and hence the trajectory, was determined using trophic level enrichments of carbon and nitrogen calculated in this study. The water type affiliation of species that only had muscle tissue analyzed for its isotopic composition was determined by applying correction factors of -1.0 and -1.5‰ to muscle $\delta^{13}\text{C}$ values in winter and summer, respectively. This correction allowed an estimation of whole body values, as muscle tissue is enriched in ^{13}C relative to the whole body. Correction factors were determined from isotopic measurements made on muscle tissue and whole bodies of several species in winter and summer (Appendix A through D). A correction factor was not applied to the nitrogen values because muscle tissue and whole body measurements did not differ enough (i.e. by 3.0‰ or greater) to alter a species' calculated trophic position and water type affiliation.

The overall organization of each food web is given in Figure 3-4, while the food chains for each fjord in the winter and summer are shown in Figure 3-5. Suspended POM in the subsurface layer was the ultimate source of organic carbon and nitrogen at the base of the food chains and webs identified in both fjords during winter and summer. The pelagic food web in Bay d'Espoir appeared to be composed of three food chains in winter and summer, while Fortune Bay had three food chains in winter and two in summer. The absence of MSW from Fortune Bay in the summer reduced its food web from three to two food chains. The trophic structure of the food webs in Bay d'Espoir and Fortune Bay in

summer and winter was similar. Only one species, *T. longicornis*, was found on the second trophic level of the food webs of Bay d'Espoir and Fortune Bay in December (Figures 3-4a, c).

3.4.1. Bay d'Espoir

3.4.1.1. December

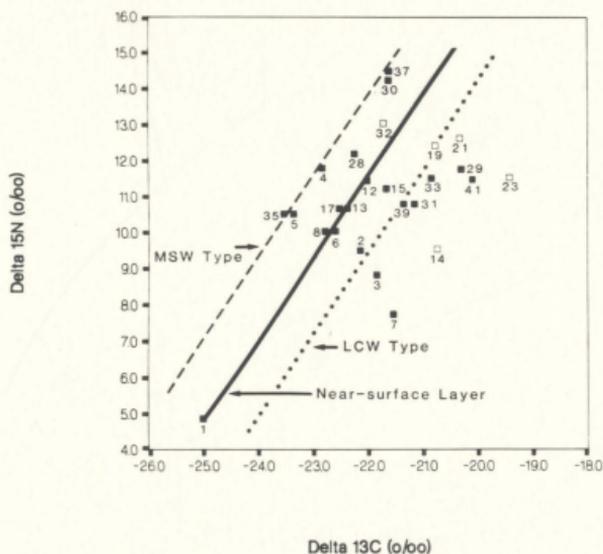
The water column of Bay d'Espoir in December consisted of a mixed subsurface layer of MSW, a mixed intermediate-depth layer of LCW and MSW (referred to as LCW type) and a layer of MSW which extended from approximately 129 m to the bottom (Figure 3-1a). The isotopic composition of the fauna suggested the affiliation of three distinct faunal assemblages, each with a particular water type. Additional information on known species' affiliations with water types came from Richard (1986), for example *C. limacina* is associated with LCW and both *B. glaciale* and *M. atlanticum* with MSW. In Figure 3-3a the lower line is the food chain associated with the LCW type, the middle line (with the subsurface POM plotted at its base) is the near-surface layer food chain, and the upper line the position of the MSW type food chain.

The food web reconstructed for Bay d'Espoir in December, shown in Figure 3-4a, had six trophic levels and consisted of three food chains (Figure 3-5a). Omnivorous copepods were at trophic levels 2 and 2.5, while the third level was occupied by carnivores and omnivores. Only carnivores were found on trophic levels 3.5 and 4. The top predators were the chaetognath *S. mazima* and the fish *M. atlanticum*. The majority of species (17 of 26) were found on trophic levels 3 and 3.5 and were carnivores.

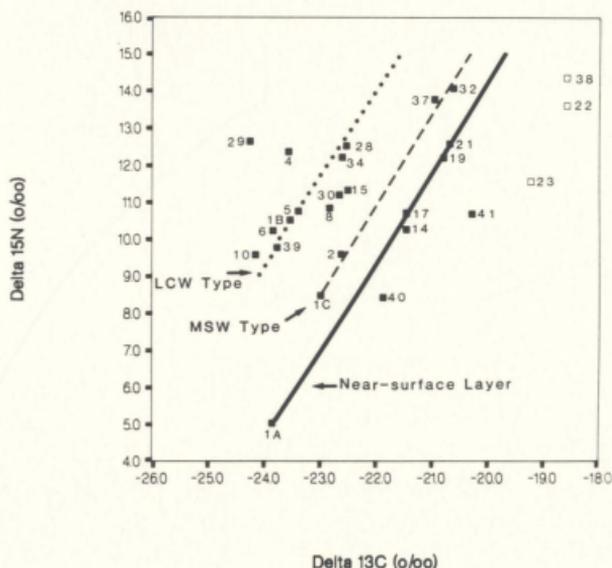
The food chain of the mixed near-surface layer was the shortest with four trophic levels, while the LCW and MSW type chains each had five levels (Figure 3-5a). The top carnivores (*M. atlanticum* and *S. mazima*) in the MSW food chain were located on the fourth trophic level. The LCW food chain had the most species associated with it (10 of 25), the most species (all carnivores) on a single trophic level (3.5), and was the only chain to have a species (*T. longicornis*) on the second trophic level. The majority of fish species were in the MSW chain,

Figure 3-3: Plots of mean stable carbon and nitrogen isotope values for species collected in Bay d'Espoir in December 1984 (a) and August 1985 (b) and in Fortune Bay in December 1984 (c) and August 1985 (d). Species associated with each water type are identified in Figure 3-5 on page 79.

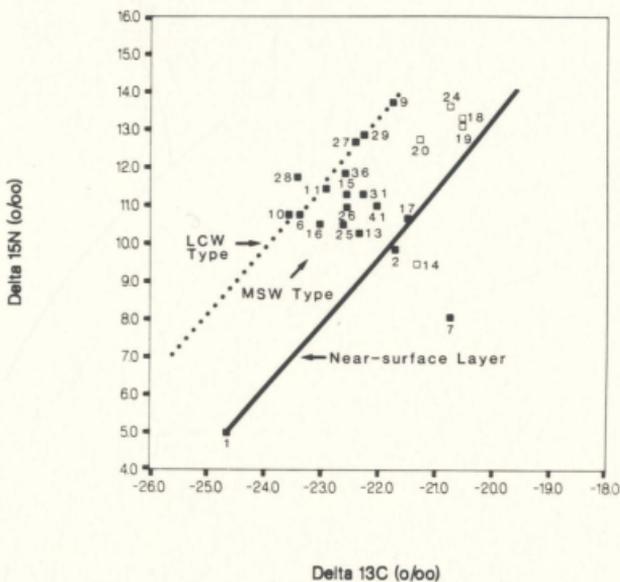
(a) Bay d'Espoir - December 1984



(b) Bay d'Espoir - August 1985



(c) Fortune Bay - December 1984



(d) Fortune Bay - August 1985

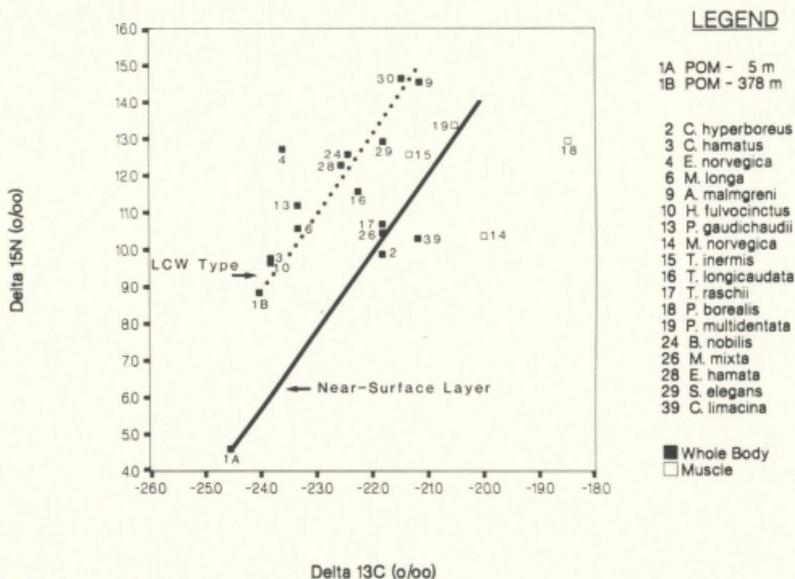


Figure 3-4: The trophic organization of the pelagic food webs in Bay d'Espoir in December 1984 (a) and August 1985 (b) and in Fortune Bay in December 1984 (c) and August 1985 (d).

(a) Bay d'Espoir - December 1984

Trophic Level

1.0

POM

2.0

T. longicornis

2.5

C. hamatus *G. tenuispinus* *G. cynoglossus* *M. longa*
Ostracod spp.

3.0

B. arctica *C. hyperboreus* *E. norvegica* *M. norvegica**
P. abyssorum *P. gaudichaudii* *T. inermis* *T. raschii*

3.5

*B. glaciale** *C. limacina* *C. harengus* Ctenophores
E. hamata *P. multidentata** *S. elegans* *S. arcticus**
T. helgolandica

4.0

M. atlanticum *S. mazima*

*Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values from Muscle Tissue.

Trophic Level

1.0

POM

2.0

2.5

Aurelia sp. *C. hyperboreus* *C. limacina* *H. fulvocinctus*
M. longa Ostracod spp.

3.0

E. hamata *G. tenuispinus* *M. norvegica** *S. elegans*
S. maxima *T. inermis* *T. raschii*

3.5

*B. arctica** Ctenophores *C. microdon* *E. norvegica*
P. multidentata *S. arcticus*

4.0

B. glaciale *M. atlanticum* Shrimp sp.*

4.5

Sebastes sp.*

*Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values from Muscle Tissue.

Trophic Level

1.0

POM

2.0

T. longicornis

2.5

H. fulvocinctus M. longa T. longicaudata

3.0

*C. hyperboreus E. hamata H. medusarum M. norvegica**
M. robusta M. mixta P. gaudichaudii T. inermis

3.5

Ctenophores *M. villosus P. propinquis* P. truncatum*
S. elegans T. raschii T. helgolandica

4.0

A. malmgreni B. nobilis P. borealis**
*P. multidentata**

*Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values from Muscle Tissue.

(d) Fortune Bay - August 1985

Trophic Level

1.0

POM

2.0

2.5

C. hamatus *H. fulvocinctus* *M. norvegica** *M. longa*
P. gaudichaudii

3.0

C. hyperboreus *C. limacina* *M. mixta* *T. longicaudata*
T. raschii

3.5

B. nobilis *E. hamata* *E. norvegica* *P. borealis**
*P. multidentata** *S. elegans* *T. inermis**

4.0

A. malmgreni *S. maxima*

*Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values from Muscle Tissue.

Figure 3-5: The trophic organization of the pelagic food chains in Bay d'Espoir in December 1984 (a) and August 1985 (b) and in Fortune Bay in December 1984 (c) and August 1985 (d).

(a) Bay d'Espoir - December 1984

<u>Trophic Level</u>	<u>Near-Surface Layer</u>	<u>LCW Type</u>	<u>MSW Type</u>
1.0	POM	POM	POM
2.0		<i>T. longicornis</i>	
2.5	<i>M. longa</i> Ostracod spp.	<i>C. hamatus</i>	<i>G. tenuispinus</i> <i>G. cynoglossus</i>
3.0	<i>T. raschii</i> <i>P. abyssorum</i> <i>P. gaudichaudii</i>	<i>B. arctica</i> <i>C. hyperboreus</i> <i>M. norvegica</i> *	<i>E. norvegica</i>
3.5	<i>P. multidentata</i> * <i>S. arcticus</i> *	<i>C. limacina</i> <i>C. harengus</i> Ctenophores <i>S. elegans</i> <i>T. helgolandica</i>	<i>B. glaciale</i> *
4.0			<i>M. atlanticum</i> <i>S. mazima</i>

*Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values from Muscle Tissue.

(b) Bay d'Espoir - August 1985

<u>Trophic Level</u>	<u>Near-Surface Layer</u>	<u>LCW Type</u>	<u>MSW Type</u>
1.0	POM	POM	POM
2.0			
2.5	<i>Aurelia</i> sp.	<i>C. limacina</i> <i>H. fulvocinctus</i> <i>M. longa</i>	<i>C. hyperboreus</i>
3.0	<i>M. norvegica</i> <i>T. raschii</i>	<i>E. hamata</i> <i>G. tenuispinus</i> <i>S. elegans</i>	
3.5	<i>B. arctica</i> * Ctenophores <i>P. multidentata</i> <i>S. arcticus</i>	<i>C. microdon</i> <i>E. norvegica</i>	
4.0	Shrimp sp.*		<i>B. glaciale</i> <i>M. atlanticum</i>
4.5	<i>Sebastes</i> sp.*		

*Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values from Muscle Tissue.

