

The Dietary Importance of Kelp-Derived Detritus to Pelagic and Benthic Consumers along the West Coast of Vancouver Island, Canada

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Abstract

Stable isotope analysis was used to determine the relative dietary importance of kelp-derived detritus to plankton and benthic organisms along a gradient of kelp abundance driven by recovering sea otter populations along the west coast of Vancouver Island (WCVI), Canada. The study used region-specific kelp isotope values (δ^{13} C and δ^{15} N) and season-specific phytoplankton isotope values to model dietary contributions of kelp-derived detritus (KDD). In general, KDD contributions were moderate to high in most plankton size fractions during the summer and decreased during the winter, particularly in the kelp sparse region. Hypothesized regional and spatial (distance from the coast) differences in kelp detritus contributions to zooplankton were not evident. Modeled estimates of the KDD contribution to benthic invertebrates were high (>40%) and independent of the organism size, among regions and between seasons, with the exception of Astraea gibberosa in the kelp abundant region. Local oceanography, natural kelp isotope signature variation, and significant overlap between kelps' and blooming phytoplankton isotope values led to a large uncertainty in the assessed KDD contributions in benthic organisms. These results highlighted the importance of the KDD as a widespread and stable year-round food source in coastal kelp populated regions.

Keywords

Kelp-Derived Detritus, Primary Production, Stable Isotopes, Vancouver Island, Particulate Organic Matter, Kelp, Benthic Organisms, Primary Consumers, Food Web

1. Introduction

Identifying drivers of nearshore ecosystem productivity, diversity and stability contribute to our understanding of food web, community and ecosystem ecology. Detritus, as an autochthonous and allochthonous subsidy, is an important bottom-up driver of trophic structure and food web dynamics by influencing energy, carbon and nutrient budgets [1] [2]. Generally, the biomass of pelagic and benthic organisms is a function of local water column productivity [2]. However, the flow of subsidies across habitats can create diverse and subsidized food webs where local productivity is low [2]. The dispersal and concentration of subsidies can be affected by local surface and bottom currents [3], regional productivity, and the ratio of habitat perimeter to area [4].

Coastal marine consumers feed directly, or indirectly, on kelp- and/or phytoplankton-derived organic matter. Kelps (Phaeophycea: Order Laminariales) are large fleshy macroalgae that occupy low intertidal and shallow subtidal rocky reef habitats of temperate coastal marine ecosystems [5]. Kelps contribute substantially to nearshore primary productivity [6], with estimates as high as 3000 g C m⁻²·yr⁻¹ [6] [7] [8] [9]. In British Columbia, bull kelp (*Nereocystis luetkeana*) sporophytes are able to assimilate 1400 g C m⁻² during summer [10] and giant kelp (Macrocystis pyrifera) productivity estimates range from 460 to 1300 g C m⁻²·yr⁻¹ [6] [7] [11]. Most of the ocean-based photosynthesis occurs along coastal margins, which occupy only 0.1% of the total ocean area but average phytoplankton productivity in upwelling regions ranges from 200 to 973 g C m⁻²·yr⁻¹ [12] [13]. Phytoplankton concentrations along the west coast of Vancouver Island (WCVI) reach a maximum during late spring to mid-summer when solar radiation is high and nutrients are readily available from winter mixing of the water column and upwelling [14] [15]. The relative contribution to particulate organic matter (POM) of these two main primary production sources (phytoplankton and macrophytes) can vary spatially and temporally [16] [17] [18] [19]. However, the year-round presence of kelp-derived detritus (KDD) could be important in the food web dynamics, and system stability, and have considerable effects on trophic structure and biodiversity [20].

With over 80% of the annual kelp production dispersed to the surrounding shallow and deep-water ecosystems through both KDD and dissolved organic matter (DOM) [21] [22] [23] [24], kelp production is important to kelp associated communities [16] [25] [26]. It may also be transported great distances from source populations as suspended POM [17] [18] [27]. Kelp-derived detritus (KDD) can be detected at great depths [3] [24] and is known to subsidize island and nearshore communities [4] [16] [28]. However, some studies have called into question the suitability of kelp as a food source because of high C:N

ratios [29], high concentrations of secondary metabolites [30], and structural rigidness [31]. Bacterial degradation of KDD can lower C:N ratios and secondary metabolite content [32], thereby increasing its nutritional quality. Relative to phytoplankton, kelp-derived carbon can contribute similarly or more to the diets of nearshore benthic invertebrate filter-feeders with estimates as high as 90% [16] [33] [34]. More importantly, KDD can increase consumer growth rates by 2 to 5-fold, relative to pure phytoplankton diets [33], and may have important consequences for population dynamics and ecosystem productivity [20].

Carbon and nitrogen stable isotope analysis is a commonly used and powerful tool in food web ecology that quantifies the incorporation of potential food sources (e.g. phytoplankton and kelp) into consumers and estimates the average trophic level of consumers [35] [36]. Variability and uncertainty in source isotope values complicate this method and have possibly led to the overestimation of KDD contribution to organisms in previous studies [37]. In marine ecosystems, δ^{13} C values typically increase by 0‰ to 1‰ per trophic level [35] [36] [38] [39]. Changes in δ^{15} N values with each trophic level transfer vary with tissue type [40] and feeding mode [39]. The average increase of δ^{15} N values with trophic level ranges from 1.4‰ for consumers of invertebrates [39] to 4‰ for filter-feeders [34].

The research aims of this study were twofold: first, to assess the KDD contributions to the tissues of plankton and benthic invertebrates near and offshore in a ~20-fold kelp productivity gradient resulting from sea otter population recovery along the WCVI; second, to investigate seasonal variability in the KDD contributions to pelagic and benthic invertebrates along the WCVI.

