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Kelp detritus: Unutilized productivity or an unacknowledged trophic resource?



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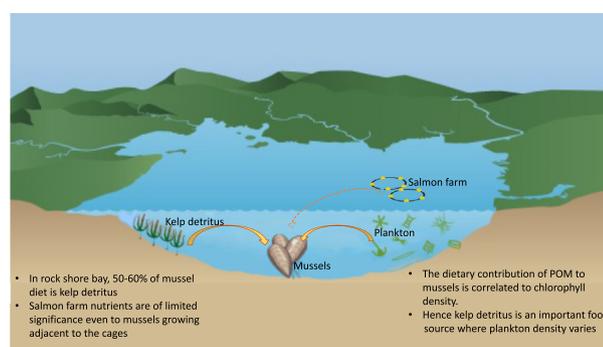
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HIGHLIGHTS

- The importance of kelp detritus in coastal food webs may have been underestimated.
- Kelp detritus formed 50–60% of the diet of suspension feeders.
- Phytoplankton and kelp productivity were similar, but <1% sustained mussels.
- Phytoplankton contribution to mussel tissue correlated with chlorophyll density.
- Applying isotopic values of kelp distal tissue reduces bias in diet source models.

GRAPHICAL ABSTRACT



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ABSTRACT

Kelp beds are one of the most productive marine systems and, while little of this production is directly consumed, there is growing evidence that kelp detritus is an essential food source for many detrital and suspension feeders, and forms an important component of offshore sedimentary carbon pools. However, the extent of the contribution of kelp detritus to the nutrition of coastal fauna is not well resolved. In this study, we compare the contribution of phytoplankton, kelp detritus, and waste from fish cages to the diet of a sentinel suspension feeder, the blue mussel (*Mytilus edulis*) using stable isotopes. We found a significant depletion in both ^{13}C and ^{15}N in kelp tissue with age (distance from stipe to the deteriorating distal end of the kelp frond) which may have biased dietary estimates in previous studies which have applied isotopic source values derived from fresh kelp. Our mixing models indicate that macroalgal detritus formed 59% of the diet of the mussels in Berehaven, Bantry Bay, Ireland. We support the isotopic mixing model results by modelling the relative production of phytoplankton, kelp, and salmon farm waste, and found the supply of C and N from kelp and phytoplankton far exceeded the requirements of the mussels with much less coming from the nearby fish cages. Monthly chlorophyll measurements indicated there was only sufficient phytoplankton density to support mussel growth during the spring and autumn, explaining our observation of patterns in the relative importance of utilization of kelp detritus. Where there is pressure to harvest kelp beds, this study highlights the supporting ecosystem service they provide as an important dietary source in coastal food webs and emphasises the need for appropriate management measures for this resource.

1. Introduction

Macrophytes (macroalgae and seagrass) represent approximately 66% of marine phototrophic biomass, but little of this is directly eaten and converted to animal biomass (Smith, 1981). Kelps (order Laminariales) are the

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most abundant macroalgae on rocky coasts in the subtidal euphotic zone, from temperate to polar seas (Billot et al., 2003). Kelp beds are also one of the most productive marine systems in the world with, for example, production of $1750 \text{ g m}^{-2} \text{ yr}^{-1}$ recorded in eastern Canada (Mann, 1972). Estimates of production to biomass ratios (P/B), indicated that globally kelp P/B ranges from 4 to 20 (Mann, 1972; Newell et al., 1995; Ortiz, 2008), signifying that the annual production of kelps can be up to 20 times the standing biomass, with *Laminaria digitata* being among the most productive with a P/B of 5.5–20.4 (Mann, 1972). *L. digitata* forms dense subtidal beds throughout the North Atlantic, with fast seasonal growth patterns that peak in the late winter to early summer with a slower rate in late summer-autumn (Pérez, 1971; tom Dieck, 1992; King et al., 2020). Light, nutrients, and water flow all have been found to influence growth rates (Schaffelke and Lüning, 1994; Smale et al., 2020), and storage of nitrate, ammonium, and phosphate occur in tissues during the winter to spring months, helping to sustain growth during the summer when ambient nutrient levels are lower (Kregting et al., 2016).

Phytoplankton P/B is normally far greater than that of kelp, in excess of 150 in the Celtic Sea (Moulllec et al., 2017), although in areas with restricted circulation such as Delaware Bay and Norwegian fjords lower P/B ratios of ~65 are reported (Frisk et al., 2011; Skaret and Pitcher, 2016). However, standing stocks of phytoplankton are likely to be orders of magnitude lower compared with that of kelps, with significant seasonal variation, so that even though P/B ratios are greater for phytoplankton, actual production can be greater in kelp beds. The balance of primary productivity in coastal systems between the benthic and pelagic components is intricately linked, with phytoplankton densities capable of influencing light transmittance to the seafloor and hence growth of benthic macroalgae (Kavanaugh et al., 2009). Likewise, macroalgal beds have been shown to modify seawater chemistry, increasing pH, and reducing both nutrient concentrations, suspended chlorophyll concentrations and the amount of C fixed by phytoplankton (Pfister et al., 2019). Removal of kelp beds that occurs during harvesting in California USA results in increased light penetration, with phytoplankton net primary production increasing as much as 1.5–2 times (Miller et al., 2011). However, this increase in phytoplankton productivity does not compensate for the loss of productivity, as these Californian kelp beds fix 3 to 15 times more carbon than phytoplankton in a comparable area during the summer (Pfister et al., 2019). The presence of suspension feeding bivalves can also influence the suspended chlorophyll concentrations (Peterson et al., 2016) and the resulting faecal material represents an important nutrient source for kelp forests (Newell et al., 1982). Bivalves may also act as a benthic-pelagic couple, capturing inaccessible Particulate Organic Nitrogen (PON) and Particulate Organic Phosphorous (POP) from the water column in the form of phytoplankton and making it available to benthic primary producers (Peterson and Heck, 1999).

It has been estimated that about 80% of kelp production is lost as detritus through the erosion of blades, breakage of the frond, or dislodgment of the algae (Krumhansl and Scheibling, 2012). On average $705 \text{ g C m}^{-2} \text{ yr}^{-1}$ is released as macroalgal detritus globally; similar to detrital export from other blue carbon habitats such as seagrass beds and mangroves, with that from salt marshes higher (Krumhansl and Scheibling, 2012). Kelp detritus may end up in the sediments forming a blue carbon stock, or enter the food web (Wilmers et al., 2012; Queirós et al., 2019). Global Net Primary Production (NPP) of macroalgae is estimated to be $1521 \text{ Tg C yr}^{-1}$, of which 173 Tg yr^{-1} are sequestered in the sediments with the majority (88%) in the deep sea (Krause-Jensen and Duarte, 2016). However, detritus from kelps has a relatively high nitrogen to carbon (N:C) ratio compared with both mangroves and saltmarsh, indicating its potential role as a nutrient source in food webs (Krumhansl and Scheibling, 2012). Evidence has been building that supports the role of kelp detritus in the nutrition of suspension feeders. Initially, assimilation of kelp detritus was supported by energy balance models that found in some habitats filter feeders could not obtain all of their nutrient requirements from phytoplankton, based on the measured phytoplankton availability and hence must be using kelp detritus (e.g. Widdows et al., 1979; Seiderer and Newell, 1985). Feeding

experiments using radio labeled kelp detritus also reinforced this theory (Stuart et al., 1982). This was further confirmed by feeding experiments that showed suspension feeders could survive and grow using macroalgal detritus as a food source, with aged macroalgal particles, where total polyphenolic concentrations were lower, in most cases promoting the best growth rates (Duggins and Eckman, 1997). Traditional analysis of gut contents of benthic grazing limpets further supported the evidence that kelp detritus is an important dietary component, with feeding experiments showing that excluding kelp detritus resulted in increased mortality (Bustamante et al., 1995). Advances in stable isotopes and their use as tracers in trophic webs has further evidenced the importance of kelp detritus as a food source for both grazers (Bustamante and Branch, 1996; Fredriksen, 2003; Norderhaug et al., 2003; Norkko et al., 2007) and filter feeders (Duggins et al., 1989; Schaffelke and Lüning, 1994; Hill et al., 2006; Kaehler et al., 2006; Kang et al., 2008; Tallis, 2009; Blight et al., 2011). Miller and Page (2012) argued that the contribution of kelp detritus may have been overestimated due to the use of offshore suspended particulate organic matter (POM), or cultured phytoplankton as a proxy for coastal phytoplankton from coastal POM in isotopic mixing models. However, many studies have also included other evidence to support the isotopic evidence. For example, the growth rates of benthic suspension feeders were shown to be twice to five times higher in areas with kelp forests compared to those areas where sea urchin grazing had created “barrens”, and isotopic ^{13}C studies indicated that it was the contribution of macroalgal C that resulted in the different growth rates (Duggins et al., 1989).