<u>Trophic Level</u>	<u>Near-Surface Layer</u>	<u>LCW Type</u>	<u>MSW Type</u>
1.0	POM	POM	POM
2.0	<i>T. longicornis</i>		
2.5		<i>H. fulvocinctus</i> <i>M. longa</i>	<i>T. longicaudata</i>
3.0	<i>C. hyperboreus</i> <i>M. norvegica</i> *	<i>E. hamata</i> <i>H. medusarum</i>	<i>M. robusta</i> <i>M. mixta</i> <i>P. gaudichaudii</i> <i>T. inermis</i>
3.5	<i>T. raschii</i>	<i>P. propinquis</i> * <i>P. truncatum</i> <i>S. elegans</i> <i>M. villosus</i>	Ctenophores <i>T. helgolandica</i>
4.0		<i>A. malmgreni</i> <i>B. nobilis</i> *	<i>P. borealis</i> * <i>P. multidentata</i> *

*Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values from Muscle Tissue.

(d) Fortune Bay - August 1985

<u>Trophic Level</u>	<u>Near-Surface Layer</u>	<u>LCW Type</u>
1.0	POM	POM
2.0		
2.5	<i>M. norvegica</i> *	<i>C. hamatus</i> <i>H. fulvocinctus</i> <i>M. longa</i> <i>P. gaudichaudii</i>
3.0	<i>C. hyperboreus</i> <i>C. limacina</i> <i>M. mixta</i> <i>T. raschii</i>	<i>T. longicaudata</i>
3.5	<i>P. borealis</i> *	<i>B. nobilis</i> <i>E. hamata</i> <i>E. norvegica</i> <i>P. multidentata</i> * <i>S. elegans</i> <i>T. inermis</i> *
4.0		<i>A. malmgreni</i> <i>S. maxima</i>

*Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Values from Muscle Tissue.

while the decapods were associated with the near-surface layer food chain. Two species, *E. hamata* and *T. inermis* were found at intermediate points between food chains and are not included in Figure 3-5a.

3.4.1.2. August

During the summer, the water types became more discrete in Bay d'Espoir (Figure 3-1b). The lower line on Figure 3-3b indicated the position of the near-surface layer, as it had subsurface POM at its base. Species associated with this water type included a jellyfish, *Aurelia* sp., ctenophores and the euphausiids *M. norvegica* and *T. raschii*. The upper line on the plot represents LCW, as the POM collected at 80 m was in the middle of this water type (Figure 3-3b). Species commonly found in this cold water type and found on the line included *C. limacina* and *E. hamata* (Richard 1986). The MSW is shown as the middle line (Figure 3-3b) and had three species (*C. hyperboreus*, *B. glaciale* and *M. atlanticum*) associated with it. The particulates collected from the bottom water (MSW type) are at the base on the line. Three species were located between the LCW and MSW type lines, Ostracod spp., *S. maxima* and *T. inermis*, and were not included in any of the food chains.

The food web in summer (Figure 3-4b) was longer than that in the winter (Figure 4-4a) by half a trophic level, although most species maintained the same trophic position between seasons. The most notable exceptions were the chaetognaths *E. hamata*, *S. elegans* and *S. maxima*, which all occupied a lower trophic position in summer (trophic level 3) than winter (trophic levels 3.5, 3.5 and 4, respectively). The top carnivores were found on trophic levels 4 and 4.5 and included an unidentified species of shrimp, and the fishes *B. glaciale*, *M. atlanticum* and *Sebastes* sp.. The majority of the fauna were on trophic levels 2.5, 3 and 3.5, and accounted for 19 of the 23 species.

In summer the pelagic food web of Bay d'Espoir appeared to consist of three food chains (Figure 3-5b). The overall structure of the food web changed slightly between seasons, due to differences in the food chains. Very few species were affiliated with the MSW food chain; the copepod *C. hyperboreus* and top carnivores *B. glaciale* and *M. atlanticum*. The trophic status of *B. glaciale*

increased from being at trophic level 3.5 in December to 4 in August. The food chain of the mixed near-surface layer, which had been the shortest, increased to six trophic levels. Instead of the winter structure, short and fat, it became long and thin in the summer. Conversely, the LCW type food chain had approximately the same number of species in winter as summer (8 versus 10) but fewer trophic levels (4 versus 5). No species were found on the second trophic level in August. Fish were found in all three food chains in summer, whereas the decapods were associated with the mixed near-surface layer.

3.4.2. Fortune Bay

3.4.2.1. December

Three water types were present in Fortune Bay in December (Figure 3-1c); a mixed near-surface layer of MSW, an layer of intermediate-depth LCW and a mixed deep layer of LCW and MSW (referred to as MSW). The plot of the December carbon and nitrogen isotope values of the fauna (Figure 3-3c) does not show a clear relationship between species and water types. Some species appear to be affiliated with the near-surface layer (*C. hyperboreus*, *M. norvegica*, *T. longicornis* and *T. raschii*) and quite a few with the LCW type (e.g. *A. malmgreni*, *P. truncatum*, *S. elegans*, and *M. longa*). The majority of species were situated between the two lines; where the line representing the MSW type should have been located.

The pelagic food web in December (Figure 3-4c) probably consisted of three food chains (Figure 3-5c) each associated with a water type. The food web consisted of six trophic levels; however, only one species, *T. longicornis*, was found on the second trophic level. The majority of species were on levels 3 and 3.5 (16 of 23 species). Omnivorous species were found throughout the food web. Four top predators were at the apex of the food web, *A. malmgreni*, *B. nobilis*, *P. borealis* and *P. multidentata*.

The food chains in the mixed near-surface layer and the MSW had four trophic levels, while the LCW type chain had an additional level. The MSW type chain had the most species associated with it and at higher levels than the other

two chains (Figure 3-5c). The majority of the species associated with the MSW type chain were omnivores.

3.4.2.2. August

By August the water column structure was simpler, and consisted entirely of LCW in a surface-warmed layer and in a colder layer that extended from 25 to 380 m (Figure 3-1d). These layers are represented as the lower and upper lines, respectively, on Figure 3-3d. Suspended near-surface layer POM is at the base of the lower line while POM collected from the bottom water (which was solely LCW in origin, Figure 3-1d) is at the base of the upper line.

The upper line representing the LCW type in the outer basin did not change its position between winter and summer. Some species found in December were also present in August, except for many of those that had been between the lower and upper lines, in the MSW type. Many of the species were in similar positions on this line as in December (e.g. *M. longa* and *A. malmgreni*). *C. hyperboreus* and *T. raschii* were still affiliated with the near-surface layer, in addition to *C. limacina* and *M. mixta*.

The pelagic food web in Fortune Bay in August had five trophic levels, one less than in December (Figure 3-4d). None of the species sampled occupied the second trophic level. Top level consumers in this ecosystem were *A. malmgreni* and *S. maxima*. Three of the four apex species on trophic level 4 in December, *B. nobilis*, *P. borealis* and *P. multidentata*, shifted to a lower level (3.5) in August. Only *A. malmgreni* remained in the same position between seasons.

Two pelagic food chains made up the food web in Fortune Bay in summer (Figure 3-5d) and were associated with the surface-warmed layer of LCW and the colder LCW that extended throughout the outer basin. The food chain of the former layer had four trophic levels compared to five in the LCW type chain. This latter water type also had more species associated with it than the surface layer. Many species did not switch food chains between seasons, although in summer the decapod species, *P. borealis* and *P. multidentata*, had different water type affiliations. In both cases, they also shifted to a lower trophic position.

3.5. Trophic Level Enrichments and Composition

Trophic level enrichments of the stable carbon and nitrogen isotopes in each fjord by season are given in Table 3-14, based on the top predators *M. atlanticum* in Bay d'Espoir and *A. malmgreni* in Fortune Bay. These enrichments were fairly consistent between fjords and seasons. Identical values for carbon (1.0‰ per trophic level) and nitrogen (2.9‰ per trophic level) enrichments were obtained from Bay d'Espoir in August and Fortune Bay in December.

The trophic composition of the fauna of the fjords is given in Table 3-15. The majority of species in Bay d'Espoir during winter and summer were carnivores (~60%), followed by omnivores (~30%), and herbivores (~10%). Between December and August the percentage of carnivores and herbivores increased slightly, while the proportion of omnivores decreased. Unlike Bay d'Espoir, the trophic composition of the fauna in Fortune Bay changed between seasons. In December, omnivores predominated in the fauna (~57%), followed by carnivores (~39%) and herbivores (~4%). This situation changed in the summer when there were an equal proportion of carnivores and omnivores (~47%). The percentage of herbivores remained much the same between seasons, although it was half of that found in Bay d'Espoir.

3.6. Stomach Contents of Melanostigma atlanticum

Stomach contents analyses were done on 34 specimens of the zoarcid *M. atlanticum* caught in Bay d'Espoir in August. The percentage of prey species found in the stomachs of fish in each size category are given in Table 3-16. A total of seven prey categories were consumed in various proportions: ostracod spp. and six copepod species (*C. hyperboreus*, *C. hamatus*, *E. norvegica*, *G. tenuispinus*, *M. longa* and *P. elongatus*). The diets of fish larger than 60-69 mm total length were made up primarily of *C. hyperboreus*. Fish 60-69 mm mainly consumed *C. hyperboreus*, *G. tenuispinus* and *M. longa*.

Data on the feeding ecology of the fish and the isotopic composition of the prey species were used to predict stable carbon and nitrogen isotope values and

Table 3-14. Trophic level enrichments of stable carbon and nitrogen isotopes in Bay d'Espoir and Fortune Bay in December 1984 and August 1985.

	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Bay d'Espoir - December	1.3	3.1
Bay d'Espoir - August	1.0	2.9
Fortune Bay - December	1.0	2.9
Fortune Bay - August	1.1	3.3

Table 3-15. The trophic composition of the fauna in Bay d'Espoir and Fortune Bay in December 1984 and August 1985.

	% Carnivores	% Herbivores	% Omnivores
Bay d'Espoir - December	60.0	8.0	32.0
Bay d'Espoir - August	63.6	9.1	27.3
Fortune Bay - December	39.1	4.3	56.5
Fortune Bay - August	47.4	5.2	47.4

Table 3-16. The percentage of prey species (by number) consumed by *Melanostigma atlanticum* in Bay d'Espoir in August 1985.

Prey Species	Length Category (mm)					
	60-69	70-79	80-89	90-99	100-109	110-119
<i>C. hyperboreus</i>	27.3	64.5	83.3	81.8	72.5	89.3
<i>C. hamatus</i>		2.1		0.5		
<i>E. norvegica</i>			2.1			
<i>G. tenuispinus</i>	27.3	12.9	2.1		5.2	7.1
<i>M. longa</i>	27.3		4.2	4.6	4.7	
Ostracod spp.	9.1	19.4	2.1	13.6	2.1	3.4
<i>P. elongatus</i>	9.1	3.2	4.2		15.0	

compare them to actual measurements (Table 3-17). Actual whole body $\delta^{13}\text{C}$ values measured in fish collected in December and August were similar to those predicted. Only fish in the largest size category, 110-119 mm, were analyzed and had a mean $\delta^{13}\text{C}$ value of $-21.2 \pm 0.8^\circ/\text{oo}$ ($n=10$) in December and $-21.0 \pm 0.8^\circ/\text{oo}$ ($n=2$) in August (Table 3-4), compared to the predicted value of $-21.7^\circ/\text{oo}$.

The actual $\delta^{15}\text{N}$ values from December ($+14.3 \pm 0.4^\circ/\text{oo}$) and August ($+13.8 \pm 0.1^\circ/\text{oo}$) samples deviated from the predicted value of $+12.5^\circ/\text{oo}$. These differences were not large enough to suggest a change in the trophic position of these fish; such that the difference between the expected and predicted nitrogen values were never greater than a trophic level enrichment of $2.9^\circ/\text{oo}$.

Table 3-17. A comparison of predicted whole body $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to actual measurements (mean \pm s.d.) of *Melanostigma atlanticum* caught in Bay d'Espoir in August 1985. Sample sizes for the actual measurements are in parentheses.

Length (mm)	Predicted*		Actual	
	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
110 - 119	-21.7	+12.5	-21.0 \pm 0.8 (2)	+13.8 \pm 0.1 (2)

*Calculated using values of 1.0 and 2.9‰ for carbon and nitrogen, respectively, to account for trophic position.