2. Materials and Methods

2.1. Study System

The research was conducted along the west coast of Vancouver Island (WCVI), British Columbia, Canada (Figure 1), situated at the northern end of the California Current Large Marine Ecosystem [41]. Complex oceanographic processes characterize this coastline. Seawater over the outer shelf, demarcated by a 100 m isobath, flows pole-ward during the winter but changes direction from northwestward to south-eastward during the spring with the seasonal onset of the coastal upwelling, and reverses again in the fall [42] [43]. The buoyancy driven Vancouver Island Coastal Current (VICC) dominates the flow over the inner (<100 m depth) continental shelf. This current flow pole-ward year-round but can be reversed in the upper 50 m by strong northwest winds that occur during upwelling favouring conditions in summer or during cold outflow conditions during winter [44].

Sea otters are voracious consumers and exert strong top-down control on many benthic invertebrates, most notably sea urchins of *Strongylocentrotus* genus. In the absence of sea otters, hyper-abundant urchin populations devastate macroalgal populations resulting in widespread urchin "barrens" [45]. In the



Figure 1. Sampling regions along the west coast of Vancouver Island (WCVI). The red lines represent summer transects (0 - 30 km). During winter, sampling was only to 10 km from the kelp forest in the kelp abundant and kelp sparse regions, and only at 4 and 8 km in the kelp intermediate region. Sampling transects indicated by KA-T1, KA-T2, etc.

presence of sea otters, sea urchins are heavily preyed upon which is followed by re-establishment of extensive kelp forests that support diverse and productive ecosystems [5] [46] [47]. As a result of the North Pacific maritime fur trade, sea otters were extirpated from the coast of British Columbia by 1929 [48]. However, between 1969 and 1972 eighty-nine animals were reintroduced to the northwest coast of Vancouver Island from western Alaska [49]. This population has increased rapidly and expanded north- and southwards along the WCVI [50] [51]. At the time of sampling, sea otters were distributed from the northern tip of Vancouver Island southward to an area just south of Clayoquot Sound (**Figure 1**) and have dramatically increased kelp populations along this coastline [52] [53].

2.2. Experimental Design

Three research cruises were conducted off the WCVI between July 2009 and July 2010. The study region included three large sounds that were characterized by large differences in kelp biomass corresponding to the sea otter occupation time [52] [53]. A "space-for-time substitution" approach [54] was used to take advantage of sea otter reintroduction and range expansion along the WCVI. Kyu-quot Sound (**Figure 1**), in the north (nearest to where sea otters were first rein-

troduced and re-established), has the highest kelp abundance and is hereafter referred to as "kelp abundant". Clayoquot Sound is hereafter referred to as "kelp intermediate", and Barkley Sound, with the lowest kelp abundance, is referred to as "kelp sparse" [27]. The kelp abundant and kelp sparse regions were approximately 170 km apart. Two transects located 10 to 12 km apart originated within kelp forests at the mouth of each sound and ran perpendicular to the coastline with sampling at 0, 0.5, 1, 2, 4, 10 and 30 km from the kelp forest. In the "kelp sparse" and "kelp abundant" regions summer sampling occurred between July 18th and 23rd, 2009; summer sampling off the kelp intermediate region was conducted between July 27th and July 28th, 2010. Winter sampling only took place off the kelp abundant and kelp sparse regions between January 23rd and 31st, 2010 due to inclement weather. It was assumed that sampled organisms were feeding on KDD produced within their respective sounds.

Regional kelp and phytoplankton isotope value estimates (δ^{13} C and δ^{15} N), see **Table 1** and [27] were used in a Bayesian mixing model (MixSIR) to quantify the percent relative contribution of kelp-versus phytoplankton-derived detritus to plankton and benthic invertebrates. It was predicted that during summer and winter nearshore and offshore organisms in the high kelp productivity, *i.e.* kelp abundant, region would have higher proportions of KDD, in comparison to a region where sea otters are absent and kelp productivity is low.

Size-fractionated plankton stable isotopes

At each station, surface size-fractionated plankton: $63 - 125 \mu m$, $125 - 250 \mu m$, $250 - 500 \mu m$, and $500 - 2000 \mu m$ were collected. One surface tow was performed at each distance by towing a 63 μm net horizontally for 5 to 10 minutes at approximately 1 knot. All samples were size-fractionated and frozen in a -20° C freezer at sea. Some samples did not have all size-fractions analyzed due to lack of sample volume.

		Summer		Winter	
POM size fraction	Phytoplankton type	Mean d ¹³ C ± SD (‰)	Mean ð⁵N ± SD (‰)	Mean δ ¹³ C ± SD (‰)	Mean ∂ ¹⁵ N ± SD (‰)
20 - 63 µm POM	Blooming phytoplankton 20 - 63 μm	-19.03 ± 0.87 (n = 22)	6.83 ± 0.63 (n = 22)	No bloom	No bloom
	Non - blooming phytoplankton 20 - 63 μm	-21.41 ± 1.48 (n = 10)	5.59 ± 1.21 (n = 10)	-22.07 ± 1.37 (n = 19)	6.27 ± 0.97 (n = 19)
0.7 - 20 µm POM	Blooming phytoplankton 0.7 - 20 μm	-21.49 ± 0.67 (n = 22)	6.66 ± 1.29 (n = 22)	No bloom	No bloom
	Non - blooming phytoplankton 0.7 - 20 μm	-22.37 ± 1.10 (n = 10)	6.34 ± 1.03 (n = 10)	-23.84 ± 0.68 (n = 20)	6.87 ± 0.91 (n = 20)
Oceanic Total POM (>0.7 μm)	Oceanic phytoplankton (37, 48 and 118 km offshore-used for summer and winter)	-25.50 ± 1.38 (n = 3)		3.83 ± 1.66 (n = 3)	

Table 1. Summer and winter phytoplankton δ^{13} C and δ^{15} N values ($\% \pm$ SD) used in the MixSIR isotope mixing model program for zooplankton and benthic organisms.

