

# $\delta^{13}\text{C}$ evidence of the origins and fates of organic carbon in estuarine and nearshore food webs\*

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**ABSTRACT:** Origins and fates of organic carbon in estuarine and nearshore marine food webs of Hood Canal, a fjord extension of Puget Sound, Washington (USA), were evaluated seasonally using stable carbon isotopes ( $\delta^{13}\text{C}$ ).  $\delta^{13}\text{C}$  was measured in: (1) autotrophic sources in terrestrial, estuarine, and nearshore marine habitats; (2) particulate and dissolved organic carbon (POC, DOC) in riverine, estuarine, and nearshore marine waters; (3) primary and secondary consumers in selected estuarine and marine littoral and neritic food webs. Autotrophic sources in terrestrial, riverine, salt marsh-meadow, and neritic habitats were generally more  $^{13}\text{C}$ -depleted (averaging  $-30$ ,  $-26$ , and  $-22$ ‰, respectively) than sources in estuarine and marine littoral habitats ( $-8$  and  $-23$ ‰). The isotopic composition of neritic consumers indicated that their food sources originated directly from phytoplankton production. In contrast, the  $\delta^{13}\text{C}$  of primary and secondary consumers ( $-11$ ‰ to  $-23$ ‰) in estuarine and marine littoral habitats suggested that the most important sources of organic carbon to these food webs were autochthonous, originating primarily from eelgrass, epiphytes, and macroalgae. Estuarine detritus deposits, sestonic POC, and sediments had widely ranging  $\delta^{13}\text{C}$  values ( $-9.7$  to  $-28.9$ ‰), indicating diverse origins. However, POC associated with surface foam in estuarine littoral waters and DOC in marine littoral waters both had isotopic values most similar to estuarine autotrophs and consumers, suggesting the potential importance of dissolved and foam organics in food-web pathways. Depletion as high as  $\Delta 8$ ‰ occurred in autotrophs, DOC, and some consumer organisms in estuarine and nearshore marine habitats during winter. This seasonal depletion in  $\delta^{13}\text{C}$  originates from variable imports of dissolved inorganic carbon (DIC) transported by freshwater and may reflect the influence of extensive freshwater storage in Hood Canal during fall and winter. These results indicate the need for further elucidation of the complex biological and chemical mechanisms of formation, cycling, and degradation of particulate and dissolved organics from autochthonous sources to estuarine and nearshore marine food webs.

## INTRODUCTION

Evidence for the importance of fluvial input of terrestrially-derived organic carbon in Pacific Northwest estuaries was provided by Naiman & Sibert's (1978, 1979) studies of the Nanaimo River estuary, British Columbia. They estimated that inputs of dissolved and particulate organic carbon (DOC & POC) from the productive conifer forest watersheds were four-fold greater than the total estuarine primary production. Recent evidence of extremely high primary production rates of micro- and macroalgae and eelgrass in Oregon and Washington (Kentula 1982, McIntire et al. 1983, Pregnall 1983, Thom 1984), higher DOC than POC

concentrations in estuaries (Wissmar & Simenstad 1984); and the importance of detritus-based estuarine food webs (Sibert et al. 1977, Kistritz 1978, Kistritz & Yesaki 1979, Northcote et al. 1979, Simenstad et al. 1979) implies, however, that contributions of autochthonous sources may be considerably underestimated. These observations indicate that the origins and fates of organic carbon in estuarine and nearshore marine food webs in the Pacific Northwest are not well known.

This paper reports our use of stable carbon isotopes in elucidating the seasonal origins and fates of different organic carbon sources in Puget Sound estuaries. We hypothesized that stable carbon isotope analysis ( $\delta^{13}\text{C}$ ; see 'Methods') offers a means of elucidating the origins and fates of organic carbon in this region's estuaries and nearshore marine waters because high riverine inputs of terrestrial carbon in fall and winter may produce a distinct, seasonally-pulsed,  $^{13}\text{C}$ -

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depleted signature ( $\delta^{13}\text{C} > -25\text{‰}$ ) separable from enriched ( $< -20\text{‰}$ ), estuarine and nearshore marine autochthonous carbon (Sackett et al. 1965, Smith & Epstein 1970).

Our primary objectives were to: (1) intensively sample  $\delta^{13}\text{C}$  of carbon sources and consumer organisms within estuarine and nearshore marine food webs; (2) determine the seasonal isotopic composition of carbon sources and consumers in the different habitats. A secondary objective included assessment of the importance of the autochthonous carbon sources to estuarine and nearshore marine food webs by comparison of the isotopic data to calculations of potential inputs of carbon by different primary producers.

## METHODS

**Sampling design.** The study sites are located in Hood Canal, an 80 km long fjord off Puget Sound (Fig. 1). Eight sampling locations include 3 riverine-

estuarine systems, a littoral marine, and a neritic habitat. The Duckabush River and estuary is the intensive study site. The Duckabush River (average annual discharge,  $3.7 \times 10^8 \text{ m}^3 \text{ yr}^{-1}$ ) drains a 172 km<sup>2</sup> coniferous forest watershed originating in Olympic National Park, almost free of anthropogenic influences. The estuary is a broad, fan-shaped delta, approximately 2.0 km<sup>2</sup> in surface area, dominated by coarse sand to gravel-cobble substrate covered by dense beds of eelgrass *Zostera marina* and macroalgae (species of *Ulva*, *Enteromorpha*) at its lower tidal elevations and salt marsh-meadow at its upper elevations. Typical July temperatures, salinities, and pH values for this region's riverine, estuarine, and neritic waters are, in respective order: 12.5, 26.0, and 20.5 °C; 00.00, 9.80, 29.88 ‰; pH 7.8, 7.2, 7.8 (Simenstad & Wissmar, unpubl.). Other river-estuarine study sites include Big Beef Creek (38 km<sup>2</sup> watershed;  $3.5 \times 10^7 \text{ m}^3 \text{ yr}^{-1}$  average annual discharge; 0.08 km<sup>2</sup> delta area) and the Skokomish River (366 km<sup>2</sup>;  $6.6 \times 10^8 \text{ m}^3 \text{ yr}^{-1}$ ; 6.0 km<sup>2</sup>). The marine littoral study site is a moderate-gradient, sand-gravel