DISCUSSION

4.1. Sources of Particulate Organic Matter

4.1.1. Subsurface POM

The stable carbon isotope values of the subsurface particulate organic matter were essentially the same as others reported for phytoplankton from high latitude ecosystems: the Bering Sea, $-24.4 \pm 0.3^\circ/\text{oo}$ (McConnaughey and McRoy 1979a); the Gulf of St. Lawrence, $-23.8 \pm 1.2^\circ/\text{oo}$ (Tan and Strain 1983); and the Scotian Shelf, $-25.3 \pm 2.8^\circ/\text{oo}$ (Mills *et al.* 1984). Alternative sources of organic matter (e.g. macrophytes, terrestrial material) were not examined directly but their contributions to the POM of the outer basins were probably minimal. Reported $\delta^{13}\text{C}$ values for *Laminaria longicuris* and *Zostera marina* in the coastal waters off Nova Scotia (Stephenson *et al.* 1984) are too positive (mean $\delta^{13}\text{C} = -15.5^\circ/\text{oo}$ and $-7.4^\circ/\text{oo}$, respectively) to be major sources of organic carbon in the outer basin of either fjord. If macrophytes had been the principal source of carbon, the $\delta^{13}\text{C}$ of consumers would have been more positive than actually observed.

The stable carbon isotopic composition of terrestrial C_3 plants ($\delta^{13}\text{C} = -23$ to $-30^\circ/\text{oo}$), peat ($\delta^{13}\text{C} = -12$ to $-28^\circ/\text{oo}$) and marine phytoplankton ($\delta^{13}\text{C} = -18$ to $-24^\circ/\text{oo}$) (Fry and Sherr 1984) all overlap, making it difficult to distinguish between these sources on the basis of carbon isotope values alone. The contribution of terrestrial material to food chains in two estuaries in Maine (Incze *et al.* 1982) and the Gulf of Mexico (Thayer *et al.* 1983) has been shown to decrease in a seaward direction and with depth (Fry *et al.* 1984). Even during spring runoff of the Mississippi River, a terrestrial signal could not be detected further than 30 km into the Gulf of Mexico (Thayer *et al.* 1983). The stations

sampled in Bay d'Espoir and Fortune Bay were both located 45 km from the outlets of their major rivers, the Conne River and Long Harbour River, respectively, and the influence of terrestrial material should have been relatively small.

The subsurface POM collected in both fjords during summer and winter cruises had stable nitrogen values characteristic of marine phytoplankton. These values ($\delta^{15}\text{N} \approx +5.0\text{‰}$) are comparable to phytoplankton ($\delta^{15}\text{N} = +5.0\text{‰}$) in the Bering Sea and Lake Ashinoko (Minagawa and Wada 1984), Slope Water particulates ($\delta^{15}\text{N} = +3.8$ to $+5.5\text{‰}$) in the euphotic zone of warm-core rings (Altabet and McCarthy 1985), and suspended material of marine origin ($\delta^{15}\text{N} = +4.96 \pm 1.3\text{‰}$) in an English estuary (Owens 1985). Sweeney *et al.* (1978) have shown that marine and terrestrially-derived suspended particulate organic matter can be distinguished on the basis of nitrogen isotope ratios.

The $\delta^{15}\text{N}$ composition of POM has been observed to change seasonally, due to variations in the input of nitrogen to the euphotic zone (Mariotti *et al.* 1984, Altabet and Deuser 1985). Seasonal variations in the nitrogen isotopic composition of POM are due to differences in the availability of nitrate to the phytoplankton and subsequent fractionations associated with assimilative processes. In winter, low $\delta^{15}\text{N}$ values in POM are observed when nitrate is not limiting and large isotopic fractionations are associated with its uptake. Higher $\delta^{15}\text{N}$ values are common in summer when nitrate is limiting and very small fractionations result from the incorporation of NO_3^- by the phytoplankton. Seasonal changes in the subsurface POM were not observed in either Bay d'Espoir or Fortune Bay. Higher $\delta^{15}\text{N}$ values may not have been found in summer due to 'wind events' upwelling nitrate into the euphotic zone and negating any fractionation associated with the uptake of nitrate by phytoplankton (Wada and Hattori 1976, Altabet and Deuser 1985).

On the basis of the stable carbon and nitrogen isotope data, the POM in Bay d'Espoir and Fortune Bay is derived from marine phytoplankton. If terrestrial material had contributed, lower $\delta^{15}\text{N}$ values, on the order of 2.5‰ (Sweeney *et al.* 1978) would have been observed. Differences in the stable carbon

isotopic composition of the subsurface POM in Bay d'Espoir from December to August may reflect seasonal changes in phytoplankton lipid levels (Smith and Morris 1980) and/or species succession in the phytoplankton assemblage (Gearing *et al.* 1984). Either of these scenarios is plausible in light of the stable nitrogen isotope ratios remaining the same between seasons.

4.1.2. Water Column Profiles

The pattern of the carbon isotope profiles taken in Bay d'Espoir and Fortune Bay in August did not follow those previously reported in other systems (Jeffrey 1969, Calder 1969, Williams and Gordon 1970, Eadie and Jeffrey 1973, Eadie *et al.* 1978, Jeffrey *et al.* 1983). Instead of the $\delta^{13}\text{C}$ values of the POM becoming more negative with depth, they became more positive. These results are similar to those reported by Bishop *et al.* (1977), who found the $\delta^{13}\text{C}$ values of POM in the equatorial Atlantic became more negative between 32 and 50 m and then got progressively more positive. Jeffrey *et al.* (1983) suggest positive $\delta^{13}\text{C}$ values reflect the breakup of large, isotopically heavy particles and the transformation of dissolved organic carbon into particulate organic carbon. Microbial degradation of the POM results in isotopically light components being removed preferentially, leaving an isotopically heavy residue (Wada 1980). The carbon isotope profiles of the POM in Bay d'Espoir and Fortune Bay reflected this process.

The nitrogen isotope profiles also do not follow the generally accepted pattern of increasingly positive $\delta^{15}\text{N}$ values with depth. Wada (1980) has shown microbial degradation of organic nitrogen leads to high $\delta^{15}\text{N}$ values in the refractory material. Saino and Hattori (1985) have suggested that this results from deamination reactions in the decaying POM, followed by the uptake of ^{15}N -enriched ammonium by nitrifiers and other bacteria. In Bay d'Espoir the increase in the $\delta^{15}\text{N}$ values between the subsurface layer and the LCW at 80 m could be attributed to the degradation of POM within the water column (Wada 1980, Owens 1985) especially if it was entrained at the thermocline. Altabet and McCarthy (1985), studying warm-core Gulf Stream rings, found entrained Slope

Water particulates shifted the isotopic composition of the ring to higher $\delta^{15}\text{N}$ values as a result of microbial degradation. The Slope Water POM had a mean $\delta^{15}\text{N}$ value of $+10.1 \pm 0.7^\circ/\text{oo}$. Particulates sampled from LCW, in this study, had a similar value of $+10.5^\circ/\text{oo}$. The LCW sampled in Bay d'Espoir at 80 m had a nitrogen isotopic composition unlike the same water sampled in Fortune Bay at 378 m ($+10.5^\circ/\text{oo}$ versus $+8.9^\circ/\text{oo}$, respectively). The reasons for this difference are not clear, although it could have been due to phytoplankton accumulating near the bottom (Pomeroy and Deibel 1986) or the resuspension of sediment. Likewise, MSW in Bay d'Espoir may have had a $\delta^{15}\text{N}$ value of $+8.3^\circ/\text{oo}$ due to the same events or as a result of Slope Water POM being modified as it was transported across the shelf and into the fjord.

4.2. Sources of Organic Matter in the Sediment

Stable carbon and nitrogen data indicate the sedimentary organic matter (SOM) in both fjords is primarily marine in origin. The stable carbon isotopic composition of the SOM was similar to values reported for arctic and boreal marine sediments in the Beaufort Sea, $-23.8 \pm 1.0^\circ/\text{oo}$ (Gearing *et al.* 1977); Hermitage Channel, Newfoundland, $-23.0^\circ/\text{oo}$ (Tan and Strain 1979); the Scotian Shelf, $-22.4 \pm 0.2^\circ/\text{oo}$ (Tan and Strain 1979) and Baffin Island fjords, -23.0 to $-21.6^\circ/\text{oo}$ (Ivany 1985). The winter and summer $\delta^{13}\text{C}$ values found in this study fall within the range of values (-22.9 to $-19.4^\circ/\text{oo}$) reported by Hunt (1966) for marine sediments along the Atlantic coast. The winter values for sediments collected from Bay d'Espoir and Fortune Bay, like the subsurface POM, are characteristic of marine material. The shift to more positive values in summer probably reflects seasonal changes in the phytoplankton in the overlying water column. McConnaughey (1978) noted that sediment values in the Bering Sea were 1 to $2^\circ/\text{oo}$ more positive than the suspended POM in the water column. Gearing *et al.* (1984) were able to show that seasonal changes in $\delta^{13}\text{C}$ values of sedimentary carbon isotope values were related to those of the phytoplankton.

The nitrogen values support the interpretation of the carbon data that the SOM is marine in origin. The stable nitrogen isotopic composition of the

sediment ($\delta^{15}\text{N}=+7.6\text{‰}$) was similar to measurements made by Macko *et al.* (1984) on marine sediments ($\delta^{15}\text{N}=+6.5\pm 0.2\text{‰}$) from the Gulf of Mexico. Ivany (1985) found marine end-member values for sediments from fjords in Baffin Island ranged from $+7.4$ to $+9.6\text{‰}$, while terrestrial values were lower, from $+5.3$ to $+5.9\text{‰}$. The consistency in the nitrogen isotopic composition of the sediment in both fjords over the two seasons provided no evidence for any significant input of terrestrial material. Major contributions of terrestrially-derived organic matter would have shifted the $\delta^{15}\text{N}$ composition of the sediment to lower values, as nitrogen from terrestrial sources typically has a $\delta^{15}\text{N}$ value of $+2.5\text{‰}$ (Sweeney *et al.* 1978).

Due to the wide range of C/N values terrestrial material can possess, Tan and Strain (1979) and LaZerte (1983) have pointed out serious limitations in using C:N ratios as indicators of sources of organic material. LaZerte (1983) has shown that stable carbon isotope tracers are better indicators of organic carbon sources in sediment. Nonetheless, the C:N ratios tend to confirm that the organic matter in the sediments is primarily marine in origin. Muller (1977) found average C/N values for marine phytoplankton range from 5.5 to 7.5, while terrestrial material has higher values from 11.9 to 36.8 (Pocklington 1976).

The organic carbon content of these fjord sediments was quite high (2.7 to 3.9%) in comparison to those from the mid-Atlantic shelf (<0.5%) or the shelf-break (1-2%), but lower than sediments receiving material from the highly productive waters off Peru (>4%) (Walsh 1981). Data do not exist on the level of primary productivity in the Newfoundland fjords, however, primary production in Newfoundland coastal waters appears to be greater than those previously reported for offshore sites (K. Pauley, personal communication).

The presence of greater proportions of organic carbon and nitrogen in the sediment from Fortune Bay than in that from Bay d'Espoir (Table 3-3) may reflect a combination of reduced microbial degradation of the POM and/or use by the fauna. Pomeroy and Deibel (1986) suggest that suppression of bacterial production during the spring bloom in colder waters makes more of the primary production available to the herbivores. Since the majority of species in Fortune

Bay were omnivores (Table 3-17) and there were only two food chains (Figure 3-5d) in the summer, compared to three in Bay d'Espoir (Figure 3-5b), an accumulation of material in the sediments was expected. However, evidence for the efficiency or inefficiency in the recycling of organic matter in each fjord is inconclusive and requires further study.

4.3. Isotopic Composition of the Fauna

Numerous studies of high latitude ecosystems have shown that environment and season have an important role in determining the availability of food to predators (Kattner *et al.* 1981) and hence their biochemical composition (e.g. Lee *et al.* 1971, Lee 1974, Bamstedt 1978, Falk-Petersen 1981, Kattner *et al.* 1981, Reinhardt and van Vleet 1986). The biochemical composition of the fauna affects its isotopic composition, because the carbon and nitrogen values are dependent on the amount of lipid and protein present in an organism. Among the species found in this study that are known to synthesize lipids seasonally were *B. arctica* (Bamstedt 1978), *C. hyperboreus* (Lee 1974), *E. hamata* (Bamstedt 1978), *M. norvegica* (Bamstedt 1976) and *M. longa* (Lee *et al.* 1972). Very few species had significant seasonal differences in their isotopic composition, so either lipid and protein synthesis only slightly altered carbon and nitrogen isotope ratios or the production of lipid was not seasonal.

There were different patterns in the isotopic composition of the same species from the two fjords during the same season. Generally whole bodies of the fauna were enriched in ^{13}C in the winter and depleted during the summer. The opposite pattern was found in Fortune Bay; from winter to summer faunal carbon isotope values became enriched in ^{13}C . This between fjords difference may reflect different feeding strategies of the fauna or the availability of isotopically distinct substrates.