In the laboratory, all samples were thawed, randomly sub-sampled in triplicates to identify and enumerate major plankton groups within each size fraction. Samples were then dried in a *Fisher Scientific* oven at 50°C for at least 24 hours, ground into a powder and packaged into 5×8 mm tin capsules for stable isotope analysis. KDD was visible microscopically, especially in the 63 - 125 μ m and 125 - 250 μ m size fractions, but was difficult to quantify and is therefore not included.

2.3. Benthic Organism Stable Isotopes

Benthic dredging was performed with a 60 cm by 30 cm dredge towed along the bottom for 5 to 10 minutes at approximate speed of 1.5 to 2 knots. This was done at all stations except within the kelp forests (0 km) and at some 30 km stations that were too deep to sample. Samples were immediately frozen in a -20° C freezer. In the laboratory, benthic samples were thawed, identified to lowest possible taxonomic level, and rinsed with distilled water. Red turban snails (*Astraea gibberosa*), hermit crabs (Infraorder Anomura) and pink scallops (*Chlamys* spp.) were the only organisms consistently abundant enough to include in analyses. The tissues of these common species/groups (muscle or, whole body minus the shell) were dried for at least 24 hours at 50°C. Dried samples were ground with a mortar and pestle or digital amalgamator, and packaged in tin capsules for carbon and nitrogen stable isotope analysis. Benthic samples from within the kelp forests were collected using SCUBA during the summer of 2009.

To test for possible acidification effects on isotope values, 7 hermit crabs were acidified with 0.1 M HCl from an eye-dropper, while the remaining 61 remained untreated. The number of drops varied from 5 to 17 and was applied until CO_2 gas stopped being released, *i.e.* stopped bubbling [55]. The sample was then re-dried without rinsing to minimize the loss of DOM and ground into a powder again [56] [57].

To test for possible lipid extraction (*i.e.* defatting) effects on red turban snail stable isotope values, five whole snails were split in half and one half was defatted, and the other remained untreated, following the method of Bligh and Dyer [58] and then lightly rinsed with distilled water on 0.7 μ m Whatman GF/F filters with light suction. Samples were re-dried and ground into a powder. Additionally, C:N ratios were used to check for excess lipids in both cases.

All isotope analyses were conducted at IsoEnvironmental in Grahamstown, South Africa. Abundances of naturally occurring carbon and nitrogen stable isotopes were determined on either a Europa Scientific Integra IRMS or Europa Scientific 20-20 IRMS linked to an ANCA SL Elemental Analyser. Beet sugar and ammonium sulphate were used as internal standards, calibrated against several International Atomic Energy Agency (IAEA) reference materials. Results are expressed in the standard delta notation, as $X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X = element in question and R = ratio of the heavy over the light isotope. Repeated analyses of homogeneous material yielded a δ^{13} C standard deviation of 0.11‰ and a δ^{15} N standard deviation of 0.16‰.

2.4. Data Analyses

<u>Size-fractionated plankton</u>: Linear regression was used to assess the relationship between distance from the kelp forest and plankton δ^{13} C values.

<u>Benthic organisms:</u> Where assumptions were met, paired t-tests were used to test for effects of acidification and lipid extraction of benthic organisms. In cases of non-normality or heterogeneous variance, Wilcoxon Matched pairs tests were used. Linear regression was used to assess relationships between stable isotope values and organism size (length or width). All statistical analyses were performed in R [59].

MixSIR: We used the isotope mixing model program MixSIR (version 1.0, [60]) to determine percent KDD contribution to plankton and benthic organisms. MixSIR is a graphical user interface that performs Bayesian analysis of stable isotope mixing models using Hilborn sampling-importance-resampling (SIR) algorithm [61]. The benefits of a Bayesian approach to stable isotope mixing models include: 1) accounting for uncertainty in source stable isotope values, 2) accounting for uncertainty in the estimates of source contributions as there is underlying uncertainty in the mixture and source isotope values, 3) determining a unique solution when more than two sources are present [62] [63]. Outputs of the program include a median percent contribution of all sources included and their respective 95% confidence intervals. The degree of overlap between confidence intervals defines the probability that two estimates are the same. Source δ^{13} C fractionation and fractionation standard deviations were set to 0% for summer and winter plankton. Source δ^{15} N fractionation and fractionation standard deviations were set to 1.47‰ \pm 0.39‰, while for winter it was 2.32‰ \pm 0.46‰. For other consumers the values used were 0.5‰ \pm 0.13‰ for δ^{13} C and $2.2\% \pm 0.3\%$ (for primary consumers), $2.13\% \pm 0.18\%$ (for omnivores and detritivores) and 3.3‰ ± 0.26‰ (for higher consumers) for δ^{15} N [64]. These values will be justified in the "Results" section.

3. Results

3.1. Surface Plankton Carbon Stable Isotopes

<u>Summer</u>: Phytoplankton species composed the largest proportional abundance of the 63 - 125 μ m plankton (0.85) surface tows and 0.35 of the 125 - 250 μ m fraction (**Figure 2(A)**). Different growth stages of copepods constituted the largest proportional abundance of plankton > 125 μ m with proportions of 0.39, 0.45, and 0.47 for the 125 - 250, 250 - 500 and 500 - 2000 μ m size fractions, respectively (**Figure 2(A)**). Cladocerans made the second largest contributions to both the 250 - 500 μ m (0.35) and the 500 - 2000 μ m fractions (0.17). Decapods were the third largest contributor to the 500 - 2000 μ m plankton (0.14).