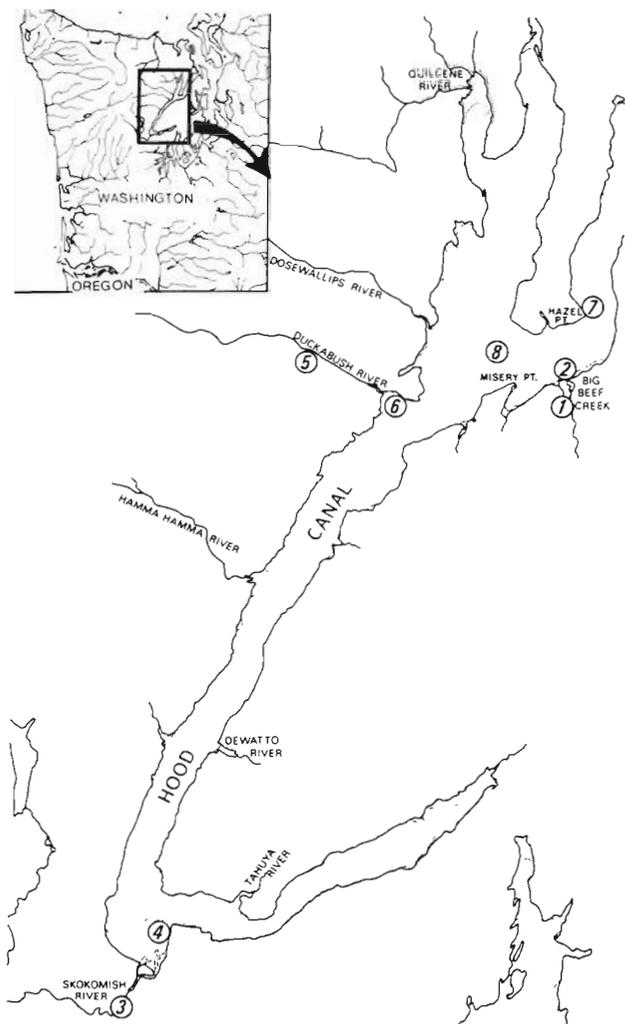


Fig. 1. Terrestrial and riverine (1, 3, 5), estuarine (2, 4, 6) and marine littoral (7), and neritic (8) habitats of Hood Canal, Washington (see insert), sampled seasonally for sources and fates of organic carbon

beach at Hazel Point and the neritic site located at Misery Point, an open water site over 100 m deep.

Sampling of primary producers, water, seston, surface foam, sediments, detritus, and biota occurred during 3 seasons: spring (April), summer (July) 1981 and winter (January) 1982. Isotopic analyses of DOC from the spring sampling were not obtained because of analytical difficulties. Due to physical and cost constraints of isotopic analyses, replicated samples from within a single sampling site were limited to sediments, DOC and POC.

*Sampling methodology.* All samples of particulates were filtered and acid-washed (5% HCl; to remove carbonates) on pre-combusted glass-fiber filters (<1.0  $\mu\text{m}$ ; Strickland & Parsons 1972). Sample filters were wrapped in pre-combusted aluminum foil and placed in polypropylene vials with desiccant. DOC samples (the filtrates of POC samples) were placed in acid-washed, presoaked polypropylene bottles, fixed with mercuric chloride, and refrigerated 2 to 4 wk prior to analysis.

Sources of autotrophic carbon included: (1) terrestrial and salt marsh-meadow vascular plants; (2) estuarine and marine algae and eelgrass; (3) neritic phytoplankton. Terrestrial plants included live conifer needles and deciduous tree leaves and salt marsh-meadow plant samples were live blades and leaves of grasses and rushes. Estuarine and marine autotrophs included living, attached macroalgae, seagrass blades, and epiphytes scraped off the seagrass blades. Benthic microalgae (diatoms) were not separated from surface sediments. Phytoplankton was sampled as POC seston passing through a 53  $\mu\text{m}$  stainless steel sieve and retained on a glass-fiber filter. Microscopic examination indicated that particles < 53  $\mu\text{m}$  in all but riverine waters were primarily phytoplankton cells (Wissmar & Simenstad 1984).

Acid-washed forceps were used to sample deposits of organic detritus randomly at various locations and microhabitats in estuarine and littoral marine sites. Samples included recognizable, large particulate organic matter (i.e. seagrass blades, deciduous and coniferous materials) that appeared to be recently deposited, as well as fine particles created by physical action and biological degradation. All organisms except microorganisms were removed from the detritus samples before acid-washing.

DOC and sestonic POC samples were obtained from estuarine and marine littoral waters with a battery-powered, portable pump, and from rivers with a 31 Van Dorn bottle. Sediment samples were obtained with 1.3 cm ID plastic cores and subsampled at the surface and 15 cm depth. Surface water foam and film samples were collected during early flood tide intrusion of the Duckabush River estuary littoral flat by suction and

decanting with sample bottles. During winter and summer of 1983, supplemental samples of water for isotopic analyses of dissolved inorganic carbon (DIC) and organic carbon (POC seston and DOC) were taken from riverine, estuarine, and neritic (1 m and 50 m depths) waters at the Duckabush River estuary.