In Bay d'Espoir, only the copepods *C. hyperboreus* and *M. longa* exhibited a significant seasonal change in their mean body $\delta^{13}\text{C}$ values. *C. hyperboreus* is known to be an omnivore while *M. longa* is a herbivore (Matthews and Bakke 1977). The shift to more negative carbon values in *C. hyperboreus* in August is

probably due to this species feeding more heavily on phytoplankton during the summer months when this food is abundant. In the winter months a greater dependence on either detritus or animal prey in the diet may occur. The shift in the body carbon values of *M. longa* probably reflects feeding on detrital POM during the winter, and switching to phytoplankton when conditions allowed.

Unlike the copepods in Bay d'Espoir, the same species in Fortune Bay did not exhibit a seasonal change in their whole body $\delta^{13}\text{C}$ values. Generally *C. hyperboreus* and *M. longa* remained the same isotopically from winter to summer, in parallel with the subsurface POM. The data suggest that these species were not switching their diets between seasons.

None of the higher trophic level species (chaetognaths, ctenophores, euphausiids and fishes) in Bay d'Espoir and Fortune Bay had significant seasonal changes in their whole body carbon isotopic composition (Tables 3-4 and 3-8). Most of the fauna in Bay d'Espoir had carbon isotope values that became more negative from December to August, while the fauna in Fortune Bay generally became more positive. In both cases the results parallel isotopic changes in the lower trophic levels and can be explained in a similar manner. The majority of the species in the higher trophic levels in Bay d'Espoir were carnivores, while omnivores dominated Fortune Bay (Table 3-15). Since many of the carnivores in Bay d'Espoir probably depend on the copepod fauna as prey, the more negative values observed in the winter, relative to those of summer, may be due to feeding on the copepods. Although the carbon ratios of the carnivores were more negative in December than August, they were actually more positive than their prey items. Likewise, higher trophic level species in Fortune Bay were generally more positive in the summer than winter due to a greater proportion of carnivores being present. This would have meant most species were omnivores in the winter when food may have been scarce, resulting in their carbon isotopic composition being lower. In summer when prey items were more abundant, one would expect $\delta^{13}\text{C}$ values to increase due to enrichments involved when feeding on prey items from higher trophic levels. Seasonal switching of diet has been observed in *M. norvegica*, (Falk-Petersen 1981) and explains why this species' carbon isotopic

composition shifted from negative to more positive values in both fjords from winter to summer. Although this species is primarily a carnivore feeding on copepods (MacDonald 1927), it switches to an omnivorous diet in the winter months (Falk-Petersen 1981). The nitrogen isotope data support this finding, as one would expect a carnivore to have a more positive nitrogen isotope ratio than an omnivore.

Evidence for the existence of resource partitioning (Schoener 1974) of food between similar species was found for the euphausiids *T. inermis* and *T. raschii*. These showed no significant seasonal changes in whole body carbon values from either fjord. However, in Bay d'Espoir, *T. inermis* and *T. raschii* exhibited a different pattern in their mean whole body $\delta^{13}\text{C}$ values. From December to August *T. inermis*' carbon value became more negative while that of *T. raschii* became positive. Therefore, their diets appeared to be different. Sargent and Falk-Petersen (1981) and Falk-Petersen (1985) have shown that both species consume phytoplankton and/or phytodetritus to varying degrees, with *T. inermis* having a greater preference for phytoplankton. The carbon isotope data appear to support the findings of these authors and suggest that *T. inermis* was consuming detritus during the winter while *T. raschii* was omnivorous. In summer *T. inermis* had a more negative $\delta^{13}\text{C}$ value than *T. raschii*, suggesting it was at a trophic level closer to phytoplankton but consuming occasional animal prey. In August, *T. raschii* appeared to be solely ingesting animal prey, probably copepods. Falk-Petersen (1981) has shown that *T. raschii*, like *M. norvegica*, primarily consumes copepods in the summer and switches to an omnivorous diet in winter.

The carbon isotopic composition of the fauna measured in this study can only be compared to two studies in the literature; McConnaughey (1978) and Mills *et al.* (1984). On the basis of similar $\delta^{13}\text{C}$ values found for the POM in these ecosystems, one might not expect differences in faunal values.

The carbon isotopic compositions of the fauna from Bay d'Espoir and from the Scotian Shelf resemble each other, possibly due to similarities in the $\delta^{13}\text{C}$ values of the POM and the hydrographic regime of both regions (Houghton *et al.*

1978, Smith *et al.* 1978). Like Bay d'Espoir, the Scotian Shelf has a water column with three major layers; a subsurface layer, an intermediate-depth cold layer and a deep layer of warm Slope Water (Houghton *et al.* 1978, Smith *et al.* 1978). Slope Water from the Scotian Shelf undergoes mixing while being transported to the Newfoundland coast and is transformed enroute into Modified Slope Water (MSW). Some fauna from the Scotian Shelf have $\delta^{13}\text{C}$ values similar to those in Bay d'Espoir and not Fortune Bay. Since the carbon isotopic composition of the POM was similar between the two fjords, differences may reflect the advection of species into Bay d'Espoir in summer and winter and Fortune Bay in winter with MSW. The pteropod *C. limacina* from the Scotian Shelf had a value of $-23.5 \pm 0.9^\circ/\text{oo}$ versus $-23.7^\circ/\text{oo}$ from Bay d'Espoir, but differed from Fortune Bay ($-21.1^\circ/\text{oo}$) in August. Likewise, *Sagitta* sp. from the Scotian Shelf ($-22.8 \pm 0.4^\circ/\text{oo}$) was similar to *S. maxima* ($-22.6^\circ/\text{oo}$) from Bay d'Espoir in August. The closest value from Fortune Bay was for *S. elegans* ($-22.2^\circ/\text{oo}$) in December. Samples of *P. gaudichaudii* from Bay d'Espoir and Fortune Bay in December were both close to those for the species from the Scotian Shelf; $-22.2 \pm 0.5^\circ/\text{oo}$ and $-22.3 \pm 0.3^\circ/\text{oo}$ compared to $-21.5 \pm 0.3^\circ/\text{oo}$, respectively. At this time of year both fjords had a layer of MSW present in the outer basin. Carbon values for the euphausiid *M. norvegica* were almost identical between Bay d'Espoir ($-21.4^\circ/\text{oo}$) and the Scotian Shelf ($-21.0 \pm 0.4^\circ/\text{oo}$) in summer.

Only a few comparisons can be made between this data set and that of McConnaughey's (1978) for the Bering Sea due to differences in the each ecosystem's species assemblage and a paucity of pelagic species sampled in that study. Ranges of the $\delta^{13}\text{C}$ values for fauna from Bay d'Espoir and Fortune Bay (Figures 3-2a,b) were not unlike those presented in a frequency histogram by McConnaughey (1978). Faunal values for the Bering Sea ranged from -26 to $-16^\circ/\text{oo}$ and were more positive than species from either fjord. This appears to be due to a large number of benthic samples measured in McConnaughey's study that are usually more enriched in ^{13}C than pelagic organisms (Fry and Sherr 1984). Species collected from the Bering Sea had $\delta^{13}\text{C}$ values similar to their counterparts from Newfoundland, although some were slightly more positive. For

example, *M. villosus* from Fortune Bay was $-21.5^{\circ}/\text{oo}$ (muscle; Table 3-12) versus $-20.3^{\circ}/\text{oo}$ (whole body) in the Bering Sea. Likewise, *T. raschii* had whole body values of $-21.4^{\circ}/\text{oo}$ and $-21.7^{\circ}/\text{oo}$ from Bay d'Espoir and Fortune Bay, respectively, in summer (Tables 3-4 and 3-8) compared to $-19.7^{\circ}/\text{oo}$ for specimens from the Bering Sea.

4.4. Trophic Level Enrichments of Stable Carbon and Nitrogen Isotopes

Trophic level enrichments calculated for carbon and nitrogen isotopes in the course of this study (Table 3-14) are similar to those reported for coastal ecosystems by other authors. Rau *et al.* (1983) found an enrichment of $1.38^{\circ}/\text{oo}$ per trophic level for food chains in the coastal waters off southern California, while Spies and DesMarais (1983) reported a value of $1.32^{\circ}/\text{oo}$ per trophic level for a benthic community. In a study of two Florida bays, Harrigan (1986) found enrichments of 1.3 and $3.3^{\circ}/\text{oo}$ per trophic level for carbon and nitrogen, respectively. A study of food chains in different habitats by Minagawa and Wada (1984) found the average enrichment for nitrogen was $3.4 \pm 1.1^{\circ}/\text{oo}$ per trophic level. These similarities in trophic level enrichments suggest that the same mechanism is involved in the fractionation of stable isotopes in food chains from similar ecosystems, independent of geographic location.

4.5. Pelagic Food Chains and Trophic Organization

4.5.1. The Effects of Environmental Variability on Food Chain Structure

Fluctuations in the physical environment affect the diversity and abundance of species, and by so doing alter and modify the trophic organization of ecosystems (Timonin 1971, Cushing 1981, Springer *et al.* 1984). The structure of individual food chains in each fjord changed between winter and summer, with the most obvious effect in Fortune Bay being the formation of an additional chain associated with MSW in December. Generally, the food chains in both fjords

during the winter were similar in their overall lengths, with species being "clumped" together on the higher trophic levels. This might be interpreted as a stabilization mechanism, as the greatest structural stability is thought to be attained in an ecosystem by having high numbers of species on a single trophic level (Cushing 1975). A similar mechanism was probably involved in stabilizing the Fortune Bay pelagic food web/chain during the summer. Although fewer species were present, they were split equally between carnivores and omnivores and spread out among the individual food chains. The increased proportion of carnivores and possible carnivorous feeding by the omnivores may have a stabilizing influence. The variability in the trophic composition of the community suggests a greater degree of trophic flexibility in Fortune Bay than Bay d'Espoir but it does not appear to have had a marked effect on the trophic structure (Matthews and Bakke 1977).

The trophic composition of the fauna differed between the two fjords, with carnivores dominating in Bay d'Espoir and omnivores in Fortune Bay (Table 3-15). Timonin (1971) noted that the trophic composition of plankton communities was related to the stability of the water regime. The introduction of a single water type (LCW) into Fortune Bay in August and the stability it provided resulted in a greater proportion of the fauna being carnivores. Diversity in a community's trophic composition is thought to contribute to ecosystem stability (Parsons and de Lange Boom 1972). Differences in the trophic composition of the two fjords reflects their different stages of ecosystem development. Odum (1969) pointed out that "a more or less regular but acute physical perturbation imposed from without can maintain an ecosystem at some intermediate point in the developmental sequence, resulting in, so to speak, a compromise between youth and maturity".

Environmental variability affected the trophic composition of the communities, although the overall organization of the food webs was not different. In retrospect, differences may not have been apparent in the food web structure of the two fjords due to dissimilar communities. Only 30 and 33% of the fauna were the same between Bay d'Espoir and Fortune Bay in December and August,

respectively (see Results, page 32). Given comparable communities in the same situations, perhaps a difference would have been observed (Pimm 1982, 1985). One can only speculate that major differences might also exist in the energy flow pathways and food chain efficiencies of each ecosystem, as a result of differences in the trophic composition (Parsons and de Lange Boom 1972).

4.5.2. Pelagic Food Chains and Water Types

Few studies have been published reporting the organization of the individual food chains of a complete food web. A common denominator in studies of marine ecosystems has been for pelagic food chains to be associated with various depth strata in the water column, such as the epi-, meso-, and bathypelagic zones (Petipa *et al.* 1970, Roger and Grandperrin 1976, Marshall 1979). The trophic organization and interactions of food chains between and within water types has yet to be fully considered. Intensive work in this area has come from studies of Gulf Stream rings (The Ring Group 1981), as it has been recognized that ecosystem processes (i.e. food chain/web development) are dependent on the history of a water type.

A dual stable isotope approach made possible the reconstruction of the pelagic food webs in Bay d'Espoir and Fortune Bay, and also the identification of individual food chains in each web. Stable isotope tracers only allow species to be assigned to a trophic level. They do not elucidate the linkages between and within levels. Single food chains never operate in isolation but continually interact with each other in the formation of various levels of complexity (Arntz 1978). This study did not provide information pertaining to the various interactions between or within the chains. To do this, a detailed study on the feeding ecology of all the species would have to be done. Evidence that species are likely to feed between chains comes from the stomach contents analysis done on *M. atlanticum* collected from Bay d'Espoir in August (Table 3-16). Prey items found in *M. atlanticum* stomachs came from the food chains in MSW (*C. hyperboreus*), as well as LCW (*E. norvegica*, *G. tenuispinus*, *M. longa* and Ostracod spp.).

The relationship outlined is speculative and requires further study, but two pieces of research make it plausible. Fontugne and Duplessy (1978) have shown that the carbon isotopic composition of plankton "is characteristic of a well-defined surface water mass and changes from one water mass to another, recording hydrologic discontinuities". The mechanism that allowed the fauna to be distinguished isotopically between water types was differences in the carbon isotopic composition of surface water POM. Altabet and McCarthy's (1985, 1986) work on warm-core rings was able to show, using stable nitrogen isotopes, that water types can be isotopically distinct. In this study, fauna within the food chains appeared to be closely associated with a specific water type, although the ultimate source of organic carbon and nitrogen came from POM originally produced in the near-surface mixed layer. Calculated $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for the fauna using stable carbon and nitrogen isotope measurements of the POM from LCW and MSW in Bay d'Espoir and LCW in Fortune Bay during the summer could not be used to reconstruct the pelagic food webs of either fjord (Appendix E through K). This finding rules out the possibility of significant contributions of carbon and nitrogen originating from those sources.