Filter feeding bivalves are a commercially important faunal group that are frequently cultured in protected coastal embayments and estuaries. They are proposed as a sustainable source of protein, being primary consumers, requiring no added food, and as they provide valuable ecosystem services (van der Schatte Olivier et al., 2018). Being suspension feeders they filter organic particles from the water column removing nutrients and reducing turbidity, permitting more light to reach the benthic macrophytes, and their often extensive colonies provide habitat for other commercially important species (Shumway et al., 2003). Individual mussels can filter about three litres of seawater h^{-1} (Saurel et al., 2013), removing about 50% of phytoplankton (Simpson et al., 2007). As such, large populations, either cultured or natural, require extensive resources of particulate organic matter and in sheltered coastal environments, these may vary according to seasonal differences in production. Traditionally, mussels are thought to feed on phytoplankton, using selective sorting to eliminate silt and other detrital particles as pseudofaeces (Jørgensen, 1996). However, there is a growing body of evidence that this may be subsidized by other sources of organic material, and while detritus from salt marsh macrophytes can only support limited growth (Williams, 1981), other sources such as seagrass, mangroves and macroalgae may be important (Walton et al., 2014; Elliott Smith and Fox, 2021). In an early review, Seed (1976) concluded that organic detritus was an important component of the diet of mussels and this was found to be particularly true when the chlorophyll a concentration decreased below the maintenance ration of $2.42 \mu\text{g l}^{-1}$ Chl a (Widdows et al., 1979).

Stable isotopes have been extensively used in trophic ecology since the early work of Deniro and Epstein (1978, 1981), who showed that carbon is useful in tracking food sources, and nitrogen in discerning trophic levels. Early studies used isotopic similarity to infer consumption of prey by a consumer (e.g. Primavera, 1996). More recently isotopic mixing models such as IsoSource (Phillips and Gregg, 2003), SIAR (Parnell et al., 2008), and lately mixSIAR (Stock et al., 2018) have enabled the calculation of the most likely proportional contribution of multiple food sources to the tissue of a consumer, and hence, dietary composition.

In this study, we compare the role of phytoplankton, kelp, and salmon cage waste in a coastal food web using suspension feeding mussels as a sentinel species. We use stable isotopes to trace the food sources of mussels sampled at increasing distances from salmon cages and related them to estimates of annual production of carbon and nitrogen from these three possible sources.

2. Methods

2.1. Site

The selected study area was Berehaven, a tidal channel that runs approximately 12 km by 1.5 km between the Beara Peninsula and Bear Island in Bantry Bay - a ria (Roycroft et al., 2004), located in southwest Ireland (51°38' N, 9° 52' W; Fig. 1). The deeper seabed in Berehaven, like Bantry Bay, is composed of mostly fine sediments such as mud and sand at a depth not exceeding 30 m. The coast is made up of coarser sediments, gravel, and rock, that provide habitat for extensive intertidal furoid and subtidal kelp beds dominated by *L. digitata*, with *Laminaria hyperborea* and *Sacchoriza polyschides* growing deeper (Crapp, 1973).

Berehaven contains multiple marine aquaculture sites including three longline mussel (*Mytilus edulis*) farms, two salmon cage sites (*Salmo salar*; Fig. 1), and a small oyster farm. Due to the proximity of the two salmon cages to the mussel farms (Fig. 1) located at the eastern end of the channel, we include them as a possible food source for suspension feeders in Berehaven.

Previous hydrodynamic modelling of Bantry Bay (Dabrowski et al., 2016; Bass, 2016), in conjunction with modelling performed as part of this research (see Gooding, 2020 for details of the model setup and simulations, but with results also plotted here in Fig. 2), has well described the bay's circulation patterns. The bay experiences a semi-diurnal tide with peak spring flows of 0.15 m s⁻¹ (flood) and 0.17 m s⁻¹ (ebb) (Fig. 2a, c; Bass, 2016). The residual circulation within Bantry bay is generally weak (<0.01 m s⁻¹) with eddy structures forming along the coast (Fig. 2e), although north-eastwards residuals were recorded along the northern shore and south-westwards residuals along the southern shore (Dabrowski et al., 2016). The average flushing time of the Bay has been estimated to be between 7 and 10 days (Dabrowski et al., 2016), indicating a well-mixed water body and suggests that production in any part of the Bay could contribute to the nutrition of the Berehaven mussels. We, therefore, have made estimates of the biomass potential food sources for the whole of Bantry Bay. Our hydrodynamic modelling shows that water flows into

and out of Berehaven from each end of Bere Island at peak spring velocities of 0.3 ms⁻¹ (south-western entrance) and 0.25 ms⁻¹ (north-eastern entrance) with convergence of currents in the middle of Berehaven resulting in almost static water in agreement with Bass (2016).

To understand the dietary availability of the three possible food sources (phytoplankton, kelp, and salmon waste), we estimated the annual production of carbon and nitrogen by phytoplankton, kelp, and salmon waste and compared it with the nutrient demands for the culture mussels.

2.2. Food sources: production versus consumption budget

2.2.1. Phytoplankton

We used the mean monthly chlorophyll density from a 19 year dataset sampled at the sea surface, and at depths of 10 m and 25 m, at the Boatyard buoy (Fig. 1) in the eastern end of Berehaven (Bass, 2011), and multiplied these values by the Bantry Bay volume (Dabrowski et al., 2016) to check whether the standing stock of chlorophyll met the required dietary maintenance ration of mussels. We used values in Arteaga et al. (2016) to convert chlorophyll to C and employed a C:N ratio of 6.625 (Dabrowski et al., 2013) to estimate the standing stock of phytoplankton N. We estimated the area of Bantry Bay using the 0 m mean sea level contour line from the Digimap database (<https://digimap.edina.ac.uk>) and excluded the islands to give a sea surface area of 231.02 km². Net Primary Productivity (NPP) m⁻³ was extracted from monthly data for 14 depth layers across the 30 horizontal cells within Bantry Bay in the Copernicus Programme dataset (CMEMS, 2021) to calculate mean monthly NPP m⁻² and total annual production for the whole bay. Total annual N production for Bantry Bay was estimated using the Redfield ratio (as above).

2.2.2. Macroalgae

As Secchi depths of greater than 7 m from April to September indicated good water clarity (Bass, 2011), and kelp beds had been reported down to 17-19 m in a nearby bay 30 km to the south (Blight et al., 2011) the subtidal area available to kelp was defined as -1 m down to -18 m (See Supplementary Information 1, F1). The kelp area was estimated using the