Among regions differences were not significant in surface plankton δ^{13} C values



Figure 2. Summer (panel A) and winter (panel B) proportional plankton by size fraction. Plankton groups that constituted < 0.5% for all size fractions were removed.

for all size fractions. Furthermore, there were no significant differences between size fraction δ^{13} C values within any of the regions. When pooling samples from all three regions there were differences among size fractions. The 63 - 125 µm size fraction was more enriched than all other size fractions (df = 4, F = 12, p < 0.05 in all cases) which is likely due to the high concentration of enriched KDD in the 63 - 125 µm fraction that was seen microscopically. All size fraction means and standard deviations are available in Table 2.

The 125 - 250 µm fraction along transect 2 in the kelp abundant region had decreasing δ^{13} C values with distance from the kelp forest (R² = 0.73, p = 0.03) (**Figure 3**). Along transect 6 in the kelp intermediate region the 250 - 500 µm fraction had decreasing δ^{13} C values with distance (R² = 0.99, p = 0.06). Transect 4 in the kelp sparse region had decreasing δ^{13} C values with distance for three size fractions as well (63 - 125 µm: R² = 0.87, p = 0.007; 125 - 250 µm: R² = 0.97, p < 0.001; 250 - 500 µm: R² = 0.59, p = 0.04) (**Figure 3**). Overall, 6 of the 20 size fraction transects showed decreasing δ^{13} C values with distance from the kelp forest.

<u>Winter:</u> Proportionally, phytoplankton species made the largest contribution to the 63 - 125 μ m (0.82) and the 125 - 250 μ m (0.54) surface tows (**Figure 2(B)**). Copepods were the second most prevalent in the 125 - 250 μ m fraction at 0.37.

Table 2. Summ	er and winte	r size-fractionated	surface plankto	on mean	δ^{13} C and	δ^{15} N val-
ues (‰ ± SD).						

	Summer		Winter		
Size fraction (µm)	Mean δ ¹³ C (±) SD ‰	Mean δ ¹⁵ N (±) SD ‰	Mean δ ¹³ C (±) SD ‰	Mean δ ¹⁵ N (±) SD ‰	
63 - 125	-18.16 ± 0.98	6.94 ± 0.93	-20.40 ± 2.32	8.56 ± 0.99	
125 - 250	-19.14 ± 0.93	8.06 ± 1.05	-21.97 ± 1.17	10.67 ± 0.52	
250 - 500 μm	-19.45 ± 0.98	8.81 ± 1.35	-22.13 ± 1.66	10.59 ± 0.60	
500 - 2000 μm	-19.16 ± 1.15	8.39 ± 1.79	-21.49 ± 1.74	11.35 ± 1.24	



Figure 3. Summer percent kelp-derived detritus contribution (median \pm 95% C.I.) to surface 63 - 125 µm, 125 - 250 µm, 250 - 500 µm, and 500 - 2000 µm plankton for all three regions. Each point is a single sample (n = 1). Kelp abundant region transects are represented by KA-1 and KA-2, kelp intermediate transects are represented by KI-1 and KI-2, and kelp sparse transects are KS-1 and KS-2. For display purposes, points are jittered horizontally.

They constituted almost the entire $250 - 500 \ \mu\text{m}$ zooplankton with a proportion of 0.94 and were the most prevalent in the 500 - 2000 μm fraction (0.75). Veliger larvae made a minor contribution to the 63 - 125 μm fraction at 0.15 and less so to the 125 - 250 μm tow (0.07). Decapod and fish larvae constituted 0.1 and 0.08 of the 500 - 2000 μm plankton, respectively (Figure 2(B)).

There were no differences in carbon enrichment for any size fractions among the three regions and there were no within region differences among the plankton size fractions. Furthermore, when kelp abundant and absent regions were combined there were no differences with respect to δ^{13} C values among size fractions (kelp intermediate region was not sampled). The kelp sparse region plankton mean δ^{13} C values ranged from -19.80‰ for 63 - 125 µm plankton to -22.39‰ for the 250 - 500 µm fraction. The kelp sparse region plankton means ranged from -19.76‰ for the 500 - 2000 µm plankton to -22.20‰ for 125 - 250 µm plankton. When all three regions combined, there were no differences in size fraction δ^{13} C values. All size fraction means and standard deviations are available in **Table 2**.

The 125 - 250 µm plankton fraction along transect 1 in the kelp abundant region had significantly decreasing δ^{13} C values with distance from the kelp forest (R² = 0.68, p = 0.04) (**Figure 4**). The 63 - 125 µm fraction along transect 3 in the kelp sparse region also had decreasing δ^{13} C values with distance from the kelp forest (R² = 0.71, p = 0.04), while transect 4 within this same region was more enriched in ¹³C with distance (R² = 0.67, p = 0.047). The 125 - 250 µm plankton along transect 3 had decreasing δ^{13} C values with distance (R² = 0.81, p = 0.04) (**Figure 4**).

3.2. Surface Plankton Nitrogen Stable Isotopes

<u>Summer</u>: With respect to plankton $\delta^{15}N$ values, the 500 - 2000 µm size fraction was more enriched in the kelp abundant region compared to the kelp sparse region (p = 0.049). The kelp abundant region's mean $\delta^{15}N$ values ranged from 8.32‰ for 125 - 250 µm to 9.75‰ for 500 - 2000 µm plankton. The kelp intermediate region's mean values ranged from 7.23‰ for 63 - 125 µm plankton to 8.08‰ for the 250 - 500 µm fraction. The kelp sparse region ranged from 6.59‰ for the 63 - 125 µm fraction to 8.86‰ for the 250 - 500 µm fraction. There were no significant within region $\delta^{15}N$ differences among the plankton size fractions. When all three regions were combined, the 63 - 125 µm was enriched in ¹⁵N when compared to all other size fractions (df = 4, F = 12, p < 0.001 in all cases), but no other fractions were different. All size fraction means and standard deviations are available in **Table 2**.