Fauna could be affiliated with a particular water type without residing in it by two possible mechanisms. Many midwater organisms are known to undertake either extensive or partial vertical migrations to feed. This mechanism has been recognized as a means of transporting near-surface organic carbon to deeper portions of the water column via the fauna (Vinogradov 1968). Organic matter can also move deeper in the water column by sinking. The position of the lines representing the near-surface layer shifted between seasons in the Bay d'Espoir plots (Figures 3-3a,b) but not in the Fortune Bay plots (Figures 3-3c,d). This reflects seasonal changes in the carbon isotopic composition of the near-surface POM in the former case and the absence of a seasonal shift in the latter (Table 3-2).

In contrast to the rather straightforward picture the trophic organization of the food webs presented, the interpretation of the pelagic food chains and their isotopic relationship with water types was difficult and has not been shown

previously. The best evidence for this relationship comes from the summer plots of the stable carbon and nitrogen isotope values of the fauna from each fjord (Figures 3-3b,d). The interpretation of the winter data in both Bay d'Espoir and Fortune Bay was difficult and reflects the dynamic nature of the water column and extensive mixing between water types that had occurred. Indeed, the mixing of water types and of the POM associated with each offers an explanation for seasonal shifts in the position of the lines in the Bay d'Espoir plots (Figures 3-3a,b) and the "clumping" of species between the upper and lower lines in the Fortune Bay winter plot (Figure 3-3c). Many of the species associated with the MSW type in that plot (Figure 3-3c) were not present during the summer, suggesting their position between the two lines was not a result of feeding from both food chains. A food chain associated with the MSW type in Fortune Bay appears to be real, although short-lived. The results of this study raise the possibility, not previously addressed in the literature, that stable isotope tracers work best in delineating food chains in stable or constant ecosystems rather than dynamic ones.

The slopes of the lines were not consistent between the plots (Figures 3-3a,b,c,d). Experimental studies using single species have provided evidence for a 1:3 trophic level enrichment for carbon (DeNiro and Epstein 1978) to nitrogen (DeNiro and Epstein 1981). However, there is no theoretical basis or empirical evidence to suggest that the food chain of a multi-species community should be characterized by a slope of 3 when $\delta^{13}\text{C}$ is plotted against $\delta^{15}\text{N}$. Indeed this study has shown that trophic level enrichments of top predators can vary seasonally for both carbon and nitrogen isotopes (Table 3-14). The assumption that enrichments are of equal magnitude at each trophic level in a food chain consisting of many species has yet to be proven.

4.5.3. The Structure of Pelagic Food Chains in Marine Ecosystems

Pelagic food chains do not exceed five or six trophic levels, although the number varies according to the type of environment and the composition of the fauna (Wyatt 1976). Petipa *et al.* (1970), in their study of the trophic organization of the Black Sea, found two discrete pelagic food chains, each with five trophic levels. Four to five steps were found between phytoplankton and pelagic invertebrate predators by Mills *et al.* (1984) on the Scotian Shelf. Arntz (1978) noted the length of food chains leading from the primary producers to cod (*Gadus morhua* L.) in the Baltic Sea ranged from three to six trophic levels. Both Steele (1974) and Mills and Fournier (1979) had four trophic levels in the pelagic component of their models for the North Sea and the Scotian Shelf and slope ecosystems, respectively. Dickie (1972) and Mills (1975) suggested that the food webs in most coastal ecosystems with fisheries would be similarly structured. Ryther (1969) felt differences in pelagic food chain lengths between coastal, oceanic and upwelling systems reflected variations in the ecological efficiency of each. Oceanic ecosystems have the longest food chains, often with no less than six levels, whereas coastal and upwelling systems have fewer trophic levels, on the order of 4 and 1.5 respectively.

The food webs in Bay d'Espoir and Fortune Bay were similarly organized and closely resembled Ryther's (1969) model of an oceanic food chain:

phytoplankton --> microzooplankton --> macrozooplankton -->
 megazooplankton --> piscivores

With the exception of Bay d'Espoir in August, the fourth trophic level was the highest attained, although the food webs consistently had six steps between the primary producers and top level consumers. The extra levels are due to the presence of intermediate steps. Thus the pelagic food webs in Bay d'Espoir and Fortune Bay appear to have a mixture of coastal and oceanic ecosystem properties in their trophic organization. Fjords are known to have similar basic properties and processes as open ocean ecosystems (Brattegard 1979).

The increased length of oceanic food chains has been attributed to the presence of mesopelagic fishes, adding an additional trophic link (Matthews and Heimdal 1979). Although this may be the case in truly oceanic ecosystems, it does not provide a valid explanation for the increased chain length in Bay d'Espoir and Fortune Bay. If this were true, Bay d'Espoir should have at least one more trophic level than Fortune Bay during winter and summer. Landry (1977) has suggested longer food chains are due to an increased number of intermediate levels. This provides an explanation for differences observed between the number of trophic steps in the two fjords compared to the Scotian Shelf (Mills *et al.* 1984) or the Bering Sea (McConnaughey 1978, McConnaughey and McRoy 1979b). The pelagic component of the Scotian Shelf ecosystem may indeed have six or more steps if microzooplankton and pelagic fishes were included in the food chain. Neither of these groups were sampled by Mills *et al.* (1984).

Steele (1974) and Mills and Fournier (1979) both suggest that microzooplankton form a direct link between the primary producers and the copepods. In a later paper, Mills (1980) proposed that an additional trophic link might be expected between the phytoplankton and herbivorous copepods due to the presence of microzooplankton species. Analysis of the data in this study revealed virtually no species on the second trophic level, between the POM and the copepods (trophic level 2.5). Improved sampling might reveal this trophic level to be occupied by microzooplankton, supporting the above contentions.

Numerous authors (Margalef 1967, Odum 1969, Parsons and de Lange Boom 1972, Steele 1974, Cushing 1975, Wyatt 1976, Matthews and Bakke 1977) have noted that the structure of food chains and webs within an ecosystem is subject to changes. Trophic reorganization often results from environmental processes directing species succession. Even the position of a species within an ecosystem's trophic framework changes seasonally and ontologically (Hardy 1924). The trophic organization of the pelagic food webs in Bay d'Espoir and Fortune Bay was similar, although subtle changes were observed with some species moving higher or lower in the webs between seasons. Variability in the community composition is thought to allow trophic flexibility in the structuring of the food

chains and webs (Matthews and Bakke 1977). The movement of species closer to the base of a food web is an important ecological step, for by moving down a species gains a size advantage over its intended prey (Wyatt 1976). The increased length of the food web in Bay d'Espoir in August relative to December resulted primarily from the addition of the redfish, *Sebastes* sp.. This species was probably present in the fjord during the winter, but avoided the net. Videotape recordings taken during submersible dives in the main outer basin of Bay d'Espoir suggest that not all of the larger pelagic fauna were sampled, i.e. pollock (*Pollachius virens*), raising the possibility that the pelagic food web is at least half to one full trophic level longer.

A comparison of the predicted to observed trophic composition and organization of Bay d'Espoir and Fortune Bay is given in Table 4-1. A greater amount of sedimentary organic matter was found in Fortune Bay than Bay d'Espoir, but as there were many unknowns (e.g. the levels of primary production in each fjord, sedimentation rates in each fjord), conclusions cannot be drawn as to the efficiency or inefficiency of these systems in their cycling of organic matter. Although the species and trophic composition of the fauna in the two fjords were different during winter and summer (Tables 3-1 and 3-15), the food web structure was remarkably similar. Briand (1983b) emphasizes that ecological networks are more similar within than between ecosystems, regardless of geographic location and taxonomic composition. Seasonal differences were found in the number of food chains present in each fjord, which appeared to be related to water column structure. The number of trophic levels in the food chains and webs did not differ between the constant (Bay d'Espoir) and fluctuating (Fortune Bay) environments. Differences may exist in the degree of connectance in each fjord's food web (Briand 1983a,b, Cohen and Briand 1984), especially as an additional food chain was found in Bay d'Espoir in summer. The number of food chains in each ecosystem may have important implications not only for energy flow pathways but also the degree of complexity and hence the resilience of each fjord to perturbations.

Table 4-1. A comparison of the observed trophic composition and organization of Bay d'Espoir and Fortune Bay to those predicted.

	Predicted	Observed
Dominant Feeding Type	Bay d'Espoir=carnivores Fortune Bay=omnivores	Bay d'Espoir=carnivores Fortune Bay=omnivores
Food Web Structure	Bay d'Espoir=long, thin with many trophic levels Fortune Bay=short, fat with few trophic levels	No difference between Bay d'Espoir and Fortune Bay
Amount of SOM	Bay d'Espoir=very little Fortune Bay=greater	A higher percentage SOM in Fortune Bay
Cycling of Organic Matter	Bay d'Espoir=efficient Fortune Bay=inefficient	Inconclusive

CONCLUSIONS

1. A progressive enrichment of ^{13}C and ^{15}N in the fauna was found with increasing trophic level. The amount of enrichment per trophic level was found to vary slightly between seasons and fjords, although comparable to previously reported values.
2. The overall trophic organization of the food webs and chains was similar in both fjords within and between seasons. Generally the top predators in each ecosystem were found on the fourth trophic level.
3. The major pelagic food chains of each food web were identified and appeared to be closely associated with specific water types. Three food chains could be distinguished in Bay d'Espoir during both seasons, while Fortune Bay had three in the winter and two in summer.
4. The trophic composition of the fauna differed between the two fjords; carnivores were dominant in Bay d'Espoir while omnivores prevailed in Fortune Bay. These differences may have important implications in the ecological energetics of each ecosystem.
5. Similarities in the trophic organization of these fjords with the Scotian Shelf and Bering Sea confirm suggestions by Dickie (1972) and Mills (1975) that in general coastal ecosystems may be structured in the same way.

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APPENDICES

Appendix A. Stable carbon and nitrogen isotope values of fauna, particulate organic matter and sediment collected in Bay d'Espoir in December 1984. The number of specimens in a sample is given as n, whereas the tissue types are coded as; B=brain, C=stomach contents, E=eggs, F=feces, K=scales and skin, M=muscle, O=ovary, S=stomach, V=viscera, W=whole body and Z=whole body with eggs.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
POM	001	2		-24.9	+4.9
POM	004	2		-25.1	
Sediment	0054	1		-23.1	+7.7
Sediment	0055	1		-23.0	+7.5
AMPHIPODS					
<i>P. abyssorum</i>	0314	5	W	-21.9	+11.3
<i>P. gaudichaudii</i>	0086	2	W	-22.6	+10.9
	0137	16	W	-22.4	+10.5
	0284	4	W	-22.6	+10.9
	0308	9	W	-22.0	+10.8
	0475	10	W	-21.5	+10.2
CHAETOGNATHS					
<i>E. hamata</i>	0290	19	W	-23.3	+12.5
	0478	19	W	-21.7	+12.4
	0489	8	W	-21.8	+12.0
	1010	17	W	-22.2	+12.0
	1038	13	W	-21.7	+11.6
<i>S. elegans</i>	0479	30	W	-20.5	+12.6
	0488	35	W	-20.0	+13.2
	1039	4	W		+9.7
<i>S. mazima</i>	0049	1	W	-21.2	+14.1

Appendix A. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
COPEPODS					
<i>C. hyperboreus</i>	0405	131	W	-22.2	+9.3
	0476	50	W	-22.3	+9.6
	0481	50	W	-21.9	+9.7
	0482	50	W	-22.1	+9.1
	0483	50	W	-21.9	+9.3
	0493	50	W	-21.9	+9.1
<i>C. hamatus</i>	1004	200	W	-22.1	+8.9
	1036	75	W	-21.5	+8.7
<i>E. norvegica</i>	0477	23	W	-22.4	+12.4
	0485	14	W	-22.6	+12.6
	1012	8	W	-22.8	+10.8
	1031	25	W	-22.9	+11.5
<i>G. tenuispinus</i>	0496	50	W	-23.3	+10.4
	1001	50	W	-23.1	+9.8
	1035	200	W	-23.1	+11.4
<i>M. longa</i>	0471	100	W	-22.7	+10.1
	0486	50	W	-22.1	+10.3
	0498	100	W	-22.4	+11.0
	1014	100	W	-22.9	+9.5
	1021	100	W	-23.1	+9.0
<i>P. elongatus</i>	1032	300	W	-21.9	
<i>T. longicornis</i>	0472	900	W	-21.2	+8.6
	1005	700	W	-22.1	+7.5
	1033	300	W	-20.9	+7.0
DECAPODS					
<i>P. multidentata</i>	0068	1	M	-20.9	+13.2
	0071	1	M	-20.6	+12.2
	0073	1	M	-20.6	+12.1
	0075	1	M	-20.4	+11.9
	0077	1	M	-21.5	+12.6
	0073	1	E	-23.5	+11.9