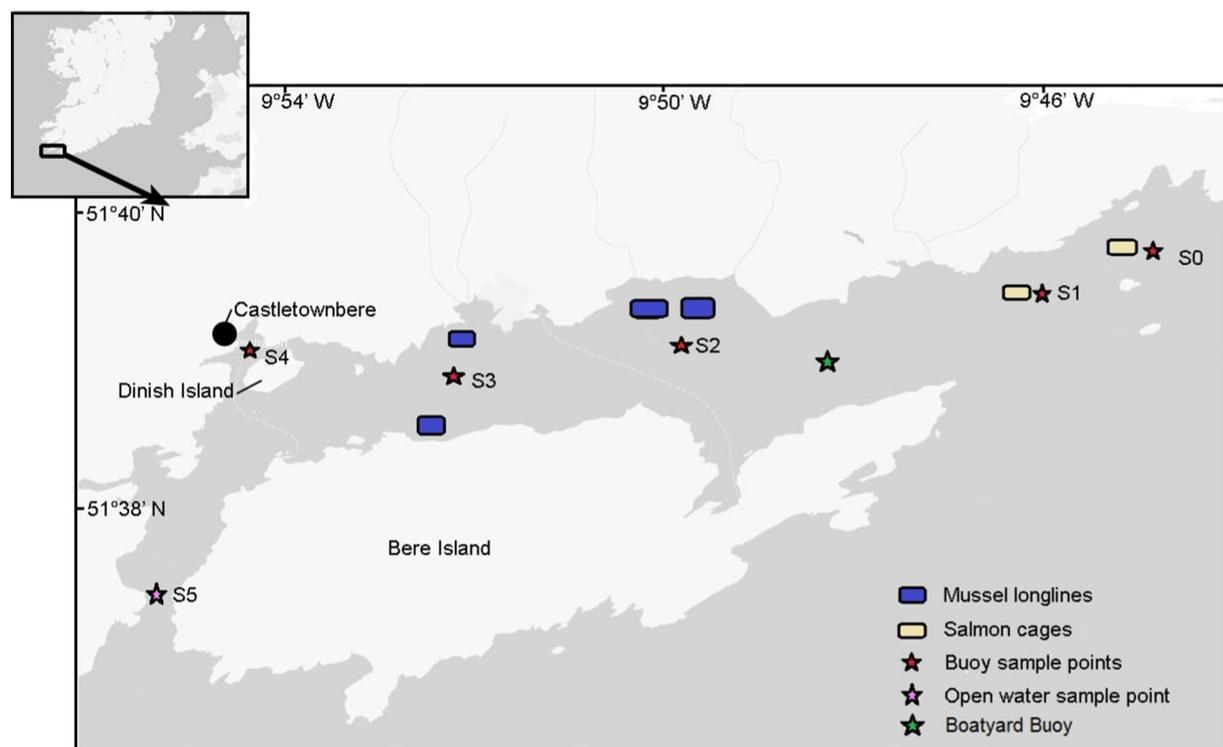


Fig. 1. Location of sampling points and aquaculture installations within Berehaven, the body of water between Bere Island to the south and the Beara Peninsula of mainland Ireland to the north.

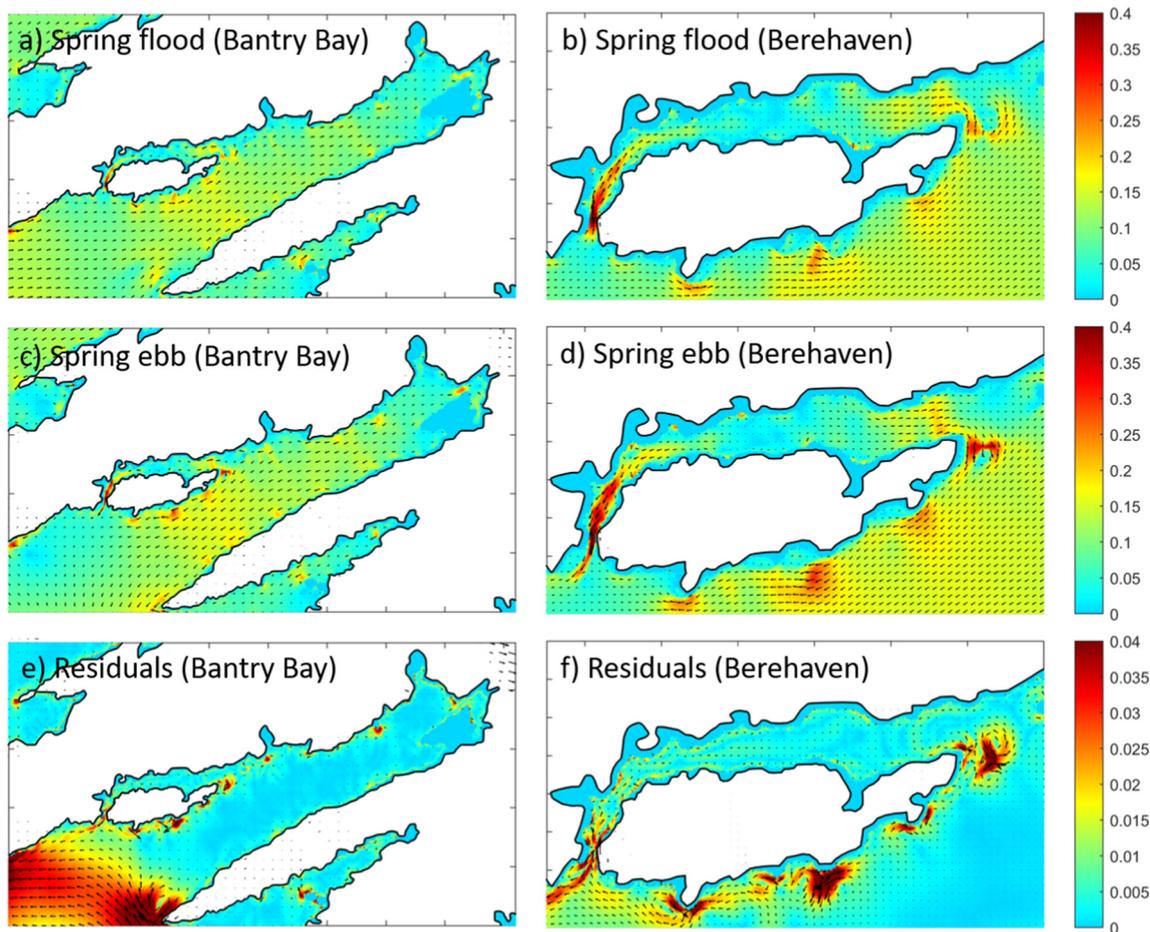


Fig. 2. Modeled current velocities (m s^{-1}) in Bantry Bay as a whole (a, c & e) and focussing in on Brehaven (b, d & f) during spring ebb and flood tides (a to d) and residual currents (e and f).

modelling software Blue Kenue with bathymetric data from the Digimap database (<https://digimap.edina.ac.uk>). The standing stock subtidal biomass of kelp was calculated by applying mean biomass estimates of mixed *L. digitata* and *L. hyperborea* beds of 3.55 kg m^{-2} from two nearby coastal sites (one sheltered and one exposed site with no significant difference reported in kelp biomass), 30 km to the south of Brehaven (Blight et al., 2011). Using a conversion rate from kelp wet weight to C of 0.054 (Birkett et al., 1998 cited in Kelly (2005) and confirmed by authors' own analysis) we estimated the standing stock of kelp carbon and kelp nitrogen and applied a conservative P/B of 4–10 (Brady-Campbell et al., 1984; Newell et al., 1995; Ortiz, 2008) to estimate annual production of carbon and nitrogen as kelp detritus (Kelly, 2005).

2.2.3. Salmon cage waste

There are two salmon farms just to the east of Brehaven: Roanarrig is licensed for 2000 t and Ahabeg for 600,000 smolts. The farms operate on a stocking, harvesting, and fallowing rotation scheme to reduce sea lice. We used published feeding rates from a very similar production facility proposed for Shothead just east of Brehaven, licensed for maximum biomass of 2800 t and where 1206.2 t of C and 146.2 t of N is supplied as feed (Bass, 2011). The C and N content of the annual feed inputs were estimated from C, N content of 53.03% and 6.79%, respectively, derived from our elemental analysis of the feed. We used the release rate of C and N from salmon cages reported by Wang et al. (2012) to quantify the amount released into Brehaven. They report 3% of the feed nutrient input is lost as DOC and DON prior to consumption, 19% of C and 15% of N defecated as POC and PON, 46% respired as DOC and 45% of N excreted as DIN (Wang et al., 2012). We assume that only particulate C and N will be directly available to suspension feeders while dissolved nutrients will be

assimilated by phytoplankton and other primary producers before they become available to suspension feeders (Troell et al., 1999).