Previous studies of estuarine food webs in British Columbia and Puget Sound facilitated selection of representative consumer organisms. One of the more important and best studied predator-prey interactions in Pacific Northwest estuaries and nearshore marine food webs involves predation by juvenile salmon (*Oncorhynchus* spp.) upon epibenthic crustaceans (harpacticoid copepods, gammarid amphipods) in littoral flat, eelgrass *Zostera marina*, and salt marsh-meadow habitats (Brown & Sibert 1977, Sibert et al. 1977, Healey 1979, 1982, Naimann & Sibert 1979, Sibert 1979, Levy & Northcote 1982, Simenstad et al. 1982). These investigators, and a recent review of the ecology of harpacticoid copepods (Hicks & Coull 1983), categorized most epibenthic crustaceans common to estuarine and littoral marine food webs of this region as detritivores. In the case of food webs involving juvenile salmon, Levy & Levings (1978), Healey (1979, 1982), Simenstad et al. (1982) have shown that particular harpacticoid copepods (e.g. *Harpacticus* sp.-cf. *uniremis* group, *Tisbe* spp.) and gammarid amphipods (e.g. *Eogammarus confervicolus*, *Anisogammarus pugettensis*, *Corophium* spp.) are uniquely important prey taxa. Food-habit studies in Puget Sound by Simenstad et al. (1979) also permitted selection of other secondary consumers that feed upon the above epibenthic crustaceans as well as infaunal and sessile invertebrates.

These diverse consumer organisms were sampled by a variety of techniques, including: (1) portable 73 cm<sup>2</sup> suction pump that retained epibenthic crustaceans > 100  $\mu\text{m}$ ; (2) vertical hauls from 25 m depth with a 0.5 m ringnet (500  $\mu\text{m}$  mesh netting) for later-stage juvenile and adult neritic zooplankton; (3) sets of a 37 m sinking beach seine or aquarium dip nets for nearshore fish, crabs, shrimp, and mysids; (4) direct removal of epibenthic and benthic macroinvertebrates. Isotope samples of sessile and motile macroinvertebrates and fish consisted for muscle tissue, while zooplankton were analysed intact.

Samples were placed in coolers and were refrigerated in the laboratory prior to filtering and processing. Stable carbon isotope samples were processed by Coastal Marine Laboratories, Inc. with a Nuclide 6-60 dual collector isotope mass spectrometer (Parker et al. 1972). Sample filters were wrapped in pre-combusted aluminum foil and dried at 60°C before being combusted. DOC was converted to CO<sub>2</sub> by potassium persulfate oxidation (Parker & Calder 1970) after being

stripped of chlorine; analytical precision was  $\pm 1\%$  to  $0.5\%$  for the DOC and  $\pm 0.2\%$  for all particulate samples. Isotopic analyses of DIC from the 1983 sampling were conducted on a triple collector gas isotope mass spectrometer by Drs Paul Quay and Mike Cafrey (Quaternary Research Center, University of Washington); analytical precision of these measurements was  $\pm 0.1\%$ .  $\delta^{13}\text{C} = (^{13}\text{C}/^{12}\text{C} \text{ sample} / ^{13}\text{C}/^{12}\text{C} \text{ standard} - 1) \times 10^3$ , expressed as  $\pm\%$  (per mille) relative to international PDB standard (fossil belemnite, *Belemnitella americana*, from Peedee formation in South Carolina) which in this paper is discussed as enriched and depleted relative to the heavier isotope,  $^{13}\text{C}$ .

*$\delta^{13}\text{C}$  technique considerations.* Interpretation of the sources and losses of organic carbon in food webs usually involves the compilation of system budgets (i.e. Teal 1962, McLusky 1981, Mann 1982). However, this approach offers little insight into the importance of different carbon sources to consumers. Alternatively, stable carbon isotope ratios which identify the photosynthetic origin of organic carbon can be used to trace the origins and fates of organic carbon in food webs (see Fry & Sherr, in press, for an excellent contemporary review). However, stable carbon analysis of food webs can be confounded by temporally and spatially complex carbon sources and variable isotopic fractionation (Fry & Sherr in press). For example, ambiguous isotopic ratios can result from: (1) mixing of more than 2 carbon sources with divergent  $\delta^{13}\text{C}$  values; (2) variable isotopic fractionation among microbes or phytoplankton due to differences in taxonomic composition (Bondar et al. 1976, Wong & Sackett 1978) and variable dissolved inorganic carbon (DIC) demand or availability (Deuser 1970, Smith & Kroopnick 1981); (3) unexplained within-plant variation in some marine algae (Stephenson et al. in press); (4) variation of animal stable carbon composition due to tissues or products analysed (Tieszen et al. 1983); (5) varying turnover rates of metazoans (Fry & Arnold 1982); (6) isotopic fractionation among trophic levels (e.g. DeNiro & Epstein 1978, McConnaughey & McRoy 1979, Rau et al. 1983).

We attempted to mediate some of these problems by: (1) examining an estuary with dominant carbon sources of divergent isotopic composition, primarily terrestrial and eelgrass carbon; (2) sampling seasonally to obtain isotopic data for sources at different times of peak riverine inflows, primary production, and detritus accumulation; (3) comparing organic carbon sources and fates for different food webs; (4) restricting isotopic sampling to aerobic environments; (5) discussing the comparative magnitudes of different allochthonous and autochthonous carbon sources for the estuarine and nearshore marine food webs of Hood Canal.