<u>Winter</u>: During the winter, there were no significant differences in plankton $\delta^{15}N$ values among the regions. The otter present region 63 - 125 µm plankton was depleted relative to the 125 - 250 µm and 500 - 2000 µm fractions (p = 0.04 and p < 0.01, respectively). There were no other size fraction differences within this region. Within the kelp sparse region, the 63 - 125 µm fraction was depleted



Figure 4. Winter percent kelp-derived detritus contribution (median \pm 95% C.I.) to surface 63 - 125 µm, 125 - 250 µm, 250 - 500 µm, and 500 - 2000 µm plankton for otter-present and absent regions. Each point is a single sample (n = 1). Kelp abundant region transects are represented by KA-1 and KA-2, kelp intermediate transects are represented by KI-1 and KI-2, and kelp sparse transects are KS-1 and KS-2. For display purposes, points are jittered horizontally.

in ¹⁵N when compared to all other fractions (df = 4, F = 32, p < 0.001 in all cases); however, no other size fractions were different. The kelp sparse region's plankton mean δ^{15} N values ranged from 9.25‰ for the 63 - 125 µm fraction to 11.12‰ for the 500 - 2000 µm fraction while the kelp sparse region's values ranged from 7.99‰ for the 63 - 125 µm plankton to 11.69‰ for the 500 - 2000 µm fraction. All size fraction means and standard deviations are available in **Table 2**.

3.3. Trophic Level Isotope Fractionation

Although summer 63 - 125 μ m plankton δ^{13} C was more enriched than the 125 - 250 μ m, 250 - 500 μ m and the 500 - 2000 μ m fractions, there was no pattern or

step-wise enrichment with size fraction. The mean ¹³C fractionation (±SD) was $-0.34\% \pm 1.51\%$ (*i.e.* values were more depleted with increasing trophic level) between 63 - 125 µm and these two fractions. There was no difference among winter plankton δ^{13} C fractions. Considering these factors, source δ^{13} C fractionation and standard deviation were "0" for summer and winter.

Because the summer and winter plankton δ^{15} N values for the 63 - 125 µm size fraction were depleted when compared to all larger size fractions, and no other fractions were significantly different, a mean fractionation (±SD) for each season was calculated by subtracting the mean of each fraction with the 63 - 125 µm within its respective season. For summer plankton, this value was 1.47‰ ± 0.39‰, while for winter it was 2.32‰ ± 0.46‰.

For benthic organisms' isotope fractionation with trophic level, values from [39] were used as this work applied to marine organisms, and had separate values for herbivores, organisms raised on invertebrates, etc. (δ^{13} C: 0.5‰ ± 0.13‰; herbivores - δ^{15} N: 2.2‰ ± 0.3‰, raised on inverts - δ^{15} N: 1.4‰ ± 0.21‰).

3.4. Kelp-Derived Detritus Incorporated by Plankton

<u>Summer</u>: During the summer in the kelp abundant region, the median KDD contributions to plankton ranged from 21% to 81% for all size fractions (**Figure 3**). Median KDD contributions to this fraction remained high and constant with distance from the kelp forest. The two largest fractions were similar in this regard with the exception of a few distances where the median KDD contribution was much higher, such as 1 km along the 250 - 500 μ m fraction. For example, for the 250 - 500 μ m fraction at 1 km the median contribution was 81% (**Figure 3**). Within a size fraction there was large overlap in confidence intervals with distance and between transects at the same distance except for the 500 - 2000 μ m fraction where there was greater variability with distance but the two transects were generally similar.

In the kelp intermediate region, median KDD contributions to plankton varied between 16% and 55% for all size fractions. It was the highest in 63 - 125 μ m plankton with the median KDD contributions ranging from 47% to 55% and remained moderately high and constant with distance from the kelp forest (**Figure 3**). Median KDD contributions slightly decreased with increasing fraction size. Samples greater than 500 μ m were not collected for this region.

In the kelp sparse region, median percent KDD contribution to plankton was highly variable with distance and between transects for all size fractions of plankton ranging from low (16%) to very high (81%) (**Figure 3**). Median contributions to the 63 - 125 μ m fraction were moderate to very high and increased with distance from the coast. Median contributions to 125 - 250 μ m plankton had large uncertainty at a number of distances (**Figure 3**). This led to large overlap in percent contributions between the two transects for this size fraction. Large confidence intervals were present for the 250 - 500 and 500 - 2000 μ m plankton. This led to a large range of possible contributions across the region for

these two size fractions.

<u>Winter</u>: In the kelp abundant region, the median KDD contributions to plankton ranged from 4% to 68% for all size fractions (**Figure 4**). Median KDD contributions to the 63 - 125 μ m fraction remained high and constant with distance from the kelp forest with large overlap in confidence intervals with distance and between transects. For the 125 - 250 μ m plankton median KDD contributions decreased moderately with distance and had relatively low overlap in confidence intervals between 0 and 10 km, indicating that there is a low probability that the contributions were similar between these two distances. The 250 - 500 μ m had smaller medians (13% - 29%) relatively to the two smaller fractions and only decreased slightly with distance within the fraction. The 500 - 2000 μ m fraction was highly variable (6% - 41%) with distance and had confidence intervals that did not overlap at certain distance.

During the winter in the kelp sparse region, KDD median contributions to plankton were from 4% to 80% for all size fractions (**Figure 4**). The 63 - 125 μ m fraction had a strong contrast with respect to KDD contribution between transects as transect 3 medians decreased, from 80% to 27%, with distance and transect 4 medians increased (from 6% to 47%, **Figure 4**). In the 125 - 250 μ m plankton, the median KDD contribution decreased with distance and had no overlap in confidence intervals between 0 and 10 km, while along the transect 4, KDD contributions remained low and constant with distance. The 250 - 500 μ m plankton showed a similar decline in contribution with distance. The precipitous decline (from 73% to 20%) was observed between 0 and 0.5 km. The 500 - 2000 μ m fraction had no trends and was highly variable with distance. The median KDD contributions were from 15% to 79% (**Figure 4**).