2.2.4. Mussel nutrient uptake

Annual bivalve production in Bantry Bay ranges between 5000 and 9500 t, with of which approximately 1300 t of mussels produced in Brehaven (UCC, 2000). We estimated the C and N contained in the meat and shell of farmed mussels and oysters, for Brehaven and Bantry Bay by applying the conversion factors provided in van der Schatte Olivier et al. (2018) to the annual harvest rate (t). To obtain the bivalve C and N requirements (i.e. the C and N content of the food consumed), the meat C and N and shell N was then multiplied by the reported consumption/biomass ratios (Q/B) of 5.11 and 10.5 for mussels (Outeiro et al., 2018) and oysters (Xu et al., 2019) respectively. Although the C incorporated into the shell is estimated, the C is not thought to be derived from food sources, but from bicarbonate dissolved in the seawater (Thomsen et al., 2018).

2.3. Determination of trophic connectivity

We sampled at six locations spread out along Brehaven, using five existing navigation and marker buoys as sampling points, from S0 at the eastern end to S4 at the western end, with a further open water sampling point (S5) identified at the Atlantic opening of Brehaven (Fig. 1). At each of the sample points; sediment was obtained using a box corer; suspended POM captured by dragging a 100 μm mesh plankton net 0.5 m below the surface for 100 m; and where present five adult mussels (*M. edulis*) and seaweed (*L. digitata*) were hand-picked from the surface of the buoys at each sample date. The timings between mussels sampling ensured isotopic equilibrium with dietary sources would be reached, as

mussels reach equilibrium within 60 days of being switched to a new diet (Dubois et al., 2007). The removal of anchorage buoys meant that mussels were not always available at stations 0, 1 and 5. In May 2019, mussels transplanted from Stn. 2 and sediment traps were suspended from three experimental buoys set up within 50 m of the salmon cages at Stn. 1 to be retrieved 4 months later in September.

We considered three possible food sources for wild and cultured mussels to be suspended POM, macroalgal detritus, and feed from the salmon cages. Feed from the salmon cages was included in the model as the feed waste concentration might be locally significant. We used suspended POM as a proxy for plankton, and included zooplankton which are regularly found in the stomachs of Bantry Bay mussels (Lehane and Davenport, 2006). We recognize that the suspended particulate organic material will contain plankton as well as kelp detritus, but this would tend to drive the mixing model to underestimate the contribution of kelp. Macroalgal samples of the kelp *L. digitata* were taken at the distal end of detached and growing blades at each sampling, and in June 2018 along three blades from the stipe to the distal end where disintegration formed kelp detritus (Fig. 3) to examine the temporal changes in isotopic signal during development and distal disintegration of the blade. In April 2018 *Laminaria* sp. detritus was additionally sampled from the strand line on the shore. Two sets of Salmon pellets were provided by Mowi ASA and field samples of mussels, algae, detritus, POM and sediment were collected in April 2018 (two weeks after salmon cages were emptied), June 2018 (no salmon present for three months), May 2019 (salmon stocked five months previously) and September 2019.

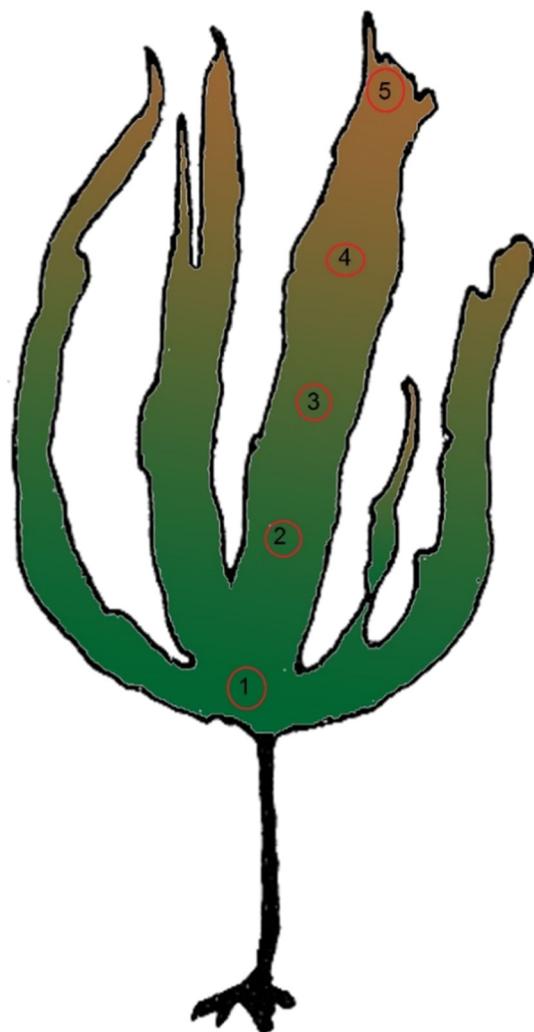


Fig. 3. Locations for isotope samples along the blade of a *Laminaria digitata* (1 to 5).

After collection POM samples were washed through a coarse (500 μm) mesh with GFC filtered seawater to remove gelatinous plankton and collected on a 45 μm mesh before being rinsed with distilled water. To avoid the influence of ingested food, mussel mantle, gill and adductor muscle were dissected out and separated from the guts and rinsed with distilled water. The isotopic enrichment of mantle, gills and muscle tissue are similar and all are significantly different from gut tissue (Cabanelas-Reboredo et al., 2009; Deudero et al., 2009). Macroalgal samples had any biofouling removed by gentle scraping before rinsing with distilled water. Half of each sediment sample was sequentially acidified with 0.1 M HCl and oven-dried repeatedly until addition of HCl resulted in no bubbling, indicating all carbonate had been removed, and used to obtain sediment organic $\delta^{13}\text{C}$ values, the remaining half was used for $\delta^{15}\text{N}$ values. All samples were oven-dried at 55 $^{\circ}\text{C}$ for a minimum of 48 h and homogenised and weighed into tin cups (Elemental Microanalysis Ltd.) before being analysed for ^{13}C and ^{15}N isotopes by Iso-Analytical Ltd. using a PDZ Europa ANCA-GSL elemental analyser linked to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Standards were run interspersed with samples which resulted in standard deviations of $<0.2\text{‰}$ for $\delta^{13}\text{C}$ and $<0.3\text{‰}$ for $\delta^{15}\text{N}$.

2.4. Data analysis

The relative contributions of potential food sources to the mantle, gill and muscle tissue of mussels (*M. edulis*) were examined using the Bayesian isotopic mixing model mixSIAR (Stock and Semmens, 2013; Stock et al., 2018). This model was selected as it can incorporate both the variance of isotopic values of sources and consumers as well as the uncertainty in the diet/tissue discrimination factors (Stock et al., 2018). MixSIAR was run in JAGS and called through R (R Core Development Team, 2016) and the 'MixSIAR' package (Stock and Semmens, 2013). The models were run with no informative priors and specified both residual and process error. Mussels tissue values were entered per station, while sources that were not found to vary by station were entered as mean values \pm standard deviation. Sampling station number was entered as a random effect. The longest Markov Chain Monte Carlo settings were used: chains = 3, chain length = 1,000,000, burn-in rate = 500,000 and thinning rate = 500, as this produces the best convergence on the true posterior distribution for each variable (Stock and Semmens, 2013). Convergence was evaluated by Gelman-Rubin diagnostics (Gelman and Rubin, 1992). We used discrimination of 0.3 ± 1.3 for $\delta^{13}\text{C}$ and 2.1 ± 1.6 for $\delta^{15}\text{N}$ as estimated by McCutchan et al. (2003) for the change in isotopic ratio between the tissue of marine primary consumer and that of the food source. For the MixSIAR model food sources, we used the mean values (\pm SD) at each sample date of the salmon pellets, POM, and for kelp detritus the distal samples of *L. digitata*. We found no difference in the isotopic values of kelp detritus and although POM isotopic signatures varied, no significant effect of sampling time, nor sample station, was discovered using a two-way ANOVA (Supplementary Information 1, F.2). Salmon pellets were also analysed at each date no isotopic variation was found.

