



REVIEW OPEN ACCESS

Macroalgae and Bivalve Interactions: A Review of Trophic and Feeding Studies to Assess the Contribution of Macroalgal Detritus to Bivalves

Fiona P. MacKechnie^{1,2}  | Andrew G. Jeffs^{1,3} ¹Institute of Marine Science, University of Auckland, Auckland, New Zealand | ²Royal Netherlands Institute for Sea Research, Yerseke, the Netherlands | ³School of Biological Sciences, University of Auckland, Auckland, New Zealand**Correspondence:** Fiona P. MacKechnie (fiona.mackechne@auckland.ac.nz)**Received:** 18 August 2025 | **Revised:** 10 April 2026 | **Accepted:** 26 May 2026**Keywords:** bivalves | feeding | macroalgae | mixing models | stable isotopes

ABSTRACT

There is growing interest in the co-culture of macroalgae and filter-feeding bivalves due to anticipated trophic benefits that may enhance the productivity of both organisms. Detritus from cultured macroalgae has the potential to supplement bivalve diets, yet few studies have directly examined this relationship in co-culture systems. This review synthesizes findings from over 70 studies encompassing a broad range of macroalgae and bivalve species to assess the potential for macroalgal material to contribute to bivalve nutrition. No consistent patterns of macroalgal utilization by bivalves were found across regions, seasons, bivalve taxa, or macroalgal groups. In situ trophic assessments using stable isotopes and fatty acids produced divergent estimates of macroalgal dietary contributions, averaging 23.7% and 6.1%, respectively. Feeding studies of bivalves fed various forms of macroalgal material found that while relatively high rates of assimilation efficiency were measured for some bivalve species, the generally poor performance of bivalves in longer term feeding studies strongly indicated that the nutritional composition of the macroalgal material is insufficient, and/or that the macroalgal material contains compounds that actively inhibit bivalve growth. The majority of feeding studies found that regardless of the diet preparation method or species of macroalgae used, bivalve growth was reduced when macroalgae was incorporated at rates higher than a 25% replacement of feed dry weight. Overall, the findings point toward a generally limited potential for filter feeding bivalves to benefit significantly from co-culture with macroalgae, although specific pairing of macroalgae and bivalve species may derive greater advantage from co-culture.

1 | Introduction

The development of the co-culture of more than one aquaculture species in the same location holds promise for increasing the efficiency and sustainability of production provided it is beneficial to the growth and health of each species [1, 2]. Bivalve aquaculture is commonly included in multi-species aquaculture initiatives because of their ability to filter feed on organic particles in the water column and their minimal requirements for husbandry [2]. However, for bivalve aquaculture to be efficient, site selection becomes very important to ensure there is sufficient

available suspended organic matter to sustain the growth of bivalves at the high densities typically used in aquaculture [3–5]. For bivalve aquaculture, there is often interest in adding macroalgal aquaculture to already existing aquaculture sites given some similarities in infrastructure requirements while adding another extractive species with low husbandry requirements [2, 6–7]. Bivalve aquaculture can take the form of bottom cage culture, rack culture, continuous longlines, raft culture, or hanging cage/lantern nets in locations ranging from intertidal to coastal waters of up to 20–30 m depth, while macroalgal aquaculture can be done on longlines or raft culture within the top first

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2026 The Author(s). *Reviews in Aquaculture* published by John Wiley & Sons Australia, Ltd.

few meters of water [7–9]. Suspension feeding bivalves generally feed on organic particulates 2–250 μm in diameter but can ingest particles up to 500 μm , which are selectively retained from the water column as they pump water across their gills using cilia [4, 10–12]. There is also the potential for positive trophic interactions between bivalves and macroalgae that can improve overall aquaculture productivity, for example, nutrient excretion from bivalves contributing to the nutrient requirements of macroalgae, and macroalgal detritus contributing suspended food particles to the diet of cultured bivalves [1, 13–15]. A detailed understanding of how macroalgae or bivalves species interact trophically in the natural environment can help to characterize the nature of the potential trophic relationship arising from the co-culture of bivalves and macroalgae, as well as other interactions that may affect normal growth and behavior [4, 7–9, 16–17]. While macroalgae are well known to benefit from increased dissolved nutrients in the water column due to the presence of bivalve species in a co-culture situation [15, 18–19], it is less clear if there is a consistently positive effect of macroalgae on bivalve growth or nutritional condition. Some bivalves have the capacity to consume organic material other than phytoplankton, although there are differences in this capacity among bivalve species, and there is also significant differences in the composition of the organic material that is available to suspension feeding organisms, such as bivalves [4, 20–22]. Research of trophic interactions, as well as feeding and growth studies, has the potential to provide insight into the nature of the potential relationship between macroalgae and bivalves in co-culture [23–25].