Estimation of total annual net production of principal

autotrophic producers in Hood Canal involved extrapolation of applicable production rate estimates from the literature to the total area of specific autotrophic habitats. Direct production rate values included those of Welschmeyer (1982) for neritic phytoplankton; Pamatmat (1968) for benthic microalgae; Thom (1981) for salt marsh-meadow plants; and Thom (1981) and McIntire et al. (1983) for macroalgae. Eelgrass production was estimated from replicated  $0.0625 \text{ m}^2$  quadrat samples of *Zostera marina* standing stock at Duckabush River estuary extrapolated by the range of P : B ratios for local populations (Phillips 1969, 1972); eelgrass epiphyte production was estimated as 5% of the eelgrass production (Kentula 1982, McIntire et al. 1983). The area of neritic habitat was estimated from planimetry of  $> 3 \text{ m}$  depth waters from NOAA chart # 18440 and all other habitats were estimated from planimetry of the habitat maps in the 'Washington Coastal Zone Atlas' (Washington Department of Ecology 1977). DOC input from rivers entering Hood Canal was estimated by extrapolating our DOC concentration data (unpubl.) by seasonal discharge data from the 3 study rivers (US Geological Survey 1983) and assigning other, unmeasured rivers to one of the 3 discharge-DOC concentration categories based upon our own familiarity with the rivers' watersheds and seasonal flow.

## RESULTS AND DISCUSSION

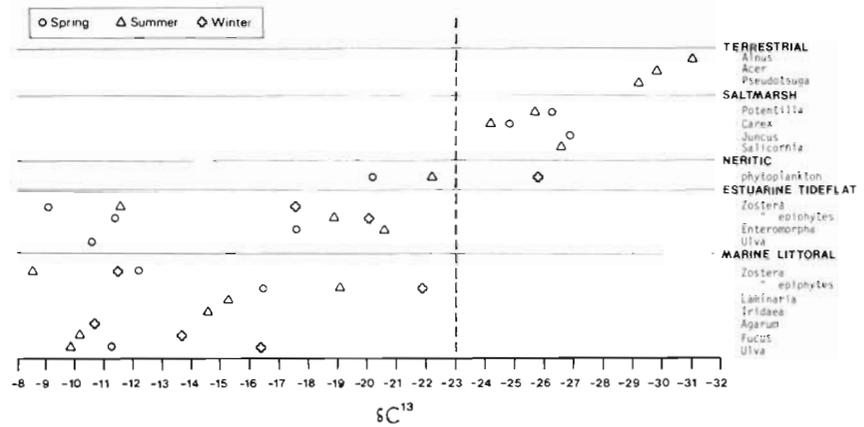
Our results indicate 2 important aspects about origins and fates of organic carbon in estuarine food webs of Puget Sound: (1) sources of organic carbon to detritus-based food webs originate primarily from  $^{13}\text{C}$ -enriched eelgrass, epiphyte, and macroalgae in estuarine and marine littoral marine beaches rather than from  $^{13}\text{C}$ -depleted sources such as terrestrial and neritic autotrophic sources; (2) the isotopic composition of estuarine primary producers, DOC, and many detritivorous consumers shows marked seasonal  $^{13}\text{C}$  depletion in winter.

### Origins and fates of organic carbon

#### Autotrophic sources

Stable carbon isotope values of living autotrophic sources were distinctly separated among terrestrial and salt marsh-salt meadow vs estuarine and marine littoral and neritic habitats (Fig. 2). Highest  $^{13}\text{C}$  depletion appeared in terrestrial and salt marsh-meadow  $\text{C}_3$  plants. Needles and leaves of douglas fir *Pseudotsuga menziesii*, big leaf maple *Acer macrophyllum* and red

Fig. 2.  $\delta^{13}\text{C}$  values for living autotrophic sources of organic carbon in terrestrial, salt marsh-meadow, estuarine and marine littoral, and neritic habitats of Hood Canal, Washington during 3 seasons, 1981 to 1982



alder *Alnus rubra* had isotopic values ranging between  $-29.2$  and  $-31.0$ ‰, and salt marsh-meadow  $\delta^{13}\text{C}$  values ranged between  $-24.2$  and  $-31.0$ ‰. In comparison, neritic phytoplankton were somewhat enriched ( $-20.2$  to  $-25.8$ ‰), while eelgrass, their epiphytes, and macrophytic algae in estuarine and marine littoral habitats were highly enriched ( $-9.1$  to  $-21.9$ ‰).

POC, DOC, sediment and detritus deposits

Both  $< 53 \mu\text{m}$  and total sestonic POC in estuarine or marine habitats were significantly ( $t = 7.82, P = 0.05, df = 17$ ) more enriched than in the rivers (Fig. 3; Table 1). Surprisingly, mean isotopic values of estuarine DOC were not significantly different ( $t = 0.06, P = 0.05, df = 5$ ) from riverine DOC. This may be due to the

absence of any DOC samples during spring (see 'Methods') when POC tended to be more enriched.

Isotopic values of sediments generally overlapped sestonic POC and DOC. Comparison of the surface and subsurface sediments indicated no significant differences in  $\delta^{13}\text{C}$  ( $t = 1.35, P = 0.05, df = 35$ ). DOC and sestonic POC associated with foam at the water surface of estuarine littoral habitats were typically enriched relative to subsurface sestonic POC, DOC, and sediments;  $\delta^{13}\text{C}$  of surface foam DOC averaged  $-19.8 (\pm 1.7)$ ‰ and sestonic POC,  $-19.0 (\pm 0.7)$ ‰.

Isotopic values of detritus deposits in estuarine and marine littoral habitats varied considerably ( $-22.2 \pm 4.7$ ‰) due to variable particle composition and no trends were evident. The most extreme  $\delta^{13}\text{C}$  values for detritus were in deciduous and coniferous debris in a side channel of Big Beef Creek estuary ( $-28.9$ ‰) and

Fig. 3.  $\delta^{13}\text{C}$  values for sestonic POC, DOC, sediments, foam DOC and POC, and detritus deposits at 5 riverine, estuarine or marine sampling sites in Hood Canal, Washington, 1981 to 1982