Pearson's correlation analysis was used to examine the relationship of the spatial variation in the isotopic signal of POM and *L. digitata* with distance from the salmon cages, the spatial variation in the isotopic values of POM and sediment, and the temporal variation in the contribution of POM to the diet of mussels and chlorophyll concentration. For the latter, the mean monthly chlorophyll concentrations, for the period 1991 to 2010, were extracted from Bass (2011) at a monitoring station close to our Stn. 2 as the spacio-temporal variability could not be captured by our point sampling. We used the average surface chlorophyll concentration of the previous 60 days, as Dubois et al. (2007) showed the mussels reach isotopic equilibrium with their diet after approximately 60 days. Analysis of variance was carried out in Minitab, followed by post hoc Tukey tests, if necessary, to test for differences in the isotopic composition and C:N ratios between tissue from the distal and stipe ends of *L. digitata* blades. Prior to statistical analyses, data were examined for normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) and were log-transformed where necessary.

3. Results

3.1. Food sources: production versus consumption budget

Phytoplankton mean carbon density was 0.03 mg C m^{-3} extrapolated to a Bay-wide standing stock of 2.64 t of phytoplankton C. Employing a molar C:N ratio of 6.625 indicates a standing stock of 0.46 t of N.

Mean monthly phytoplankton NPP for the whole bay varied from 4 to $34 \text{ g C m}^{-2} \text{ month}^{-1}$ with annual productivity of $238 \text{ g C m}^{-2} \text{ yr}^{-1}$. We estimated a total annual phytoplankton production estimate of 55,189 tC and 9719 tN.

Kelp beds extend over an area of 4680 ha in Bantry Bay with an estimated standing stock subtidal biomass of 166,140 t, equivalent to a standing stock of 9020 tC and 424 tN with an annual production of 36,080–90,202 t of carbon and 1698–4243 t of nitrogen, or kelp detrital production rates of $771\text{--}1927 \text{ g C m}^{-2} \text{ yr}^{-1}$.

Salmon cage waste: We estimate the annual release of particulate waste products directly available to the suspension feeders are 229 tC and 22 tN. The annual release of dissolved nutrients is estimated as 1033 t DOC and 66 t DIN which is available to phytoplankton and other primary producers and in turn to the suspension feeders.

In summary, we estimate total annual primary production in Bantry Bay to be 55,189 tC and 9719 tN for phytoplankton and 36,080–90,202 tC and 1698–4243 tN for kelp, while salmon waste released as POC is estimated to be 229 tC yr^{-1} with 22 tN yr^{-1} as PON. 1070 tC and 70 tN from fish feed are also released in a dissolved form that may be assimilated by phytoplankton.

Farmed suspension feeders. After estimating the C and N content of the bivalves and applying reported Q/B values we estimate C and N consumed by Bantry Bay mussels annually to be 248 tC and 111 tN, while oysters consumed 198 tC and 99 tN. This excludes the C required for shell growth and maintenance that is not derived from food sources (Table 1).

3.2. Determination of trophic connectivity

POM values varied from $\delta^{13}\text{C} -22.3$ to -19.2‰ and $\delta^{15}\text{N} 10.3$ to 7.8‰ , whereas kelp detrital values ranged from -19.2 to -22.2‰ for $\delta^{13}\text{C}$ and 7.8 to 10.3‰ for $\delta^{15}\text{N}$. There was no discernible gradient in the isotopic values of POM or *L. digitata* with distance from the salmon cages (Pearson correlation: $p \geq 0.6$ for $\delta^{13}\text{C}$ and $p \geq 0.5$ for $\delta^{15}\text{N}$).

For the macroalga *L. digitata* the isotopic values of both ^{15}N and ^{13}C changed from the stipe growth (meristematic) region to the disintegrating distal tips (Fig. 4) and with ^{15}N becoming significantly more depleted at the distal tip (Anova $F = 14.15$, $p < 0.001$). Hence the isotopic values for the distal tip were used in isotopic modelling. We also found no significant difference in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the shoreline kelp detritus and the sampled distal ends of the blades of *L. digitata*. We also found that the distal parts of the blade were significantly enriched (t -test: $t = -3.69$, $p = 0.003$) in nitrogen compared to the growth region around the stipe (mean: 2.05% vs 1.85% N, respectively). In June 2018 samples of *L. digitata* the C:N ratio was significantly reduced at the distal tip (Anova $F = 8$, $p = 0.02$) and pairwise comparisons indicated that blade C:N ratios were on average 3.2 ($95\% \text{ CI } \pm 2.5$) less at the distal tip. May 2019 samples from detached

Table 1

Annual harvest rates (tonnes year⁻¹), carbon and nitrogen content of dry weight of meat and shells of mussels and oysters in Bantry Bay and Berehaven, and the C and N consumption estimates based on consumption/biomass rates.

		Dry Wt	C	N	Required C	Required N
Berehaven mussels (1300 t/yr)	Meat	34.4	15.8	3.1	80.9	16.0
	Shell	470.6	59.7	4.0	304.9	20.2
Total Bantry Bay mussels (incl. Berehaven) (4000 t/yr)	Meat	105.9	48.7	9.6	248.8	49.1
	Shell	1448.0	183.6	12.2	938.2	62.2
Total Bantry Bay oysters (4500 t/yr)	Meat	42.1	18.9	3.3	198.0	34.7
	Shell	3828.1	335.0	6.1	3517.1	64.3

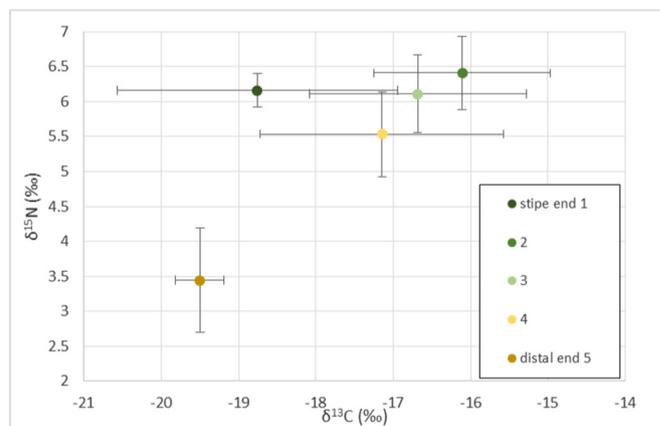


Fig. 4. Mean and standard deviation of $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰) values of samples, collected at low water spring tide, taken along three blades of *Laminaria digitata* from the stipe (meristematic) region to the disintegrating distal end (see Fig. 3 for position on the kelp blade).

and growing blades indicated that C:N ratios in the distal tip of detached blades (C:N 23.8) were less than the ratios of distal tip of attached blades (C:N 33.2) ($F = 5.8$, $p = 0.009$) with a mean difference of 9.4 ($95\% \text{ CI } \pm 8.6$). The kelp fragments sampled from the tidal strand line during the April 2018 sampling had a mean ($\pm \text{SD}$) C:N ratio of 18.7 ± 1.7 and were not significantly different to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the sampled distal ends of the blades of *L. digitata*.

Mean isotopic values of all sources and mussel tissue varied very little between the four sampling times, with sources having distinct and well separated mean isotopic values (Fig. 5). Sediment isotopic values were not correlated with POM values, but showed a pattern of depletion in $\delta^{15}\text{N}$ values towards the middle of Berehaven, being most depleted at the harbour area, and most enriched at either end (Supplementary Information 1, F.3). Some mussels were much depleted in ^{13}C and included those from S1 in June 2018 when no salmon were present and from S0 in May 2019 five months after the restocking of salmon had occurred. In general mussel signatures showed a pattern of enrichment in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the eastern to the western stations in the centre of Berehaven (Stn. 4), in both June 2018 (no salmon) and May 2019 (with salmon) (Supplementary Information 1, F.4). Between May and September 2019, storms resulted in only partial harvesting of two of the three buoys and the incomplete isotopic results for September 2019 samples are presented in supplementary material (F.5).