3.5. Kelp-Derived Detritus Incorporated by Benthic Organisms

<u>Astraea</u>: Paired defatted and untreated Astraea gibberosa samples showed no differences in δ^{13} C and δ^{15} N values. Further analyses were only on the untreated samples.

Astraea mean lengths (±SE) differed among regions (df = 2, F = 29, p < 0.001). The kelp abundant region individuals (3.43 ± 0.19 cm) were smaller in size compared to the kelp intermediate (5.4 ± 0.15 cm) and absent regions (5.59 ± 0.23 cm; p < 0.001 in both cases). When all regions were pooled, Astraea δ^{13} C and δ^{15} N values increased with length (R² = 0.47, p < 0.001, and R² = 0.11, p = 0.03, respectively).

There was considerable within region δ^{13} C variation among sampling sites (df = 7, F = 9, p < 0.001) which did not allow samples from within the same region to be pooled for modeled KDD contribution estimates because it led to bimodal posterior probability distributions. This variation did not exist for δ^{15} N values.

Percent KDD incorporated by *Astraea* showed among and within region variation with large differences in percent KDD contribution among all region (**Figure 5**). *Astraea* collected in the kelp abundant region had 0% to 27% (range



Figure 5. Percent kelp-derived detritus contribution (median \pm 95% C.I.) to the diet of *Astraea gibberosa* (red turban snail) during the summer. Within region sites are represented by different symbols. Samples sizes from left to right are Grassy: 1, Kamils: 7, Morton: 3, Thorton: 2, Chetarpe: 5, La Croix: 1, D14: 5, G.F.I.: 3, Prasiola: 5 and Seppings: 11.

of medians) of KDD subsidy. In the kelp intermediate region, KDD contribution medians ranged from 64% to 71%. The kelp sparse region samples were composed of the largest percent KDD with median contributions from 68% to 97% (**Figure 5**). Seppings Island had the highest median percent KDD contribution (97%) compared to any sampling site.

<u>Chlamys</u>: When all three regions were combined, scallop summer δ^{3} C values increased with shell width (R² = 0.43, p < 0.001). This led to modeling KDD contribution to scallops grouped by shell width. Generally, during the summer percent KDD contribution to pink and spiny scallops was higher in the kelp sparse region, especially in the larger size classes (**Figure 6**). When all otter present-region size classes were combined, median percent KDD contributions were from 25% to 60% with the smallest size class (1.1 - 1.5 cm) having the largest median percent contribution of 60%. Only one size class was collected from the kelp intermediate region during the summer. This size fraction (2.6 - 3 cm) had a percent KDD contribution of 62%. Median percent KDD contributions to the kelp sparse region scallops ranged from 75% to 92%. There was a trend towards increasing KDD contribution with size-class. Scallops of the smallest size class (1.1 - 1.5 cm) had a median percent contribution of 62% and the largest size class (3.6 - 4 cm) had a contribution of 81%.

During the winter, scallops were only retrieved during dredging in the kelp abundant region. Percent KDD contribution to these scallops ranged from 40 to



Figure 6. Percent kelp-derived detritus contribution (median \pm 95% C.I.) to the diet of *Chlamys* sp. (pink scallops) by shell width (cm). Winter samples were only retrieved from the kelp abundant region. Sample sizes from left to right are: 1, 1, 9, 1, 1, 3, 1, 2, 4, 3, 1, 6, 7 and 1. Samples of the same size class are jittered for display purposes.

73% and there was no trend of increasing contribution with larger size classes (**Figure 6**). There was a trend of higher contribution during the winter relative to the summer in the kelp abundant region.

<u>Anomurans</u>: Paired t-tests of hermit crab samples that were split in half and one half was treated with acid and the other half left untreated showed no change in δ^{13} C and δ^{15} N values. Further analyses were only performed on untreated samples.

Hermit crab δ^{13} C and δ^{15} N values increased with carapace width during the summer (R² = 0.40, p < 0.001 and R² = 0.14, p < 0.001, respectively) and during the winter with δ^{13} C (R² = 0.35, p = 0.003). Therefore, modeled KDD contribution estimates were determined for hermit crabs grouped in 0.1 cm bin intervals.

During the summer in the kelp abundant region, the two smallest size classes (0.2 and 0.3 cm) had the lowest contribution of KDD with the 0.2 cm size class having a median percent contribution 47%. There was a trend towards increasing KDD contribution with increasing size (little confidence interval overlaps) as

the 0.8 cm size class having a possible median contribution of 76% (**Figure 7**). In the kelp intermediate region, median percent

KDD contributions to hermit crabs were from 56% to 79%. The 0.3 cm size class had the lowest contribution at 56%, while the 0.4 cm size class had the largest at 79%. In the kelp sparse region, the percent KDD contribution was high in all size classes. The median contributions were from 69% to 89% with 3 size classes having possible KDD contributions \geq 90% for 3 size classes (0.3, 0.4 and 0.6 cm). The kelp sparse region 0.3 and 0.4 size classes had a larger percent KDD contribution than the similar kelp abundant region size classes.