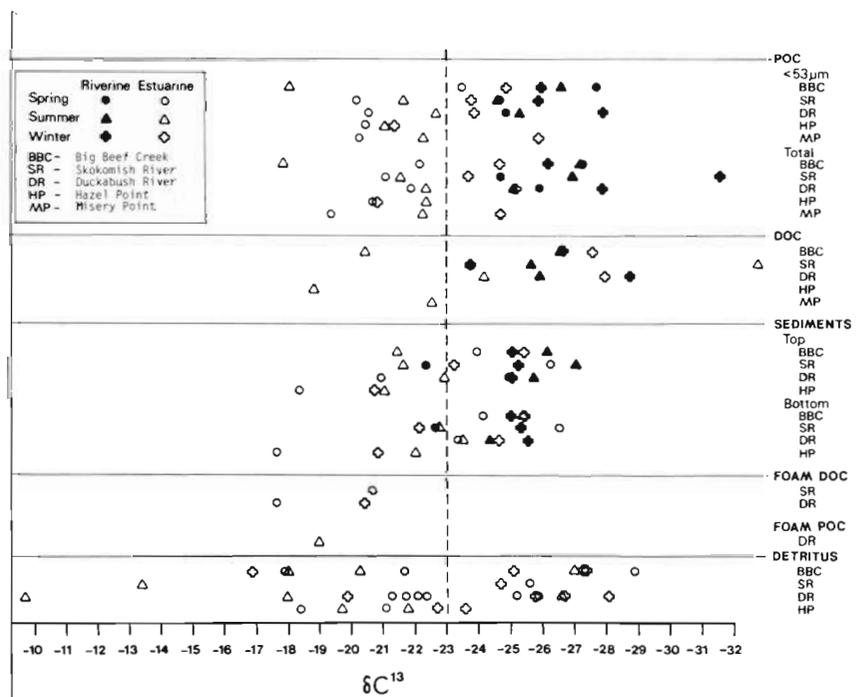


Table 1. Summary ( $\bar{x} \pm SD$ ; sample size in parentheses) of  $\delta^{13}C$  values of sestonic POC, DOC, sediments, detritus deposits, and foam in riverine, estuarine, and marine habitats in Hood Canal, Washington. nd = no data

Carbon source	Habitats				Overall
	Riverine	Estuarine littoral	Marine littoral	Neritic marine	
Sestonic POC < 53 $\mu$ m	-25.9 $\pm$ 1.2 (9)	-22.2 $\pm$ 2.1 (11)	-20.9 $\pm$ 0.5 (3)	-22.7 $\pm$ 2.8 (3)	-23.4 $\pm$ 2.6 (26)
Total	-26.9 $\pm$ 1.9 (10)	-22.3 $\pm$ 2.1 (12)	-21.2 $\pm$ 0.9 (3)	-22.0 $\pm$ 2.7 (3)	-23.7 $\pm$ 3.1 (28)
DOC	-26.2 $\pm$ 2.0 (8)	-26.3 $\pm$ 4.0 (7)	-18.8 (1)	-24.5 $\pm$ 3.5 (3)	-25.6 $\pm$ 3.4 (19)
Sediments	-25.0 $\pm$ 1.2 (28)	-23.8 $\pm$ 1.8 (46)	-20.3 $\pm$ 1.6 (11)	nd	-23.5 $\pm$ 1.3 (85)
Detritus deposits	nd	-22.6 $\pm$ 5.1 (32)	-21.2 $\pm$ 2.4 (9)	nd	-22.3 $\pm$ 4.7 (41)
Foam POC	nd	-18.3 $\pm$ 1.4 (4)	nd	nd	-18.3 $\pm$ 1.4 (4)
DOC	nd	-20.5 $\pm$ 0.2 (4)	nd	nd	-20.5 $\pm$ 0.2 (4)

in eelgrass fragments in low tidal elevation eelgrass bed in the Duckabush River estuary (-9.7‰).

Consumers and their predators

Epibenthic crustaceans and benthos in estuarine and marine littoral habitats were enriched (-16.2  $\pm$  2.5‰)

relative to sestonic POC, DOC, sediment, and most detrital carbon (Fig. 4). In general, epibenthic crustaceans, including harpacticoid copepods (*Harpacticus uniremis* group) and gammarid amphipods (*Eogammarus confervicolus* and *Anisogammarus pugettensis*), were enriched (-16.6  $\pm$  2.9) compared to infaunal and sessile suspension-feeding bivalves (-19.7  $\pm$  1.8‰). A specimen of *Phyllaplysia taylori*, an epiphyte-grazing

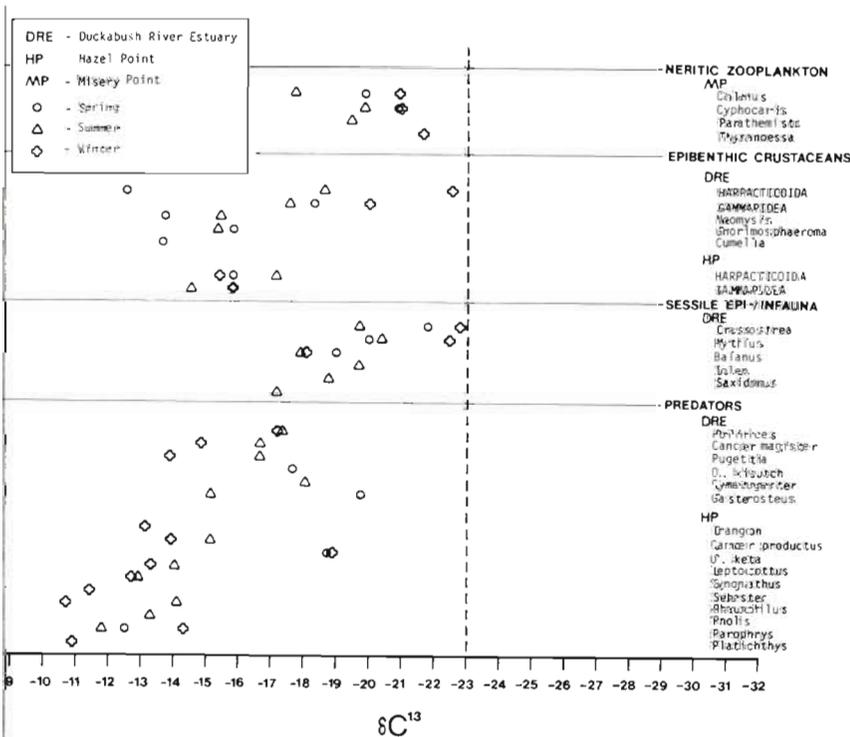


Fig. 4.  $\delta^{13}C$  values of consumer organisms and their predators in estuarine (DRE) and marine littoral (HP) and neritic (MP) habitats of Hood Canal, Washington, during 3 seasons, 1981 to 1982

sea hare, in eelgrass beds at Hazel Point was extremely enriched ( $-5.7\text{‰}$ ).