Results from the mixing model mixSIAR suggested that in April 2018, two weeks after the salmon cages were harvested, kelp detritus accounted for the majority of the C and N analysed in the tissue of the sampled mussels, with the salmon feed playing a small, but significant role (Fig. 5). In June 2018, the salmon cages had been empty for three months, kelp detritus still accounted for the majority of the diet, but the contribution of POM increased to 35% (Table 2). We checked to see whether the contribution from salmon waste was an artefact of the mixing model by rerunning the June 2018 results and including salmon feed as a source, but the results showed the contribution from salmon feed was low (4%) and not significant. In the following year (May 2019), when the salmon cages had been stocked for five months, results of the mixSIAR modelling were less constrained with wider confidence intervals and, for all mussel sampled within Berehaven, the mean dietary contribution of kelp detritus had decreased to 43.7%, while POM had increased to 50.7%, and salmon feed to 5.6% ($0.1\text{--}36.3\%$). However, the only mussels that received a significant dietary contribution from the salmon waste were those at Stn. 0, close to the cages. This observation was confounded by values for mussels sampled directly from the salmon cage structure, where a fish feed contribution to mussel tissue could not be confirmed, as the Bayesian credible interval included zero (2% with $95\% \text{ CI } 0\text{--}7.1\%$).

The isotopic mixing models found that the contribution of kelp detritus to the mussel tissue declines from the eastern end of Berehaven (Stn. 0) to

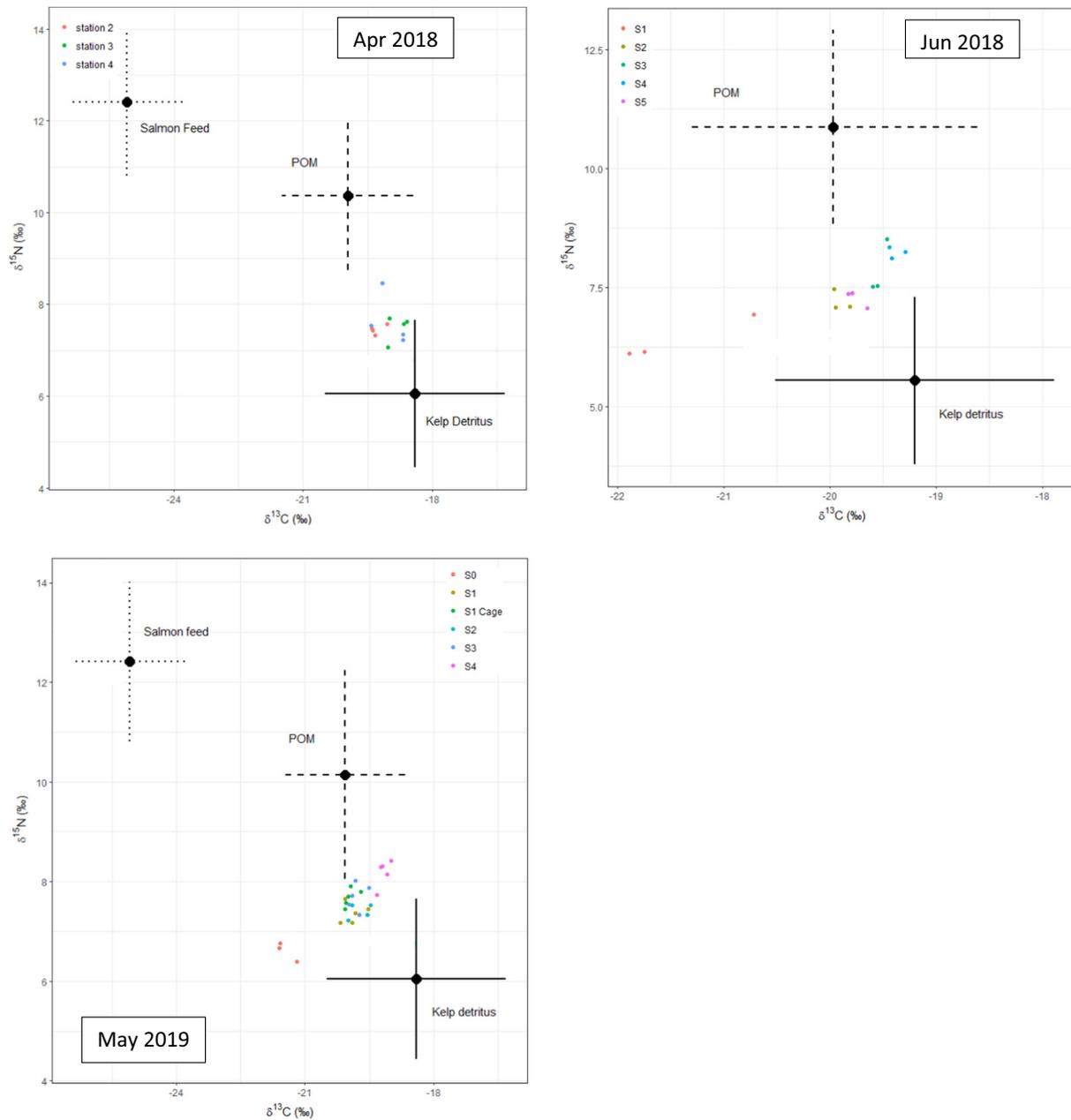


Fig. 5. Stable isotope values (‰) of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) for mussel samples from buoys within Berehaven, Ireland (corrected for isotopic discrimination) and mean (\pm SD) values for sources (Kelp detritus, particulate organic material (POM) and salmon feed). Samples were collected in April and June 2018, and in May 2019.

the Castletownbere harbour (Stn. 4). This spatial trend was especially noticeable in June 2018 and May 2019, though an increase at the westernmost and relatively well-mixed station (Stn. 5) was observed in June 2018 (Fig. 5). Conversely, the contribution of POM to the tissue of mussels increases towards the central region of Berehaven. The dietary contribution of the salmon feed was only significant to mussels sampled from S0 in May 2019 (credible intervals did not include zero). The April 2018 samples (not

shown), showed no similar pattern to that of June 2018 or May 2019, with dietary proportion of kelp detritus, POM, and salmon feed to mussel did not vary between stations, however mussels were only available for sampling at stations 2, 3, and 4.

To examine how the dietary contribution of POM to the mussel tissue is related to phytoplankton concentration, we plotted our values of the dietary contribution of POM against the mean surface chlorophyll concentration from the preceding two months. Although only four data points are available they were highly correlated indicating a possible relationship between phytoplankton density and the dietary contribution of POM (Fig. 7).

Table 2

Mean dietary contribution and 95% Bayesian credible intervals from kelp detritus, particulate organic matter (POM) and salmon feed to the gill and mantle tissue of mussels resulting from the isotopic Bayesian mixing model (mixSIAR).

Sample	Kelp detritus	POM	Salmon feed
April 2018	67.7% (41–80.4%)	21.9% (2–46.8%)	10.5% (0.6–27.7)
June 2018	65% (38.8–87.7%)	35% (12.3–61.2%)	
May 2019	43.7% (8.8–80.8%)	50.7% (13.1–86.9%)	5.6% (0.1–36.3%)

4. Discussion

This study has demonstrated that the high primary production in coastal kelp forests is a potentially important resource with subsequent detrital production acting as a major food source for suspension feeders such as

mussels. Krumhansl and Scheibling (2012) reported primary production of kelps to range from 10 to 5622 g-C m⁻² yr⁻¹ with that of *L. digitata* ranging from 289 to 2287 g-C m⁻² yr⁻¹ (Mann, 1972; Krumhansl and Scheibling, 2012), which is similar to the estimated range in our study of 771–1927 g-C m⁻² yr⁻¹. Although lower estimates of 135 to 402 g-C m⁻² year⁻¹ were reported for British *L. digitata* sites (King et al., 2020). Phytoplankton primary production is classically thought to approximate 50 g-C m⁻² yr⁻¹ in the open ocean, 100 g-C m⁻² yr⁻¹ in coastal waters, and 300 g-C m⁻² yr⁻¹ in upwelling areas (Ryther, 1969). More recently the median annual phytoplankton primary productivity in a global review of 131 estuarine-coastal marine ecosystems was estimated to be 252 g-C m⁻² yr⁻¹ (Cloern et al., 2013). Our estimates of phytoplankton primary productivity for Bantry Bay of 239 g-C m⁻² yr⁻¹ indicates a relatively productive area and are similar to those estimated for the surrounding Celtic-Biscay shelf LME of 272 g-C m⁻² yr⁻¹ (TWAP, 2015) and the North Sea of 119 g-C m⁻² yr⁻¹ (Rodhouse et al., 1984).