During the winter, samples were only obtained in the kelp abundant and absent regions. Possible percent-kelp derived detritus contributions remained as high as during the summer. The median percent contribution for the 0.7 cm size class in the kelp abundant region was 73% (**Figure 7**), which was within the confidence intervals for most summer size-classes. In the kelp sparse region, the



Figure 7. Percent kelp-derived detritus contribution (median \pm 95% C.I.) to the diet of hermit crabs (Anomurans) by shell width (cm) for summer and winter along the kelp abundance gradient. Samples are pooled from a variety of distances from the kelp forests. Summer sample sizes from left to right; kelp abundant: 3, 5, 6, 1, 2, 1, 1; kelp intermediate: 1, 4, 5, 3, 2, 1; kelp absent: 2, 14, 2, 1, 4, 1, 1. Winter sample sizes from left to right; kelp abundant: 1; kelp sparse: 2, 1, 5, 6, 3, 2, 1. Samples of the same width are jittered for display purposes.

median percent KDD contributions were from 69% to 91% when all size classes were combined. The 0.2 cm size class had the lowest contribution 69% and the 0.5 cm size class had the highest contribution at 91%. However, in general, there was high overlap in confidence intervals among most size-classes.

4. Discussion

Contrary to expectation, regional differences in kelp contribution to primary consumers were not detected despite a 20-fold difference in the giant kelp (*Macrocystis pyrifera*) abundance between regions. Furthermore, no consistent decrease in kelp contribution to primary consumers with increasing distance from source kelp forests within any region was evident. Nevertheless, during the winter, the KDD contribution to plankton was lower than during the summer with pronounced variability between regions and along transects away from kelp forests. The KDD contribution to benthic organisms was also high in all regions during both summer and winter. The exception was Astraea in the kelp abundant region where KDD contribution was on average more than 3-fold lower than the kelp sparse region.

4.1. Plankton δ^{13} C Variability

In general, some size fractions of plankton along a particular transect during both summer and winter showed significant decreases in δ^{13} C values with the distance from kelp forests. This was expected in the kelp abundant region because of higher kelp production, hence lateral transport and faster dissipation of the ¹³C enriched organic matter away from the kelp forest. The shelf currents may facilitate this as shown for the POM [27] [64]. The coastal upwelling and downwelling conditions could further control the KDD contribution to the POM [65]. The kelp intermediate region only had decreasing δ^{3} C values with distance from the kelp forest for one (250 - 500 µm) size fraction along both transects. While, this may reflect the inability of small plankters of this fraction to feed on kelp-derived production, other explanations are likely in play. For example, accumulation of lipids that are ¹³C depleted [66] may affect their isotopic ratios [67]. Plankton δ^{13} C from the kelp sparse region was more depleted along one transects oceanward for all plankton smaller than 500 µm. This coincides with their food source (surface POM) being more depleted with distance along this transect [27]. On the other hand, along the nearby transect, plankton remained relatively enriched in ¹³C with distance from the kelp forest. This may result from the presence of KDD or blooming phytoplankton in these samples [27] [68]. Wide confidence intervals, due to similar isotopic values of KDD and blooming phytoplankton as well as highly dynamic oceanographic environment in this region do not allow answering this question with high certainty [22] [27] [69].

4.2. Plankton δ^{15} N Variability

Plankton $\delta^{15}N$ variability is affected by the $\delta^{15}N$ variability of its food sources

[70], isotope fractionation during assimilation [71], excretion [72], and their trophic level [36] [73]. A wide variety of animals are enriched in ¹⁵N by ~3.4‰ relative to their diet and trophic position can be estimated from their δ^{15} N values [36] [39].

KDD can support higher densities of consumers at higher trophic levels [4] [20] [52]. In this study, only $\delta^{15}N$ differences within plankton size fractions were found during the summer between the kelp abundant and absent regions. For example, the 500 - 2000 µm size fraction within the kelp abundant region was 1.9‰ enriched compared to <250 µm size fractions. However, this is likely not biologically significant, nor is it prevalent enough to conclude whether or not kelp abundant region plankton are feeding at higher trophic levels. There were no within-region differences among $\delta^{15}N$ values of plankton size fractions, which inhibits the conclusion that larger size fractions of plankton were feeding at higher trophic levels [74].

4.3. Incorporation of Kelp-Derived Detritus by Plankton

KDD contribution to majority size fractions of zooplankton was moderate to high during the summer in all regions. Contrary to our predictions but in agreement with the surface POM, no regional and along transects differences in kelp contribution were evident. The two largest zooplankton size fractions (250 - 500 and 500 - 2000 µm) showed the largest spatial variability. Furthermore, uncertainties in the KDD contribution estimates were greatest for the kelp sparse region. This, however, could be misleading to how important KDD is in this region because the high uncertainty in the modeled estimates likely resulted from the inclusion of *Nereocystis* being the major, and possibly the only, kelp species contributing to POM. This species had a mean δ^{13} C value of -18.31%, which was the closest to blooming phytoplankton values of -18.91% than in any other region [27]. Similarity in source isotope values leads to uncertainty (*i.e.* large confidence intervals) in modeled contribution estimates [62]. In general, for a given distance and region, median KDD contributions to plankton were similar to median KDD contributions to POM [27].

During winter, there was a greater spatial variability within regions and pronounced differences in detritus contributions between transects. In general, the KDD contribution was similar during both seasons. Nevertheless, during the winter, kelp contribution was patchier, especially in the kelp sparse region.