Appendix A. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>S. arcticus</i>	0082	1	M	-21.1	+12.1
	0421	1	M	-20.0	+13.1
	0422	1	M	-19.8	+12.7
EUPHAUSIIDS					
<i>M. norvegica</i>	0044	9	M	-20.6	+9.2
	0045	9	M	-20.6	+8.9
	0046	9	M	-21.7	+9.4
	0047	11	M	-20.4	+9.7
	0048	8	M	-20.7	+9.7
<i>T. inermis</i>	1006	5	W	-22.5	+10.9
	1015	5	W	-22.0	+10.8
	1025	5	W	-20.7	+11.6
	0283	27	M	-21.0	+12.1
	0303	33	M	-21.9	+12.4
	0311	17	M	-21.5	+12.1
<i>T. raschii</i>	0138	8	W	-22.2	+10.6
	0141	14	W	-22.6	+10.7
	0143	13	W	-22.0	+10.6
	0282	32	M	-21.5	+11.2
	0304	24	M	-21.9	+11.5
	0305	26	M	-21.5	+11.2
FISHES					
<i>B. glaciale</i>	0384	1	M	-21.6	+13.7
	0387	1	M	-21.5	+13.0
	0390	1	M	-21.7	+12.5
	0412	1	M	-21.7	+12.9
	0385	1	O	-22.0	+11.5
	0386	1	S	-23.1	+11.2
	0388	1	O	-21.9	+11.1
	0389	1	V	-22.9	+10.3
	0391	1	O	-22.1	+11.1
	0392	1	V	-21.9	+10.2
	0413	1	O	-22.1	+11.4
	0414	1	V	-22.9	+10.5

Appendix A. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>C. harengus</i>	1024	3	W	-20.9	+11.6
<i>G. cynoglossus</i>	0379	2	W	-23.3	+10.8
	0411	2	W	-23.5	+10.2
<i>M. atlanticum</i>	0374	1	W	-20.3	+14.3
	0375	1	W	-21.0	+14.3
	0376	1	W	-20.7	+14.0
	0377	1	W	-22.1	+14.4
	0378	1	W	-22.7	+14.2
	0434	1	W	-21.7	+14.7
	0435	1	W	-20.6	+14.2
	0436	1	W	-21.4	+14.8
	0436	1	W	-21.4	+15.2
	0437	1	W	-20.2	+13.7
	0435	1	M	-21.0	+14.9
	0437	1	M	-19.1	+14.2
MYSIDS					
<i>B. arctica</i>	0083	1	W	-25.2	+10.8
	1000	2	M	-19.3	+11.7
MISCELLANEOUS					
Ctenophores	0490	34	W	-18.4	+11.1
	1016	38	W	-20.1	+11.1
	1040	30	W	-21.7	+11.7
<i>C. limacina</i>	1017	1	W	-21.3	+10.9
Ostracod spp.	0473	50	W	-22.7	+10.0
	1034	150	W	-22.8	+10.0
<i>T. helgolandica</i>	0460	20	W	-21.7	+10.5
	0480	30	W	-20.5	+11.3

Appendix B. Stable carbon and nitrogen isotope values of the fauna, particulate organic matter and sediment collected in Fortune Bay in December 1984. The number of specimens in a sample is given as n, whereas the tissue types are coded as; B=brain, C=stomach contents, E=eggs, F=feces, K=scales and skin, M=muscle, O=ovary, S=stomach, V=viscera, W=whole body and Z=whole body with eggs.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ ($^{\circ}/\text{oo}$)	$\delta^{15}\text{N}$ ($^{\circ}/\text{oo}$)
POM	0007	2		-25.3	+5.2
POM	0011	2		-24.1	+4.7
Sediment	0051	1		-23.0	+7.4
Sediment	0052	1		-23.0	+7.3
AMPHIPODS					
<i>A. malmgreni</i>	0101	1	W	-21.1	+13.1
	0344	1	W	-21.9	+13.7
	0358	1	W	-22.2	+14.6
<i>H. fulvocinctus</i>	0056	7	W	-24.7	+11.4
	0059	4	W	-24.8	+10.7
	0060	4	W	-22.8	+10.8
	0100	27	W	-22.5	+10.8
	0114	14	W	-22.8	+10.8
	0196	2	W	-23.0	+11.0
	0058	3	Z	-24.3	+10.6
	0090	1	Z	-23.5	+10.2
	0183	3	Z	-23.6	+10.2
	0257	1	Z	-23.5	+9.7
<i>H. medusarum</i>	0354	4	W	-22.9	+11.6
	0359	2	W	-22.8	+11.1
<i>P. gaudichaudii</i>	0112	3	W	-21.9	+10.1
	0164	16	W	-22.5	+9.9
	0274	6	W	-22.2	+10.4
	0362	5	W	-22.3	
	0365	4	W	-22.6	+10.5

Appendix B. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	
CHAETOGNATHS						
<i>E. hamata</i>	0199	3	W	-23.4	+11.9	
<i>S. elegans</i>	0129	40	W	-22.4	+12.3	
	0192	29	W	-22.3	+13.3	
	0316	104	W	-22.7	+12.9	
	0347	120	W	-23.1	+13.4	
	1045	53	W	-20.7	+12.8	
COPEPODS						
<i>C. hyperboreus</i>	1053	9	W	-21.8	+10.6	
<i>M. longa</i>	1042	300	W	-23.1	+10.1	
	1046	300	W	-23.4	+11.2	
	1049	300	W	-23.6	+10.8	
	1050	300	W	-23.3	+11.3	
	1051	300	W	-23.0	+11.1	
<i>T. longicornis</i>	1043	1000	W	-20.8	+8.0	
EUPHAUSIIDS						
<i>M. norvegica</i>	0015	1	M	-20.3	+9.6	
	0016	1	M	-20.6	+8.9	
	0020	1	M	-22.2	+8.9	
	0022	1	M	-21.1	+9.9	
	0023	1	M	-22.5	+9.5	
	0024	1	M	-20.4	+9.4	
	0025	1	M	-21.3	+8.9	
	0026	1	M	-22.5	+9.9	
	0033	11	M	-21.0	+9.8	
	0033	13	M	-20.3	+9.6	
	<i>T. inermis</i>	0106	8	W	-22.0	+10.8
		0116	10	W	-22.1	+11.7
0123		21	W	-22.6	+11.5	
0162		26	W	-22.8	+11.3	

Appendix B. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
	0132	33	M	-21.5	+12.3
	0144	72	M	-21.3	+11.9
	0194	16	M	-21.9	+12.3
	0208	19	M	-21.1	+11.2
	0236	10	M	-23.1	+12.3
	0249	9	M	-21.1	+12.4
	0264	21	M	-22.0	+12.6
	0319	20	M	-23.3	+12.4
	0328	17	M	-21.2	+12.2
	0350	19	M	-21.6	+12.1
	0361	20	M	-20.9	+12.4
	0368	12	M	-22.0	+12.3
<i>T. raschii</i>	0117	14	W	-21.9	+11.0
	0161	24	W	-21.4	+10.7
	1054	16	W	-20.9	+10.4
	0089	72	M	-21.4	+11.3
	0145	105	M	-21.5	+11.6
	0193	17	M	-21.7	+11.8
	0209	21	M	-21.0	+11.5
	0230	13	M	-21.3	+11.5
	0259	15	M	-21.0	+11.4
	0265	21	M	-21.7	+11.8
	0320	21	M	-21.0	+11.7
	0340	17	M	-21.5	+11.5
<i>T. longicaudata</i>	0103	25	W	-23.6	+10.8
	0349	6	W	-23.4	+11.0
	1055	4	W	-22.0	+9.6
DECAPODS					
<i>P. borealis</i>	0036	1	M	-21.4	+13.1
	0393	1	M	-20.0	+13.3
	0396	1	M	-19.8	+11.5
	0397	1	M	-21.5	+14.1

Appendix B. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
	0398	1	M	-20.1	+13.6
	0399	1	M	-20.1	+14.1
<i>P. propinquis</i>	0037	1	M	-21.2	+12.7
<i>P. multidentata</i>	0035	1	M	-20.5	+13.3
	0038	1	M	-20.2	+13.1
FISH					
<i>M. villosus</i>	0220	1	W	-24.2	+11.5
	0373	1	W	-21.7	+11.6
	0433	5	W	-21.7	+11.9
	0371	1	M	-22.4	+13.7
	0372	1	M	-20.3	+13.0
	0381	1	M	-21.4	+12.9
	0382	1	M	-22.0	+12.9
	0383	1	V	-22.2	+13.9
MYSIDS					
<i>B. nobilis</i>	0029	1	M	-20.5	+13.2
	0039	8	M	-20.8	+13.6
	0042	6	M	-20.9	+14.1
<i>M. robusta</i>	0095	1	W	-22.6	+10.6
	0043	2	Z	-24.4	+11.7
	0221	2	Z	-22.1	+11.3
<i>M. mixta</i>	0122	6	W	-23.6	+11.1
	0190	4	W	-22.6	+11.2
	0251	1	W	-22.0	+10.4
	0345	4	W	-21.9	+11.4
	0369	9	M	-21.6	+11.4
<i>P. truncatum</i>	0191	2	W	-22.3	+12.7
MISCELLANEOUS					
Ctenophores	0188	12	W	-21.9	+9.3

Appendix B. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
	0244	5	W	-22.7	+10.6
	0261	8	W	-22.4	+10.9
	0333	22	W	-22.8	+13.4
	1048	21	W	-20.2	+11.4
<i>T. helgolandica</i>	1044	20	W	-22.2	+11.2

Appendix C. Stable carbon and nitrogen isotope values of the fauna, particulate organic matter and sediment collected in Bay d'Espoir in August 1985. The number of specimens in a sample is given as n, whereas the tissue types are coded as; B=brain, C=stomach contents, E=eggs, F=feces, K=scales and skin, M=muscle, O=ovary, S=stomach, V=viscera, W=whole body and Z=whole body with eggs.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
POM (5m)	0552	2		-23.8	+5.1
POM (5m)	0554	2		-24.0	+4.6
POM (80m)	0546	2		-23.5	+10.5
POM (745m)	0547	2		-23.1	+7.9
POM (745m)	0548	2		-22.9	+8.6
Sediment	0577	1		-21.8	+7.6
AMPHIPODS					
<i>H. fulvocinctus</i>	0856	14	W	-24.1	+9.5
CHAETOGNATHS					
Chaetognath sp.	0812	27	W	-20.4	+12.7
<i>E. hamata</i>	0752	25	W	-22.3	+12.2
	0766	10	W	-22.2	+12.3
	0768	29	W	-22.8	+12.9
<i>S. elegans</i>	0765	15	W	-25.9	+12.1
	0767	7	W	-22.4	+13.2
COPEPODS					
<i>C. hyperboreus</i>	0780	100	W	-22.4	+9.6
	0786	100	W	-22.9	+9.3
	0815	100	W	-22.4	+9.5
<i>E. norvegica</i>	0759	25	W	-23.6	+11.5
	0775	30	W	-24.4	+13.0
	0777	30	W	-23.8	+11.7

Appendix C. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
	0802	30	W	-22.3	+12.9
<i>G. tenuispinus</i>	0782	600	W	-24.0	+10.1
	0821	600	W	-23.1	+11.1
	0835	300	W	-22.9	+11.2
<i>M. longa</i>	0781	200	W	-24.1	+9.6
	0823	300	W	-23.8	+9.9
	0836	100	W	-23.7	+10.7
Mixed Copepods	0761	100	W	-21.1	+9.5
	0762	200	W	-22.4	+9.0
DECAPODS					
<i>P. multidentata</i>	0527	1	W		+12.1
	0517	1	M	-19.2	+11.6
	0523	1	M	-18.4	+13.1
	0525	1	M	-19.3	+12.2
	0526	1	E	-22.1	+11.6
<i>S. arcticus</i>	0519	1	W	-20.6	+12.6
	0509	1	M	-19.4	+12.2
	0510	1	M	-20.0	+10.9
	0511	1	M	-19.4	+12.1
EUPHAUSIIDS					
<i>M. norvegica</i>	0516	3	W	-21.4	+10.1
	0505	5	M	-19.7	+9.7
	0514	9	M	-19.7	+10.2
	0515	10	M	-19.6	+10.2
	0513	50	F	-20.7	+8.5
<i>T. inermis</i>	0801	5	W	-23.1	+11.5
	0624	10	M	-20.3	+12.3
	0625	10	M	-20.4	+12.2
	0626	10	M	-20.5	+12.6
<i>T. raschii</i>	0800	5	W	-21.7	+10.8