The relative scale of benthic and pelagic productivity in the study area is reflected in nutrient uptake by farmed mussels within the Bay, which relied on the kelp detritus as a dominant food source forming 59% of the diet of wild and cultured mussel within Berehaven, with most of the balance being provided by consumption of POM (Table 2). Similar estimates for the dietary contribution from kelp detritus were reported for mussels of 46–63% in nearby northern France (Schaal et al., 2010) and 45–50% for suspension feeders in general (reviewed data, Elliott Smith and Fox, 2021). We found the nutrient waste released by the salmon cages contributed relatively little to C and N to the nutritional requirements of cultivated mussels within Berehaven. Intertidal suspension feeding bivalves were scarce in the study area (Cartwright, 2017), suggesting that mussel culture systems represent the dominant biomass of bivalve suspension feeders in Berehaven. In Bantry Bay, kelp primary productivity was similar to that of the phytoplankton productivity and far exceeded the nutrient requirements of the cultured mussels. The consumption of NPP by 8500 t of bivalves represents approximately 1% of C and 3% and 12% of N produced by phytoplankton and kelp within the Bay, respectively. The remaining detritus is available to other suspension feeders, and the detrital food web, and may remain within the kelp beds or is transported to other habitats (Krumhansl and Scheibling, 2012), with some deposited in deeper water sediments forming part of the blue carbon pool (Wilmers et al., 2012; Hill et al., 2015; Queirós et al., 2019). Earlier research had reported kelp detrital food webs to occur close to kelp beds (Bustamante and Branch, 1996; Kaehler et al., 2000; Fredriksen, 2003), but more recently export of kelp detritus has been shown to support fauna kilometres from the kelp beds (Vanderklift and Wernberg, 2008; Filbee-Dexter and Scheibling, 2014).

The annual amount of carbon released into the water column by kelp is related to the production with peak growth reported in early summer (Werner and Kraan, 2004) with varying, but continuous detrital production occurring throughout the year (Filbee-Dexter et al., 2018). In ecosystem modelling, macroalgal production is estimated using a production to biomass ratio (P/B) (Kelly, 2005). P/B ratios for other kelp forests around the globe range from 4 to 10 (Brady-Campbell et al., 1984; Newell et al., 1995; Ortiz, 2008), while a P/B of 5.5 to 20.4 was recorded for *L. digitata* (Mann, 1972) signifying that that annual production for Canadian kelp can be up to 20 times the standing biomass, with production decreasing with depth.

Many studies have evidenced the importance of kelp detritus to a variety of different feeding guilds including grazers and suspension feeders and these were recently reviewed by Elliott Smith and Fox (2021). However, subtidal benthic coastal mussels that used detritus as a food source exhibited growth four times slower than raft grown individuals, but were able to support gamete development during the winter months and a partial spring spawning, whereas raft mussels did not spawn until the summer (Rodhouse et al., 1984). Others argue that that kelp contribution has been overestimated by the difficulties in obtaining the correct isotopic values for phytoplankton and advise caution in the use of offshore POM isotopic values as a proxy for those of inshore phytoplankton (Miller and Page, 2012). In our study, we use inshore POM values in our three source mixing

model, and acknowledge that the samples will contain kelp detritus as well as plankton. However, this will most likely result in an over-estimation of the contribution of phytoplankton to mussel tissue in the isotopic mixing model. An increase in the proportion of kelp detritus in the POM sample would cause the isotopic values to shift closer to that of the kelp and hence the mussels, and would result in an increased dietary contribution from POM in order to balance isotopic values of the dietary sources with those of the consumer.

We looked at the mean monthly variation in the chlorophyll *a* values over a 19 year period to examine if there was any correlation between chlorophyll *a* concentration and the contribution of POM to mussel tissue (Fig. 7). We found a strong relationship ($R^2 = 92\%$), although the sample size was small, indicating when chlorophyll density is low the dietary contribution of POM for mussels is reduced. It may be that where/when phytoplankton production is nutrient or light-limited the large biomass of kelp and other seaweeds present throughout the year could form an important food reserve that releases detritus throughout the year through the gradual degradation of the distal ends of the kelp blades. Chl *a* concentrations in Berehaven only exceed the required maintenance ration for mussels of 2.42 µg l⁻¹ (Widdows et al., 1979) in April and August/October, so the elevated seasonal contribution of kelp detritus to the diet of mussels is not unexpected. Maximal Secchi depths of >7 m that are reported from April to September in Berehaven also suggest that phytoplankton growth is nutrient limited or extensively grazed during the summer (Bass, 2011), but may allow for increased benthic productivity. Seasonal differences in relative benthic and pelagic productivity may also be compounded by seasonal patterns of resuspension of kelp detritus, which can influence availability for consumption by suspension feeders. In the present study, there was a greater contribution of kelp during the April (Fig. 6) sampling following the seasonal period of higher wind velocities and wave energy experienced in SW Ireland in spring and winter (O'Connor et al., 2012; Remmers et al., 2019). Similarly, the proportion of kelp detritus in POM was reported to be significantly higher on exposed shores where water movement and turnover were greater compared with sheltered area (Bustamante and Branch, 1996). In the current study, although no isotopic gradients in POM samples were obvious along the length of Berehaven, mussels from areas with greater water movement had a higher reliance on kelp detritus than mussels from areas with low residual current speeds (Fig. 1) which had higher POM contributions. This spatial pattern is reflected in the changes in the isotopic values of the mussels within Berehaven (Fig. 5). Few studies on bivalve diets have looked at how localised temporal changes in phytoplankton availability are reflected in dietary shifts as indicated by changes in the isotopic signature as found in the mussels in Berehaven (Fig. 7). However some studies have reported similar increases in phytoplankton contribution to the diets of suspension feeders with increased phytoplankton availability. In Antarctica the diet of the bivalve *Lanternula elliphium* was found to be more reliant on detrital material under the ice sheet, but shifted to one that consumed more phytoplankton and macroalgae in open water (Norkko et al., 2007). The authors suggested that detritus is an important food source where there is strong seasonality in primary production (Norkko et al., 2007). Earlier it had been proposed that kelp detrital contributions to the diet of filter feeders should be higher during winter in Alaska, USA, than during summer when phytoplankton density was at its greatest, (Duggins et al., 1989). This hypothesis was confirmed in Washington state, where kelp detritus was found to form 86–88% of the diet of mussels in winter, but only 22–73% in the summer (Tallis, 2009). Similar results were obtained around the South African coast with isotopic values of mussels on the east and south coast indicating reliance on the coastal particulate material dominated by macroalgal detritus, whereas mussels along the west coast showed greater reliance on offshore phytoplankton, where phytoplankton production is driven by Benguela current upwelling (Hill et al., 2006). Likewise, isotopic values of ribbed mussels (*Geukensia demissa*) indicated that individuals in the marsh centre were more reliant on *Spartina* detritus while those on the seaward edge obtained more of their nutrition from phytoplankton (Peterson et al., 1985). It is unclear whether these increases in the dietary contribution of phytoplankton as a

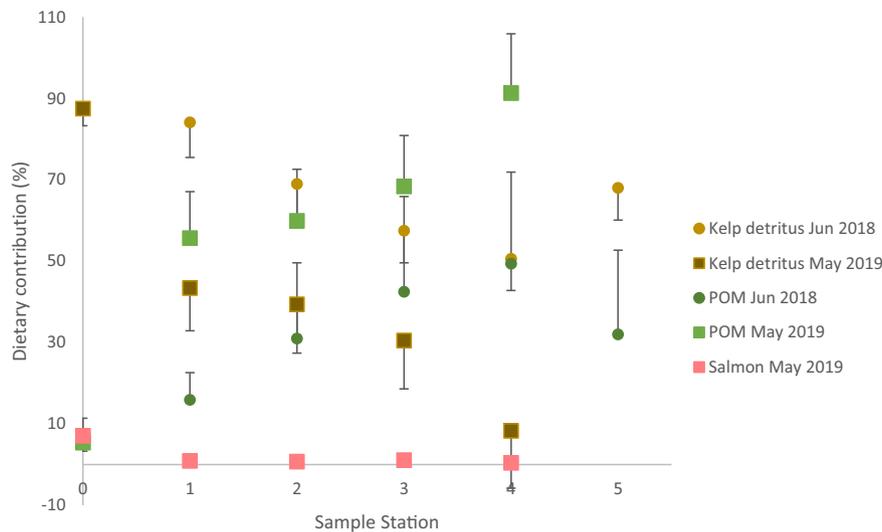


Fig. 6. Mean (\pm SD) contribution of kelp, POM, salmon waste to the tissue of mussels sampled at stations in June 2018, and May 2019.

result of increasing availability are driven by active preference or merely a passive response.