Trophic interaction studies measuring tracers, such as stable isotopes (SI) and fatty acids (FA), offer a snapshot of interactions of species through the flow of carbon and nitrogen in an ecosystem, helping to elucidate how energy and nutrients are utilised by different organisms within an environment [26]. These methods are especially useful for indirectly determining the food sources utilized by bivalves, as direct measures of the food resources used by suspension or filter feeders are difficult to obtain and are often extremely variable across temporal and spatial scales [26–28]. Meta-analyses of trophic studies using SI indicate that carbon from macroalgae makes a large contribution to coastal ecosystems, including trophic contributions to many organisms, such as suspension feeders [25]. The results of these studies indicate that suspension feeders, such as bivalves, would be able to benefit from consuming and incorporating macroalgal detritus if it is available in an aquaculture setting. However, the broad trophic classifications in SI studies can result in estimates of an individual carbon source categorized by the type of feeding method, thus the category of suspension feeders often includes bivalves, sponges, polychaetes, crustaceans, and so forth [25, 29–30]. Hence, the actual contribution of macroalgae to the nutrition of bivalves may not be consistent with other groups of suspension feeders [25, 29–30]. Stable isotope analysis has been widely used to investigate trophic interactions, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ being the most commonly measured isotopes. The isotope $\delta^{13}\text{C}$ is primarily used to identify the sources of primary production in a food chain, while $\delta^{15}\text{N}$ decreases when passing through each successive trophic level [26, 31–32]. Analyses of SI of animal tissues reflect the isotope values of food that is consumed and utilized to some degree, providing an integrated representation of the diet and trophic level

of an organism [26, 31–33]. However, it becomes more complex when attempting to make estimates of dietary contributions for individual species and when the SI signatures of primary producers overlap [26, 27]. The overlap of SI signatures for primary producers is problematic when determining dietary sources for suspension feeders because there are many potential sources of particulate organic matter in coastal waters, including phytoplankton, zooplankton, decaying macroalgae, terrestrial matter and suspended sediments [21, 22, 34–37].

Fatty acid analyses (FAA) can provide qualitative and “semi-quantitative” markers of dietary and trophic linkages in marine food webs due the conservation of some fatty acids (FA) through trophic levels [38]. Fatty acid analysis can be an effective tool to use alongside SI analyses to help provide deeper insights of trophic interactions in an ecosystem [39–42]. Primary producers (i.e., phytoplankton, macroalgae, vascular plants, and bacteria) are the main sources of fatty acids within the marine environment and specific FAs and ratios of specific FAs can be used as trophic markers for tracing sources of food [38]. There is some overlap between sources of FA, because the amounts of FAs produced by algae can be affected by light, nutrients, and growth phase, and there are often similarities within taxa [38–40]. The FA profile of trophic sources is conserved to some degree between food source and consumers due to the limited ability of most animals for the *de novo* synthesis and conversion of some FAs, which helps in retaining the unique ratios of FAs specific to phytoplankton and macroalgal food sources [38–40, 43]. In general SI and FA analyses face similar constraints, whereby too much overlap can confound the mixing models that are used for translating the SI and/or FA data into estimating relative trophic contributions from different sources, and therefore sampling across temporal and spatial scales is encouraged to help parse out natural variation [38, 39, 41–42]. Rather than just reporting the differences between the isotopic composition between sources, mixing models can be used to estimate the contributions of different food sources to organisms based on the isotopic composition of the consumers and their possible food sources, often by using trophic discrimination factors (TDFs) which provide an estimate of how an organism incorporates food sources [26, 44–45]. These estimates are typically used to determine how much an organism may utilize or rely upon a specific food source.

Feeding and growth studies of bivalves can contribute to an understanding of their feeding biology, including particle selection and rejection, as well as ingestion and assimilation efficiency of different carbon sources, which are important considerations to understanding the role bivalves have in marine ecosystems [2, 46–47]. Macroalgae have an important role in providing habitat and food for other organisms and contribute significantly to the dissolved and particulate organic matter in the environment, and are significant sources of detritus in coastal ecosystems [14, 48]. Understanding the potential connections between bivalves and macroalgae aids in clarifying how these organisms interact with each other in natural and aquaculture environments. Hence, by reviewing the existing body of literature of trophic field studies and laboratory feeding studies, it should be possible to determine the potential contribution of macroalgal material to bivalve nutrition.