Appendix C. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
	0806	5	W	-21.8	+10.8
	0807	5	W	-21.0	+10.8
	0631	10	M	-20.1	+11.0
	0663	10	M	-20.4	+11.3
	0778	17	M	-21.3	+11.3
FISHES					
<i>B. glaciale</i>	0600	1	W	-20.6	+11.0
	0582	1	M	-20.7	+13.3
	0589	1	M	-20.4	+13.4
	0593	1	M	-20.6	+13.5
	0581	1	K	-18.5	+13.0
	0585	1	S	-20.6	+13.4
	0585	1	S	-20.7	+13.4
	0586	1	C	-20.0	+10.7
	0587	3	B	-21.7	+14.3
<i>C. microdon</i>	0731	2	W	-22.5	+12.1
<i>M. atlanticum</i>	0651	1	W	-21.5	+13.9
	0652	1	W	-20.4	+13.7
	0636	1	M	-20.1	+13.3
	0650	1	M	-20.2	+14.2
	0655	1	M	-18.6	+14.3
<i>Sebastes</i> sp.	0500	1	M	-18.6	+14.2
MYSIDS					
<i>B. arctica</i>	0565	3	M	-19.0	+11.8
	0566	3	M	-19.1	+11.1
	0567	6	M	-19.6	+11.6
MISCELLANEOUS					
<i>Aurelia</i> sp.	0512	1	W	-21.9	+8.3
<i>C. limacina</i>	0730	1	W	-23.7	+9.7
Ctenophores	0784	30	W	-20.1	+11.0

Appendix C. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
	0811	60	W	-20.4	+10.6
Ostracod spp.	0820	100	W	-22.3	+11.0
	0848	100	W	-23.1	+10.8

Appendix D. Stable carbon and nitrogen isotope values of the fauna, particulate organic matter and sediment collected in Fortune Bay in August 1985. The number of specimens in a sample is given as n, whereas the tissue types are coded as; B=brain, C=stomach contents, E=eggs, F=feces, K=scales and skin, M=muscle, O=ovary, S=stomach, V=viscera, W=whole body and Z=whole body with eggs.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
POM (5m)	0575	2		-24.5	+4.6
POM (378m)	0569	2		-24.0	+8.9
POM (378m)	0570	2		-23.9	
Sediment	0579	1		-21.8	+7.7
Sediment	0580	1		-22.0	+7.5
AMPHIPODS					
<i>A. malmgreni</i>	0908	1	W	-20.5	+14.0
	0909	1	W	-21.7	+15.2
	0911	1	W	-21.0	+13.9
<i>H. fulvocinctus</i>	0890	15	W	-24.0	+8.9
	0897	2	W		+10.3
	0924	21	W	-23.9	+9.5
	0930	2	W	-23.1	+10.0
<i>P. gaudichaudii</i>	0855	9	W	-23.6	+10.6
	0875	5	W	-23.2	+11.0
	0896	6	Z	-23.2	+11.0
	0927	6	Z	-23.0	+11.6
CHAETOGNATHS					
<i>E. hamata</i>	0928	3	W	-22.4	+12.2
<i>S. elegans</i>	0861	30	W	-21.4	+13.4
	0863	30	W	-22.1	+13.3
	0873	41	W	-21.6	+13.0
	0878	50	W	-22.2	+11.8

Appendix D. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>S. maxima</i>	0891	100	W	-21.6	+13.0
	0894	4	W	-21.4	+14.6
COPEPODS					
<i>C. hyperboreus</i>	0860	50	W	-22.1	+9.8
	0889	50	W	-21.5	+10.0
	0921	50	W	-21.6	+9.8
	0932	20	W	-21.6	+9.9
<i>C. hamatus</i>	0916	500	W	-23.7	+9.7
<i>E. norvegica</i>	0858	19	W	-23.9	+11.4
	0887	30	W	-23.7	+13.2
	0923	16	W	-23.3	+13.5
<i>M. longa</i>	0859	300	W	-23.8	
	0862	300	W	-23.4	+10.8
	0865	300	W	-23.3	+11.0
	0877	300	W	-22.9	+10.8
	0881	300	W	-23.3	+10.7
	0883	300	W	-23.2	+9.6
DECAPODS					
<i>P. borealis</i>	0538	1	M	-18.4	+12.9
<i>P. multidentata</i>	0537	1	M	-20.5	+13.2
Shrimp sp.	0539	1	M	-18.4	+14.3
	0540	1	M	-18.8	+12.9
EUPHAUSIIDS					
<i>M. norvegica</i>	0534	3	M	-20.1	+10.6
	0535	5	M	-20.0	+10.3
	0536	5	M	-19.8	+10.1
<i>T. inermis</i>	0937	3	M	-21.3	+12.6
<i>T. raschii</i>	0904	5	W	-21.5	+10.7
	0905	10	W	-21.9	+10.5

Appendix D. Continued.

Sample	I.D. #	n	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
	0867	26	M	-20.7	+10.8
	0868	15	M	-20.7	+10.7
	0902	15	M	-20.9	+12.0
<i>T. longicaudata</i>	0900	14	W	-21.7	+11.1
	0936	11	W	-22.5	+11.9
MYSIDS					
<i>B. nobilis</i>	0853	1	W	-22.3	+12.6
<i>M. mixta</i>	0530	1	W	-21.8	+10.4
MISCELLANEOUS					
<i>C. limacina</i>	0884	2	W	-21.1	+10.1

Appendix E. Calculated $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for mean stable carbon and nitrogen isotope values of whole body (W) and muscle (M) tissue from fauna collected in Bay d'Espoir in December 1984. Where $\Delta\delta^{13}\text{C}=(\delta^{13}\text{C}_{\text{ANIMAL}}-\delta^{13}\text{C}_{\text{POM}})$ and $\Delta\delta^{15}\text{N}=(\delta^{15}\text{N}_{\text{ANIMAL}}-\delta^{15}\text{N}_{\text{POM}})$. The subsurface POM was; $\delta^{13}\text{C}=-25.0\text{‰}$ and $\delta^{15}\text{N}=+4.9\text{‰}$.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
AMPHIPODS					
<i>P. abyssorum</i>	W	-21.9	3.1	+11.3	6.4
<i>P. gaudichaudii</i>	W	-22.2	3.8	+10.7	5.8
CHAETOGNATHS					
<i>E. hamata</i>	W	-22.1	2.9	+12.1	7.2
<i>S. elegans</i>	W	-20.3	4.7	+11.8	6.9
<i>S. maxima</i>	W	-21.2	3.8	+14.1	9.2
COPEPODS					
<i>C. hyperboreus</i>	W	-22.1	2.9	+9.4	4.5
<i>C. hamatus</i>	W	-21.8	3.2	+8.8	3.9
<i>E. norvegica</i>	W	-22.7	2.3	+11.8	6.9
<i>G. tenuispinus</i>	W	-23.2	1.8	+10.5	5.6
<i>M. longa</i>	W	-22.6	2.4	+10.0	5.1
<i>P. elongatus</i>	W	-21.9	3.1		
<i>T. longicornis</i>	W	-21.4	3.6	+7.7	2.8
DECAPODS					
<i>P. multidentata</i>	M	-20.8	4.2	+12.4	7.5
<i>S. arcticus</i>	M	-20.2	4.7	+12.6	7.7
EUPHAUSIIDS					
<i>M. norvegica</i>	M	-20.8	4.2	+9.4	4.5

Appendix E. Continued.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
<i>T. inermis</i>	W	-21.7	3.3	+11.1	6.2
	M	-21.5	3.5	+12.2	7.3
<i>T. raschii</i>	W	-22.3	2.7	+10.6	5.7
	M	-21.6	3.4	+11.3	6.4
FISHES					
<i>B. glaciale</i>	M	-21.6	3.4	+13.0	8.1
<i>C. harengus</i>	W	-20.9	4.1	+11.6	6.7
<i>G. cynoglossus</i>	W	-23.4	1.6	+10.5	5.6
<i>M. atlanticum</i>	W	-21.2	3.8	+14.3	9.4
	M	-20.1	4.9	+14.6	9.7
MYSIDS					
<i>B. arctica</i>	W	-25.2	-0.2	+10.8	5.9
	M	-19.3	5.7	+11.7	6.8
MISCELLANEOUS					
<i>C. limacina</i>	W	-21.3	3.7	+10.9	6.0
Ctenophores	W	-20.1	4.9	+11.3	6.4
Ostracod spp.	W	-22.8	2.2	+10.0	5.1
<i>T. helgolandica</i>	W	-21.1	3.9	+10.9	6.0

Appendix F. Calculated $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for mean stable carbon and nitrogen isotope values of whole body (W) and muscle (M) tissue from fauna collected in Bay d'Espoir in August 1985. Where $\Delta\delta^{13}\text{C}=(\delta^{13}\text{C}_{\text{ANIMAL}}-\delta^{13}\text{C}_{\text{POM}})$ and $\Delta\delta^{15}\text{N}=(\delta^{15}\text{N}_{\text{ANIMAL}}-\delta^{15}\text{N}_{\text{POM}})$. The subsurface POM was; $\delta^{13}\text{C}=-23.9\text{‰}$ and $\delta^{15}\text{N}=+5.0\text{‰}$.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
AMPHIPODS					
<i>H. fulvocinctus</i>	W	-24.1	-0.2	+9.5	4.5
CHAETOGNATHS					
<i>E. hamata</i>	W	-22.4	1.5	+12.5	7.5
<i>S. elegans</i>	W	-24.2	-0.3	+12.7	7.7
<i>S. maxima</i>	W	-22.6	1.3	+11.1	6.1
COPEPODS					
<i>C. hyperboreus</i>	W	-22.6	1.3	+9.5	4.5
<i>E. norvegica</i>	W	-23.5	0.4	+12.3	7.3
<i>G. tenuispinus</i>	W	-23.3	0.6	+10.8	5.8
<i>M. longa</i>	W	-23.9	0.0	+10.1	5.1
Mixed Copepods	W	-21.8	2.1	+9.3	4.3
DECAPODS					
<i>P. multidentata</i>	W	-20.7	3.2	+12.1	7.1
	M	-19.0	4.9	+12.3	7.3
<i>S. arcticus</i>	W	-20.6	3.3	+12.6	7.6
	M	-19.6	4.3	+11.7	6.7
Shrimp sp.	M	-18.6	5.3	+13.6	8.6
<i>M. norvegica</i>	W	-21.4	2.5	+10.1	5.1
	M	-19.7	4.2	+10.0	5.0

Appendix F. Continued.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
<i>T. inermis</i>	W	-22.4	1.5	+11.2	6.2
	M	-20.4	3.5	+12.4	7.4
<i>T. raschii</i>	W	-21.4	2.5	+10.8	5.8
	M	-20.6	3.3	+11.2	6.2
FISHES					
<i>B. glaciale</i>	W	-20.6	3.3	+14.0	9.0
	M	-20.6	3.3	+13.4	8.4
<i>C. microdon</i>	W	-22.5	1.4	+12.1	7.1
<i>M. atlanticum</i>	W	-21.0	2.9	+13.8	8.8
	M	-19.6	4.3	+13.9	8.9
<i>Sebastes</i> sp.	M	-18.6	5.3	+14.2	9.2
MYSIDS					
<i>B. arctica</i>	M	-19.2	4.7	+11.5	6.5
MISCELLANEOUS					
<i>Aurelia</i> sp.	W	-21.9	2.0	+8.3	3.3
<i>C. limacina</i>	W	-23.7	0.2	+9.7	4.7
Ctenophores	W	-20.3	3.6	+10.8	5.8
Ostracod spp.	W	-22.7	1.2	+10.9	5.9

Appendix G. Calculated $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for mean stable carbon and nitrogen isotope values of whole body (W) and muscle (M) tissue from fauna collected in Bay d'Espoir in August 1985. Where $\Delta\delta^{13}\text{C}=(\delta^{13}\text{C}_{\text{ANIMAL}}-\delta^{13}\text{C}_{\text{POM}})$ and $\Delta\delta^{15}\text{N}=(\delta^{15}\text{N}_{\text{ANIMAL}}-\delta^{15}\text{N}_{\text{POM}})$. The intermediate-depth POM was; $\delta^{13}\text{C}=-23.5\text{‰}$ and $\delta^{15}\text{N}=+10.5\text{‰}$.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
AMPHIPODS					
<i>H. fulvocinctus</i>	W	-24.1	-0.6	+9.5	-1.0
CHAETOGNATHS					
<i>E. hamata</i>	W	-22.4	1.1	+12.5	2.0
<i>S. elegans</i>	W	-24.2	-0.7	+12.7	2.2
<i>S. maxima</i>	W	-22.6	0.9	+11.1	0.6
COPEPODS					
<i>C. hyperboreus</i>	W	-22.6	0.9	+9.5	-1.0
<i>E. norvegica</i>	W	-23.5	0.0	+12.3	1.8
<i>G. tenuispinus</i>	W	-23.3	0.2	+10.8	0.3
<i>M. longa</i>	W	-23.9	-0.4	+10.1	-0.4
Mixed Copepods	W	-21.8	1.7	+9.3	-1.2
DECAPODS					
<i>P. multidentata</i>	W	-20.7	2.8	+12.1	1.6
	M	-19.0	4.5	+12.3	1.8
<i>S. arcticus</i>	W	-20.6	2.9	+12.6	2.1
	M	-19.6	3.9	+11.7	1.2
Shrimp sp.	M	-18.6	4.9	+13.6	3.1
<i>M. norvegica</i>	W	-21.4	2.1	+10.1	-0.4
	M	-19.7	3.8	+10.0	-0.5