Secondary consumers possessed isotopic values similar to their prey (Fig. 4). Fishes feeding on epibenthic crustaceans in estuarine and marine littoral habitats – including juvenile chum *Oncorhynchus keta* and coho salmon *O. kisutch* – had  $\delta^{13}\text{C}$  values ( $-10.7$  to  $-18.9\text{‰}$ ) overlapping those of their prey. Other fishes (*Leptocottus armatus*, *Syngnathus leptorhynchus*, *Sebastes caurinus*, *Rhacochilus vacca*, *Pholis laeta*, *Parophrys vetulus*, *Platichthys stellatus*) in the littoral eelgrass bed at Hazel Point were enriched ( $-12.7 \pm 1.2\text{‰}$ ) relative to their prey, harpacticoid copepods and gammarid amphipods. Macroinvertebrate predators on the littoral flat of Duckabush River estuary had enriched  $\delta^{13}\text{C}$  values ( $-16.5 \pm 1.1\text{‰}$ ) compared to some of their potential prey, sessile epifauna and benthic infauna ( $-19.8 \pm 1.7\text{‰}$ ), but were similar to epibenthic crustaceans ( $-16.6 \pm 3.0\text{‰}$ ).

Herbivorous calanoid copepods (*Calanus* spp.) and juvenile euphausiids (*Thysanoessa* sp.) in neritic waters at Misery Point had  $\delta^{13}\text{C}$  values ( $-20.0 \pm 1.7\text{‰}$ ) overlapping those phytoplankton ( $-20.9 \pm 0.5\text{‰}$ ) (Fig.

4). Invertebrate predators upon these herbivores, hyperiid (*Parathemisto pacifica*) and gammarid amphipods (*Cyphocaris challergeri*), had almost identical values ( $-20.1 \pm 0.7\text{‰}$ ).

The frequency of occurrence of all seasonally-averaged  $\delta^{13}\text{C}$  values for samples of autotrophic sources, sestonic POC, DOC, detritus deposits, sediments, consumers and their predators in all habitats (Fig. 5) indicates the prominence of autochthonous carbon sources to food webs in estuarine and marine littoral and neritic habitats. All terrestrial, salt marsh-meadow, riverine DOC, POC, and sediment sources had  $\delta^{13}\text{C}$  values above  $-23\text{‰}$ , compared to less than  $-23\text{‰}$  for all consumers, indicating minor incorporation of allochthonous carbon in estuarine and nearshore marine food webs.  $\delta^{13}\text{C}$  values of primary consumers and their predators ( $-11$  to  $-23\text{‰}$ ) in estuarine and marine littoral habitats suggested that the most important sources were carbon from eelgrass, epiphytes, and macroalgae. Isotopic values of POC and DOC associated with surface foam in estuarine and marine littoral habitats paralleled those of autotrophs and consumers in these habitats, suggesting the importance of these

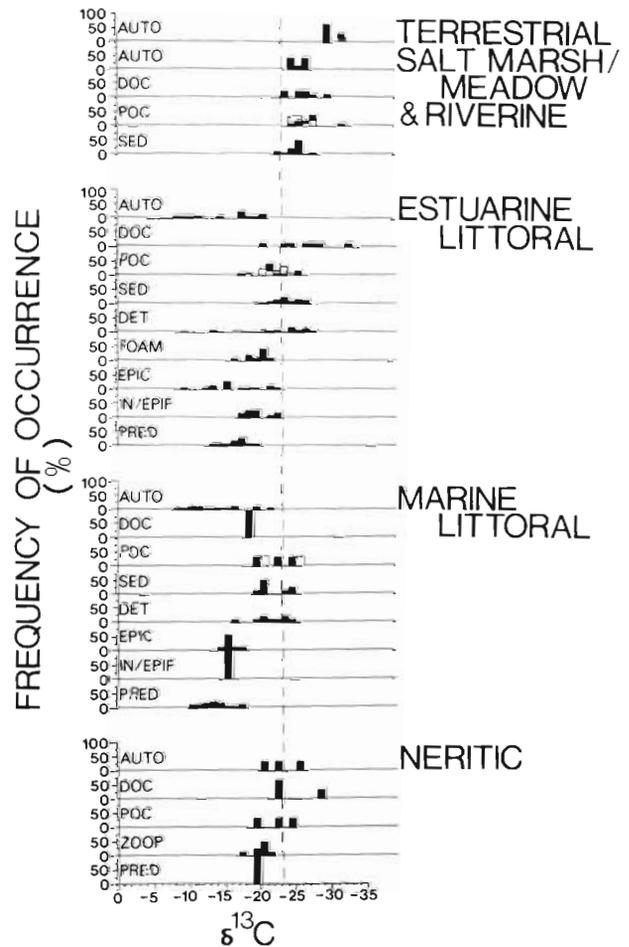


Fig. 5. Seasonally-averaged frequency distributions of  $\delta^{13}\text{C}$  values for sources and fates of organic carbon in terrestrial, salt marsh-meadow, riverine, estuarine and marine littoral, and neritic habitats in Hood Canal, Washington, 1981 to 1982. AUTO autotrophs; DOC dissolved organic carbon; POC particulate organic carbon; SED sediments; DET detritus deposits; FOAM surface water foam; EPIC epibenthic crustaceans; IN/EPIF infauna and epifauna; ZOOP pelagic zooplankton; PRED predators. Open bars:  $< 53 \mu\text{m}$  POC

carbon forms in food web pathways. Isotopic values of detritus, sestonic POC, and sediments suggested that only their autochthonous portions were important as food resources in both of these habitats. The wide-ranging isotopic values ( $-9.7$  to  $-28.9$ ‰) of detritus, sestonic POC, and sediments in the estuaries reflected strong, variable input of riverine carbon.