These results indicate that the moderate to high KDD contribution to plankton year-round at all distances offshore of the kelp abundant region is likely due to the oceanographic conditions specific to this region, that alter the abundance of KDD. Although our estimates are potentially high, it was predicted that the KDD contribution would be consistently higher, particularly during upwelling events [64] [65] [69]. Summer growth and accumulation of kelp biomass are released into the environment through senescence and dissolved organic carbon [23] [75]. Winter storms accelerate the breakdown of kelp and release the biomass gained in the summer during the winter [5] [69]. Harris [76] postulated that the water beyond the continental shelf off northern Vancouver Island was similar to shelf water due to the narrowing (to \sim 5 km) continental shelf along the northern part of Vancouver Island. Wind driven upwelling filaments and eddies regularly form off Brooks Peninsula, just north of the kelp abundant region, moving a significant proportion of the nutrients, phytoplankton and zooplankton off the shelf into the adjacent pelagic environment [44] [77]. Similarly, this mechanism would draw the nearshore KDD away from shore. During our study, we collected total POM near the ocean floor in the kelp abundant region (data not presented here), with ¹³C depleted by 1.6% relative to surface POM during the summer and 1.1‰ during the winter. Harris [76] explained the SST gradient along the WCVI, with lower temperatures of the kelp abundant region, as a result of the narrow shelf because upwelled water off the kelp abundant region has a shorter distance to travel and less time to warm before being transported off the shelf. This could have implications for water residence time over the shelf and upwelled water and particles with depleted ¹³C being in the nearshore area depleting the surface POM δ^{13} C. Although KDD production may be relatively high in this region it is possible that the retention of this production in the region is reduced by regional oceanography and/or diluted by upwelled, ¹³C depleted POM [27].

4.4. Incorporation of Kelp-Derived Detritus by Benthic Invertebrates

KDD incorporated by the snail Astraea gibberosa differed greatly within regions and among sites within the kelp abundant region and therefore could not be combined for mixing model estimates. Individuals from Kamils Island had the highest KDD (median 27%) contribution compared to other sites (\leq 5%). Surprisingly, the KDD contribution to the other two regions was high with a median contribution of 68% - 97%. One explanation for these results may be that abundant kelp populations in the kelp abundant region is also associated with abundant understory red algae in the kelp abundant region [78]. Red algae are highly depleted in ¹³C (~-30‰; [79]) and could be an abundant food source in the kelp abundant region leading to the low contribution of kelp-derived production to these organisms, or, as some have suggested, there is superiority in mixed diets compared to single foods [80] [81] [82]. Second, the individuals in the kelp abundant region were approximately 2 cm smaller and thus more ¹³C depleted. Sea otter populations at equilibrium density are thought to be food limited [83] and changes in prey availability will influence sea otter foraging behavior [84]. Sea otters preferentially feed on sea urchins when available [46] [84]. However, in areas where otters have been established for quite some time large urchins are absent [46] and otters consume less preferred prey that has become more energetically profitable [85] [86]. It is therefore plausible that in the kelp abundant region large Astraea heavily preyed upon and reduced in abundance. Finally, smaller Astraea may eat less kelp tissue but consume diatoms and bacteria on kelp blades that are relative ¹³C depleted [33] [87] [88]. Also, smaller *Astraea* could be structurally limited due to smaller or weaker mouth parts and not be able to consume, or possibly even digest kelp, due to its rigidness [31].

In general, modeled estimates of KDD contribution to benthic invertebrates were similar, among regions and between seasons. The incorporation of KDD by *Calliostoma* was similar and high (>60%) for all regions. This was not the case for *Chlamys* spp. as kelp sparse region scallops had higher contributions of KDD than the kelp abundant region for most size classes. The kelp intermediate region was midway between the other two regions. During the winter there was a trend towards a higher contribution of KDD for all size classes of scallop in the kelp abundant region. Hermit crabs showed a similar pattern except for the two smallest size classes (0.2 and 0.3 cm) in the kelp abundant region were composed of less KDD than the kelp sparse region. This is evidence of possible hermit crab body size effects with respect to KDD consumption. Again, during the winter the contribution remained as high as during the summer, which was consistent across all size classes.

The surprisingly high contribution of KDD to consumers from the kelp sparse region during the summer and winter may be explained as follows. First, although giant kelp abundance is 20-times higher in the kelp abundant region, there is still an ample standing stock of other kelp species present in the kelp sparse region [78] contributing to this region's POM pool. Second, the δ^{13} C values of the most abundant *Nereocystis* in this region appeared similar to the values of blooming phytoplankton resulted in highly uncertain modeled KDD contributions. Altering the kelp proportions in this region from 100% Nereocystis to include *Macrocystis* would enrich the kelp δ^{13} C value used in the mixing model and potentially decrease the maximum possible contribution of the giant kelp KDD to organisms within this region. Estimated uncertainty was higher in both regions during the winter because kelp values used in the mixing model had larger within region variability. The presence or absence of sea otters indirectly alters kelp forest species composition and grazer-kelp interactions through successional processes [53] [89], and therefore, may affect consumer diets and isotope values. Drift kelp and KDD are known to accumulate on gentle slopes and depressions as well as in areas of low current velocities suggesting importance of local hydrodynamics [90]. Biber [91] reports that areas with low standing stock of drift macroalgae and high currents can still have significant fluxes of drift pass through. These processes can lead to shifts in consumer spatial distributions in response to food availability [90] leading to isotope enrichment and potentially obscuring predicted patterns.

In conclusion, it appears that the local oceanography, kelp forest species composition, kelp species isotope variation, and kelp's similarity with blooming phytoplankton isotope values led to highly variable and at times counterintuitive results leading to uncertainty in the modeled KDD contributions. Nevertheless, in regions with dynamic hydrodynamics (*i.e.* fast currents, upwellings/downwellings, filament and eddy formation) that characterize narrow shelf regions, the KDD contribution to the various pelagic and benthic ecosystems is modestly high irrespective of the sea otter occupation. This is largely driven by the redundancy in the kelp species composition when multi-year *Macrocystis* species can be replaced by the annual species such as *Nereocystis*. Our study could uncover the inter-annual variability in the KDD contributions, which may hypothetically be more pronounced in the absence of *Macrocystis* kelp forests [22]. Ultimately, our findings speak to how widespread or limited the indirect effects of otters (e.g., kelp forest community succession), and other sources of ecosystem change, can be and are helpful in applications of ecosystem based coastal management.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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