Norderhaug et al. (2003) demonstrated that the nutritional importance of kelp detritus depends on bacterial degradation making kelp more palatable as food. The current study also found that C:N ratios decreased at the distal end of the kelp blade, indicating bacterial-related increases in N with the disintegration of the blade with age. Similar enrichment with nitrogen at the distal end were reported for the kelp *L. saccharina* (Gevaert et al., 2001), and the brown macroalga *Ascoseira mirabilis* (Gómez and Wiencke, 1998). The isotopic differences between the stipe and distal ends of the *Laminaria* blade found in the current study of $\sim 2.5\%$ for $\delta^{15}\text{N}$ (Fig. 4) were very similar to that found for *Laminaria hyperborea* in Norway of -16.7 vs -18.7% for $\delta^{13}\text{C}$ and 5.5 vs 3.5% for $\delta^{15}\text{N}$, respectively (Fredriksen, 2003). Stephenson et al. (1984) also reported isotopic variations within the blade of *Laminaria longicuris*, and suggested that it may result from differential storage of biochemical compounds. In contrast Elliott Smith and Fox (2021) reported that the isotope change during the decay of kelp was generally small (-1.5 to 1.5%) and detrital material had a similar isotopic value to live kelp. However, we found with *L. digitata*, only the very distal ends of the blade had significantly different isotopic values, and were enriched in nitrogen, perhaps indicating that the changes are associated with degradation and bacterial colonization as postulated by Norderhaug et al. (2003). These isotopic changes might indicate that previous studies that did not use samples from the distal ends of

kelp blades may have biased estimates of their contribution to the diets of the target organisms.

The isotopic mixing model showed the contribution of salmon waste to the diet of mussels had distinct spatial patterns across sampling stations at each sample time. In April 2018 (just after harvesting the salmon) the salmon feed contribution was consistent at approximately 10% across the three stations (Stns. 2, 3, and 4) where mussels were found, this was likely the result of the highest salmon biomass and feed inputs and circulation patterns (Fig. 2). Whereas in May 2019, the biomass of salmon was low only having been stocked 5 months previously, and hence only mussels at Stn. 0 had a significant dietary contribution from salmon feed. It appears that either the effect from the cages is very distance limited and particulate outputs from the farms are rapidly dispersed in the water column, or that the isotopic signal from the salmon feed is significantly modified, so that it is indistinguishable from that of other sources. A recent review by Reid et al. (2018) suggested that impacts from aquaculture in areas of high water flow can be short-lived, and where commercial feeds are used, are rarely detectable beyond 100 m from the cage (Price et al., 2015). However, the April 2018 samples are not consistent with these reports, where even samples at Stn. 4 some 9 km to the west of the salmon cages showed a small, but significant, influence from the salmon feed. The bulk of C and N released from the cages is in the form of DOC and DON, which then have to be assimilated in phytoplankton biomass to be available to filter feeders. It is probable that this assimilation process would result in the loss of the isotopic identity of salmon feed and be significantly diluted. Sanz-Lazaro and Sanchez-Jerez (2017) also found that mussels did not directly assimilate fish farm waste products. They proposed that rather than thinking about direct nutrient flows between mussels and algae in conjunction with fed species in IMTA systems, IMTA should be thought of more in terms of regional nutrient pools where nutrient inputs from fed species are indirectly balanced by withdrawals by the culture of extractive species like suspension feeders and kelp. On this basis, for the Berehaven study area, the annual nutrient uptake by farmed mussels ($248.8 \text{ t-C yr}^{-1}$ and 49.1 t-N yr^{-1}) balances the particulate nutrient inputs from farmed fish (229 t-C yr^{-1} and 22 t-N yr^{-1}), indicating the aquaculture is having a neutral impact in terms of regional nutrient input to coastal waters.

In conclusion, we estimated that kelp production was equivalent to that of the water column phytoplankton. Furthermore, kelp detrital material was an important resource for suspension feeders supplying an estimated 59% of the diet of the mussels in Berehaven. The proportion that macroalgal detritus contributed to mussel tissue varied consistently with the position within Berehaven, and across sampling dates. Hydrodynamic models indicated that stations located in areas of higher water movement coincided with stations at which mussels received a great proportion of

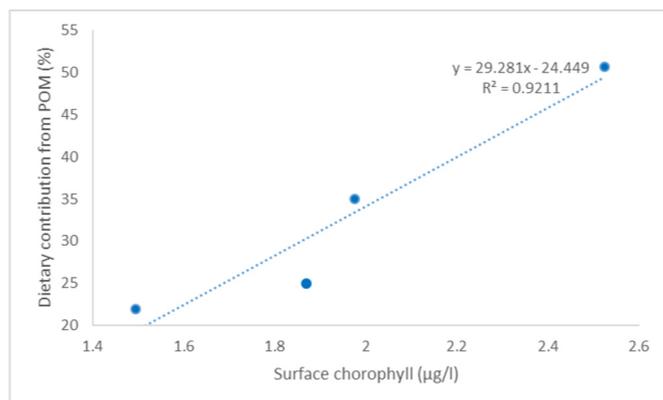


Fig. 7. Relationship between the mean surface chlorophyll concentration from the preceding two months at the Boatyard buoy (N51°38.98', W 09°48.00'), between stations S1 and S2, and the mean dietary contributions of POM to the tissue of mussels in Berehaven in April and June 2018, May and September 2019.

their diet from macroalgal detritus. We found similar patterns of enrichment in ^{13}C and depletion in ^{15}N in the older degrading kelp tissue at the distal end of the kelp blade compared with the growth tissue at the stipe end as previously reported which emphasises the need for careful selection of kelp samples when examining their contribution to the food web. The release of particulate waste products from the salmon cages was detected in the mussels, although there was no gradient in contribution and even those mussels growing on the cages had an isotopic signal that was no different from those growing several kilometres distant. It may be that the hydrodynamics of Berehaven result in the dispersal of salmon farm nutrients too rapidly for gradients to be assimilated in mussel tissues given the time taken for inorganic nutrients to enter the food web. As the cultured mussels, thought to be the dominant suspension feeding biomass in Berehaven, only consume $\sim 1\%$ of the kelp production, this resource is likely to play an important role in providing trophic subsidy to other habitats and may be a significant source for offshore blue carbon pools. The importance of kelp detritus needs to be recognised in relation to the controversial issuing of kelp harvesting licences both in UK and Ireland (Siggins, 2018; Sim, 2018) and continued harvesting worldwide (Barilotti and Zertuche-González, 1990; Rothman et al., 2006; Lorentsen et al., 2010) especially as kelp forests are declining in many areas (Vergés et al., 2014; Krumhansl et al., 2016) and are further threatened by climate change driven marine heatwaves (Arafah-Dalmau et al., 2020; Smale et al., 2020).

CRediT authorship contribution statement

M.E.M. Walton: Writing - Original Draft, Formal analysis, Investigation, **R. Browne:** Investigation, Writing - Review & Editing, **J.N. Griffiths:** Investigation, Formal analysis, Writing - Review & Editing, **D. Cartwright:** Investigation, Formal analysis, Writing - Review & Editing, **P. Robins:** Formal analysis, Writing - Review & Editing, **S.K. Malham:** Writing - Review & Editing, Funding acquisition, **L. Le Vay:** Investigation, Conceptualization, Supervision, Writing - Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.153191>.

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