Both primary and secondary consumers tended to be enriched relative to their food resources (Fig. 5). This trend lends support to earlier observations of small-scale fractionation between trophic levels (DeNiro & Epstein 1978, Haines & Montague 1979, McConnaughey & McRoy 1979, Teeri & Schoeller 1979, Rau et al. 1983, Theyer et al. 1983), although in several instances (e.g. epibenthic detritivores vs total POC) the enrichment (as high as  $9.4$ ‰) was more than has been reported in the literature. However, this apparent anomaly does lend support for more direct (i.e. DOC) or alternative food web pathways between these consumers and isotopically enriched macrophytes. Accordingly, the neritic phytoplankton-primary consumer (calanoid copepods) food chain illustrated a more typical (i.e.  $x = 3.4$ ‰) enrichment. While enrichment was relatively common at the first trophic level, enrichment between primary and secondary consumer levels was not consistent. This probably reflects consumption of a diverse spectrum of prey with divergent isotopic composition or, in the case of omnivorous consumers such as mysids and hyperiid and gammarid amphipods, mixed feeding upon living autotrophs, detritus, and other metazoans. The isotopic composition of more long-lived secondary consumers such as fish also integrates a longer, and possibly more diverse, period of food carbon consumption.

### Seasonality of $\delta^{13}\text{C}$

Seasonal fluctuations in  $\delta^{13}\text{C}$  were evident in all estuarine and littoral marine autotrophic sources (Fig. 2). The highest depletion was evident in eelgrass, eelgrass epiphytes, macroalgae, and phytoplankton samples collected in the winter, when eelgrass and *Ulva* showed as much as  $\Delta 6$ ‰ increased depletion over summer samples.

Seasonality of isotopic values in sestonic POC were not evident (Fig. 3). In contrast, values of estuarine and neritic DOC appeared more depleted during winter, while riverine values were variable.

Seasonal isotopic variation in consumer organisms was confined to relatively short-lived primary consumers (Fig. 4). Epibenthic crustaceans and sessile bivalves on littoral flat of the Duckabush River estuary showed increased depletion of as much as  $\Delta 3.9$ ‰ between summer and winter. In contrast, their pre-

dators in both littoral habitats at the Duckabush River estuary and at Hazel Point showed no such trend. Slightly increased depletion was also evident for neritic herbivores and predators at Misery Point ( $\Delta 1.1$  to  $3.2$ ‰).

The increased  $\delta^{13}\text{C}$  depletion in autotrophic carbon and DOC during winter may be related to seasonal variation in photosynthetically-fixed isotopic carbon and in sources of DIC in freshwaters (Spiker & Schemel 1979). Seasonal differences in  $\delta^{13}\text{C}$  composition of DIC in Hood Canal may arise from longer storage of freshwater in the fjord during the winter and fall (Friebertshausen & Duxbury 1972). These investigators suggested that, in addition to direct river discharge, the freshwater content of Hood Canal is also influenced by freshwater inflow from the adjacent and larger Whidbey Island basin, whose freshwater content is regulated by the seasonal discharge of the Skagit River.

We measured  $\delta^{13}\text{C}$  of DIC in 3 different habitats during winter and summer 1983 to assess seasonal variability (Table 2). During winter,  $\delta^{13}\text{C}$  of DIC in the Duckabush River ( $-6.4$ ‰) was depleted by  $5.1$  to  $6.0$ ‰ relative to DIC in the estuary and neritic surface waters. In summer, however,  $\delta^{13}\text{C}$  of DIC in all 3 surface waters were enriched by between  $1.9$  and  $2.6$ ‰. The depleted DIC in riverine, estuarine, and neritic waters in winter and lower salinities in the neritic habitat further indicates the probable influence of freshwater DIC in Hood Canal on autotrophs.

Examples of seasonal variation in  $\delta^{13}\text{C}$  values of estuarine and nearshore marine autotrophs and DOC are not common in the literature (see, however, Fry 1984). Changing species composition or photosynthetic pathways, production rates, and influences of temperature and pH have all been shown to cause  $^{13}\text{C}$  enrichment in oceanic phytoplankton (Degens et al. 1968; Deuser et al. 1968, Parker & Calder 1970, Wong & Sackett 1978). Observations of seasonal changes in the species composition and temperatures in Hood Canal (Shuman 1978, Copping 1982) implies that these factors, as well as freshwater storage, may have contributed to the seasonal  $^{13}\text{C}$  enrichment ( $\Delta 5.6$ ‰) observed in this study.