Appendix G. Continued.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
<i>T. inermis</i>	W	-22.4	1.1	+11.2	0.7
	M	-20.4	3.1	+12.4	1.9
<i>T. raschii</i>	W	-21.4	2.1	+10.8	0.3
	M	-20.6	2.9	+11.2	0.7
FISHES					
<i>B. glaciale</i>	W	-20.6	2.9	+14.0	3.5
	M	-20.6	2.9	+13.4	2.9
<i>C. microdon</i>	W	-22.5	1.0	+12.1	1.6
<i>M. atlanticum</i>	W	-21.0	2.5	+13.8	1.6
	M	-19.6	3.9	+13.9	3.4
<i>Sebastes</i> sp.	M	-18.6	4.9	+14.2	3.7
MYSIDS					
<i>B. arctica</i>	M	-19.2	4.3	+11.5	1.0
MISCELLANEOUS					
<i>Aurelia</i> sp.	W	-21.9	1.6	+8.3	-2.2
<i>C. limacina</i>	W	-23.7	-0.2	+9.7	-0.8
Ctenophores	W	-20.3	3.2	+10.8	0.3
Ostracod spp.	W	-22.7	0.8	+10.9	0.4

Appendix H. Calculated $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for mean stable carbon and nitrogen isotope values of whole body (W) and muscle (M) tissue from fauna collected in Bay d'Espoir in August 1985. Where $\Delta\delta^{13}\text{C}=(\delta^{13}\text{C}_{\text{ANIMAL}}-\delta^{13}\text{C}_{\text{POM}})$ and $\Delta\delta^{15}\text{N}=(\delta^{15}\text{N}_{\text{ANIMAL}}-\delta^{15}\text{N}_{\text{POM}})$. The bottom water POM was; $\delta^{13}\text{C}=-23.0\text{‰}$ and $\delta^{15}\text{N}=+8.3\text{‰}$.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
AMPHIPODS					
<i>H. fulvocinctus</i>	W	-24.1	-1.1	+9.5	1.2
CHAETOGNATHS					
<i>E. hamata</i>	W	-22.4	0.6	+12.5	4.2
<i>S. elegans</i>	W	-24.2	-1.2	+12.7	4.4
<i>S. maxima</i>	W	-22.6	0.4	+11.1	2.8
COPEPODS					
<i>C. hyperboreus</i>	W	-22.6	0.4	+9.5	1.2
<i>E. norvegica</i>	W	-23.5	-0.5	+12.3	4.0
<i>G. tenuispinus</i>	W	-23.3	-0.3	+10.8	2.5
<i>M. longa</i>	W	-23.9	-0.9	+10.1	1.8
Mixed Copepods	W	-21.8	1.2	+9.3	1.0
DECAPODS					
<i>P. multidentata</i>	W	-20.7	2.3	+12.1	3.8
	M	-19.0	4.0	+12.3	4.0
<i>S. arcticus</i>	W	-20.6	2.4	+12.6	4.3
	M	-19.6	3.4	+11.7	3.4
Shrimp sp.	M	-18.6	4.4	+13.6	5.3
<i>M. norvegica</i>	W	-21.4	1.6	+10.1	1.8
	M	-19.7	3.3	+10.0	1.7

Appendix H. Continued.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
<i>T. inermis</i>	W	-22.4	0.6	+11.2	2.9
	M	-20.4	2.6	+12.4	4.1
<i>T. raschii</i>	W	-21.4	1.6	+10.8	2.5
	M	-20.6	2.4	+11.2	2.9
FISHES					
<i>B. glaciale</i>	W	-20.6	2.4	+14.0	5.7
	M	-20.6	2.4	+13.4	5.1
<i>C. microdon</i>	W	-22.5	0.5	+12.1	3.8
<i>M. atlanticum</i>	W	-21.0	2.0	+13.8	5.5
	M	-19.6	3.4	+13.9	5.6
<i>Sebastes</i> sp.	M	-18.6	4.4	+14.2	5.9
MYSIDS					
<i>B. arctica</i>	M	-19.2	3.8	+11.5	3.2
MISCELLANEOUS					
<i>Aurelia</i> sp.	W	-21.9	1.1	+8.3	0.0
<i>C. limacina</i>	W	-23.7	-0.7	+9.7	1.4
Ctenophores	W	-20.3	2.7	+10.8	2.5
Ostracod spp.	W	-22.7	0.3	+10.9	2.6

Appendix I. Calculated $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for mean stable carbon and nitrogen isotope values of whole body (W) and muscle (M) tissue from fauna collected in Fortune Bay in December 1984. Where $\Delta\delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{ANIMAL}} - \delta^{13}\text{C}_{\text{POM}})$ and $\Delta\delta^{15}\text{N} = (\delta^{15}\text{N}_{\text{ANIMAL}} - \delta^{15}\text{N}_{\text{POM}})$. The subsurface POM was; $\delta^{13}\text{C} = -24.7\text{‰}$ and $\delta^{15}\text{N} = +5.0\text{‰}$.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
AMPHIPODS					
<i>A. malmgreni</i>	W	-21.7	3.0	+13.8	8.8
<i>H. fulvocinctus</i>	W	-23.4	1.3	+10.9	5.9
<i>H. medusarum</i>	W	-22.9	1.8	+11.4	6.4
<i>P. gaudichaudii</i>	W	-22.3	2.4	+10.2	5.2
CHAETOGNATHS					
<i>E. hamata</i>	W	-23.4	1.3	+11.9	6.9
<i>S. elegans</i>	W	-22.2	2.5	+12.9	7.9
COPEPODS					
<i>C. hyperboreus</i>	W	-21.8	2.9	+10.6	5.6
<i>M. longa</i>	W	-23.3	1.4	+10.9	5.9
<i>T. longicornis</i>	W	-20.8	3.9	+8.0	3.0
DECAPODS					
<i>P. borealis</i>	M	-20.5	4.2	+13.3	8.3
<i>P. propinquis</i>	M	-21.2	3.5	+12.7	7.7
<i>P. multidentata</i>	M	-20.4	4.3	+13.2	8.2
EUPHAUSIIDS					
<i>M. norvegica</i>	M	-21.3	3.4	+9.4	4.4
<i>T. inermis</i>	W	-22.4	1.3	+11.3	6.3
	M	-21.8	2.9	+12.2	7.2
<i>T. longicaudata</i>	W	-23.0	1.7	+10.5	5.5

Appendix I. Continued.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
<i>T. raschii</i>	W	-21.4	3.3	+10.7	5.7
	M	-21.3	3.4	+11.6	6.6
FISH					
<i>M. villosus</i>	W	-22.5	2.2	+11.7	6.7
	M	-21.5	3.2	+13.1	8.1
MYSIDS					
<i>B. nobilis</i>	M	-20.7	4.0	+13.6	8.6
<i>M. robusta</i>	W	-22.6	2.1	+10.6	5.6
<i>M. mixta</i>	W	-22.5	2.2	+11.0	6.0
	M	-21.6	3.1	+11.4	6.4
<i>P. truncatum</i>	W	-22.3	2.4	+12.7	7.7
MISCELLANEOUS					
Ctenophores	W	-22.0	2.7	+11.1	6.1
<i>T. helgolandica</i>	W	-22.2	2.5	+11.2	6.2

Appendix J. Calculated $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for mean stable carbon and nitrogen isotope values of whole body (W) and muscle (M) tissue from fauna collected in Fortune Bay in August 1985. Where $\Delta\delta^{13}\text{C}=(\delta^{13}\text{C}_{\text{ANIMAL}}-\delta^{13}\text{C}_{\text{POM}})$ and $\Delta\delta^{15}\text{N}=(\delta^{15}\text{N}_{\text{ANIMAL}}-\delta^{15}\text{N}_{\text{POM}})$. The subsurface POM was; $\delta^{13}\text{C}=-24.5\text{‰}$ and $\delta^{15}\text{N}=+4.6\text{‰}$.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
AMPHIPODS					
<i>A. malmgreni</i>	W	-21.1	3.4	+14.4	9.8
<i>H. fulvocinctus</i>	W	-23.7	0.8	+9.7	5.1
<i>P. gaudichaudii</i>	W	-23.3	1.2	+11.1	6.5
CHAETOGNATHS					
<i>E. hamata</i>	W	-22.4	2.1	+12.2	7.6
<i>S. elegans</i>	W	-21.8	2.7	+12.9	8.3
<i>S. maxima</i>	W	-21.4	3.1	+14.6	10.0
COPEPODS					
<i>C. hyperboreus</i>	W	-21.7	2.8	+9.9	5.3
<i>C. hamatus</i>	W	-23.7	0.8	+9.7	5.1
<i>E. norvegica</i>	W	-23.6	0.9	+12.7	8.1
<i>M. longa</i>	W	-23.3	1.2	+10.6	6.0
DECAPODS					
<i>P. borealis</i>	M	-18.4	6.1	+12.9	8.3
<i>P. multidentata</i>	M	-20.5	4.0	+13.2	8.6
EUPHAUSIIDS					
<i>M. norvegica</i>	M	-20.0	4.5	+10.3	5.7
<i>T. inermis</i>	M	-21.3	3.2	+12.6	8.0
<i>T. raschii</i>	W	-21.7	2.8	+10.6	6.0

Appendix J. Continued.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
<i>T. longicaudata</i>	M	-20.8	3.7	+11.2	6.6
	W	-22.1	2.4	+11.5	6.9
MYSIDS					
<i>B. nobilis</i>	W	-22.3	2.2	+12.6	8.0
<i>M. mixta</i>	W	-21.8	2.7	+10.4	5.8
MISCELLANEOUS					
<i>C. limacina</i>	W	-21.1	3.4	+10.1	5.5

Appendix K. Calculated $\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$ values for mean stable carbon and nitrogen isotope values of whole body (W) and muscle (M) tissue from fauna collected in Fortune Bay in August 1985. Where $\Delta\delta^{13}\text{C}=(\delta^{13}\text{C}_{\text{ANIMAL}}-\delta^{13}\text{C}_{\text{POM}})$ and $\Delta\delta^{15}\text{N}=(\delta^{15}\text{N}_{\text{ANIMAL}}-\delta^{15}\text{N}_{\text{POM}})$. The bottom water POM was; $\delta^{13}\text{C}=-24.0\text{‰}$ and $\delta^{15}\text{N}=+8.9\text{‰}$.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
AMPHIPODS					
<i>A. malmgreni</i>	W	-21.1	2.9	+14.4	5.5
<i>H. fulvocinctus</i>	W	-23.7	0.3	+9.7	0.8
<i>P. gaudichaudii</i>	W	-23.3	0.7	+11.1	2.2
CHAETOGNATHS					
<i>E. hamata</i>	W	-22.4	1.6	+12.2	3.3
<i>S. elegans</i>	W	-21.8	2.2	+12.9	4.0
<i>S. mazima</i>	W	-21.4	2.6	+14.6	5.7
COPEPODS					
<i>C. hyperboreus</i>	W	-21.7	2.3	+9.9	1.0
<i>C. hamatus</i>	W	-23.7	0.3	+9.7	0.8
<i>E. norvegica</i>	W	-23.6	0.4	+12.7	3.8
<i>M. longa</i>	W	-23.3	0.7	+10.6	1.7
DECAPODS					
<i>P. borealis</i>	M	-18.4	5.6	+12.9	4.0
<i>P. multidentata</i>	M	-20.5	3.5	+13.2	4.3
EUPHAUSIIDS					
<i>M. norvegica</i>	M	-20.0	4.0	+10.3	1.4
<i>T. inermis</i>	M	-21.3	2.7	+12.6	3.7
<i>T. raschii</i>	W	-21.7	2.3	+10.6	1.7

Appendix K. Continued.

Species	Tissue	$\delta^{13}\text{C}$ (‰)	$\Delta\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta\delta^{15}\text{N}$ (‰)
<i>T. longicaudata</i>	M	-20.8	3.2	+11.2	2.3
	W	-22.1	1.9	+11.5	2.6
MYSIDS					
<i>B. nobilis</i>	W	-22.3	1.7	+12.6	3.7
<i>M. mixta</i>	W	-21.8	2.2	+10.4	1.5
MISCELLANEOUS					
<i>C. limacina</i>	W	-21.1	2.9	+10.1	1.2