$\delta^{13}\text{C}$  seasonality in estuarine autotrophs, primarily *Zostera marina* and associated epiphytes, was even greater ( $\Delta 8$ ‰; Fig. 2) than in phytoplankton. This suggests considerable differences in photosynthetic pathways (Smith & Epstein 1970, McMillian et al. 1980) and environmental influences such as temperature, salinity, and sediments on production (McRoy & Helfferich 1977, Benedict et al. 1980). Indirect evidence of the influence of temperature upon enrichment includes observations by Thayer et al. (1978) for *Z. marina* in North Carolina ( $\Delta 1$ ‰ winter-spring enrichment) compared to *Z. marina* in colder northern

Table 2.  $\delta^{13}\text{C}$  of dissolved inorganic carbon (DIC) in riverine, estuarine, and neritic waters in the vicinity of the Duckabush River estuary, winter and summer. Physical conditions indicated by temperature ( $^{\circ}\text{C}$ ) and salinity (‰)

Location	Temperature ( $^{\circ}\text{C}$ )		Salinity (‰)		$\delta^{13}\text{C}$ (‰)	
	Winter	Summer	Winter	Summer	Winter	Summer
Duckabush River	5.0	12.9	0	0	-6.4	-4.5
Duckabush River estuary	7.9	15.5	10	10	-1.3	+0.7
Neritic marine						
surface (-1 m)	8.5	20.5	15.6	25.5	-1.1	+1.5
mid-depth (-50 m)	9.5	11.5	27.8	29.5	-0.4	-0.7

latitudes of eastern Canada ( $\Delta 6$ ‰; Stephenson et al. in press).

Seasonal variation in  $^{13}\text{C}$  was common in autotrophs and primary consumers but  $\delta^{13}\text{C}$  of secondary consumers showed neither wide nor consistent seasonal variation (Fig. 3). This indicates integration of  $\delta^{13}\text{C}$  composition from diverse prey resources by predators, as well as differences in turnover rates of populations and tissue carbon. For instance, predators usually have long life spans exceeding 1 yr, compared to less than 3 mo for most primary consumers (Parsons et al. 1977).

#### Annual rates of primary production in estuarine and nearshore marine habitats of Hood Canal

The potential total net production of autotrophs in Hood Canal was estimated to be  $9.1$  to  $9.5 \times 10^7$  kg C  $\text{yr}^{-1}$  (Table 3). This production was mainly due to neritic phytoplankton production (63 to 66%), with benthic macroalgae in estuarine and littoral habitats accounting for the remainder. In comparison, we estimated total riverine inputs of DOC to be  $1.1 \times 10^5$  kg C  $\text{yr}^{-1}$ . Thus, in contrast to Naiman & Sibert (1978, 1979), who estimated that the major source of estuarine carbon in the Nanaimo River estuary was riverine DOC, our estimates for Hood Canal suggest that carbon input

from benthic primary production alone was several orders of magnitude greater than the total riverine inputs of DOC. We expect that primary production is the dominant carbon source of DOC and labile particulate detritus in these estuaries. Dissolved carbon may be transformed to POC through flocculation at the freshwater/saltwater interface (Sieburth & Jensen 1968; Gardner & Menzel 1974; Sholkovitz 1976; Mulholland 1981) and through the interaction of surface-active agents and air bubbles (Baylor & Sutcliffe 1963; Riley 1963, McIntyre 1974, Velimirov 1980), both common mechanisms in estuaries.

Estimates of extracellular release of DOC range from 5 to 70% of net primary production for phytoplankton (Antia et al. 1963, Hellebust 1965, Thomas 1971, Wallen & Geen 1971, Fuast & Chrost 1981), 1.5% for *Zostera marina* and 2.1% for associated epiphytes (Penhale & Smith 1977), 25% for salt-marsh vascular plants (Turner 1974), and 2 to 40% for benthic macroalgae (Sieburth & Jensen 1968, Sieburth 1969, Pregonall 1983). Applying these ranges of DOC release to the various estimates of net annual primary production (Table 3) suggests that a total of  $4.2$  to  $56.4 \times 10^6$  kg C  $\text{yr}^{-1}$  could be released annually by autotrophs within Hood Canal, a potential input two fold greater than riverine DOC.

Several factors potentially influencing release of

 Table 3. Estimated total annual net production ( $\text{gC yr}^{-1}$ ) of principal autotrophic producers in Hood Canal, Washington; see 'Methods' for details of calculations

Producer category	Annual incremental production ( $\text{gC m}^{-2} \text{yr}^{-1}$ )	Surface area ( $10^6 \text{m}^2$ )	Total annual net production ( $10^3 \text{kg C}$ )	% of total
Neritic phytoplankton	229	260.6	59,677	63-66
Benthic microalgae	143-266	20.6	2,943-5,477	3-6
<i>Zostera</i> eelgrass meadows	20-165	11.5	231-1868	1-2
Eelgrass epiphytes	1-8	11.5	12-92	1
<i>Carex</i> salt marsh	529	2.8	1,497	2
<i>Juncus-Potentilla</i> salt meadow	956-1,108	0.7	707-820	1
<i>Ulva-Enteromorpha</i> macroalgae	4,644	5.5	25,449	27-28
		Total	90,516-94,877	

extracellular organics from estuarine and littoral autotrophs might be tidal exposure and resubmergence. Pregnall (1983) indicated that an intense pulse (15 min in duration) of DOC occurs immediately after reimmersion of *Enteromorpha* sp. exposed to moderate desiccation during low tide. He also showed that benthic and epiphytic microbes utilized 40 % to 47 %, respectively, of the available DOC over a 3 h period after DOC release. Similarly, our studies of surface water foam in the Duckabush River estuary suggest that foam originates from DOC excreted by highly productive macrophytes – such as species of *Ulva*, *Enteromorpha*, *Zostera*, and associated epiphytes (Wissmar & Simenstad 1984). This corresponded well with our evidence that, in comparison to autotrophs and detritus deposits,  $\delta^{13}\text{C}$  of foam DOC and entrained POC ( $-15.1$  to  $-19.5$ ‰) overlapped more with the isotopic composition of most consumers and their predators (Fig. 5). We suggest that, although the chemical biological mechanisms of conversion of DOC and POC into forms utilizable as food by consumers have not been well defined, such transformations of organic matter from autochthonous autotrophs may constitute a significant food web pathway in estuarine and nearshore marine habitats of the region.

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