2 | Methods

2.1 | Trophic Studies

For locating publications regarding trophic studies—the keywords “stable isotopes” OR “fatty acids” AND “suspension feeder” AND “macroalgae” were used in Google Scholar and Scopus searches up to 09/2024 and limited to publications in English. Publications were reviewed by titles, and if relevant, then the abstracts and the body of the text of the manuscript were reviewed. Additional sources were obtained from the references cited in publications that were identified to be directly relevant. In total, 75 publications (i.e., peer-reviewed journal articles and theses) were selected that investigated the contribution of macroalgal material to individual or collective taxa of bivalves using stable isotopes (SI), fatty acids (FA), or both. In all, 63 papers analysed SI only, eight analysed only FA, and four analysed both SI and FA, for a total of 75 studies. Information on the species of bivalves, species of macroalgae, types of organic tissues collected, type of mixing model used, trophic enrichment factors for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (TEFs), and phytoplankton/POM sampling methods were collated. If possible, individual data points were separated by month, and months were classified by seasons (winter, spring, summer, autumn) according to the appropriate global Hemisphere (Northern or Southern). Global ecoregions were assigned based on Marine ecoregions classified by Spalding et al. [49]. Data from publications were extracted using Data digitizer (<https://apps.automeris.io/wpd/>) and included: means/medians, range or confidence intervals of the estimates of consumption of macroalgae by suspension feeders were extracted from graphs using Data digitizer if values were not explicitly provided in the text.

If possible, estimates for macroalgal contribution to bivalve nutrition were separated for different bivalve and macroalgal species, but this was not always the case due to the type of taxonomic groupings used by the mixing models that estimate trophic contributions from SI and/or FA data. For this review, the species of suspension feeding bivalves were classified into orders of bivalves to make broader groupings, while macroalgae were grouped by Class or Division. If macroalgal species were not identified in publications, or listed as an entity (e.g., turfing algae), the reference was listed as a mix and taxonomically unknown. Species of macroalgae and suspension feeders were checked and updated with currently accepted taxonomic names according to the World Register of Marine Species (<https://www.marinespecies.org/>) and AlgaeBase (<https://www.algaebase.org/>). If the date/month of the sampling was identified, the data were classified according to the season in the respective Hemisphere, and if presented, means were averaged over more than three seasons, the mean was considered a yearly estimate. The bivalve tissues sampled were classified as whole soft body, muscle, or by the specific organs. The amount and type of macroalgal tissue sampled was noted when specified, otherwise samples were classified as whole or partial samples. It was also recorded when corrections were made to $\delta^{13}\text{C}$ values due to lipid content for trophic models using SI [50]. If studies only used FAs or included both FAs and SIs analyses, the estimates of algal contribution to bivalves were grouped separately from the SI analyses alone.

To determine if there was any relationship between the bivalve orders, macroalgal Phylum/Class, and seasons, the mean estimates of macroalgal contribution were limited to the largest groups that contained sufficient data for comparisons. Likewise, the most common estimates for the separate seasons (i.e., spring, summer, autumn, winter) and the publications with yearly measurements were segregated. The bivalve orders with more than 10 estimates for macroalgal trophic contribution, and macroalgal Phylum/Class estimates with more than 10 estimates for the selected orders were isolated. The selected mean estimates for macroalgal trophic contribution to bivalves were compared with generalized linear mixed models using the R package *glmmTMB*. The model was run for the interaction of Phylum/Class $\times$ Bivalve order with seasons and carbon TEFs as a covariates and study ID as a random effect. The model was run with a Tweedie (log transformed) distribution. The R package *Dharma* was used to confirm the residuals and dispersion of the data complied with model assumptions. All means are presented as $\pm$ standard error.

2.2 | Feeding Experiments

To identify publications regarding bivalve feeding experiments the search terms “bivalves” AND “macroalgae” AND “detritus” AND “feeding” and minus the terms – “ascidian”, – “sponges” “holothurian”, – “cnidaria”, – “coral”, – “polychaete” were used as search terms in Google Scholar and Scopus. The term detritus was used in addition to macroalgae to address the consumption by bivalves of organic material other than phytoplankton, as well as the terminology for kelp derived-detritus used to characterize the contribution kelp detritus has in some coastal locations [4, 20, 25, 51]. Publications that included only vascular plants as food sources were excluded, but studies that included both macroalgae and vascular plants (i.e., seagrasses) were included. Information regarding the species of bivalves and macrophytes were extracted along with diet preparation, absorption efficiencies (AE), and mortality rates if provided. Information on feeding duration (hours, days, weeks) and relative measures of growth in bivalves were recorded, as well as any comparisons for measurements of growth against phytoplankton controls. Feeding experiments were diverse and generally divided into three categories that is, feeding of fresh/freeze-dried material, feeding aged material with natural bacteria, or feeding single cell detritus following bacterial or enzymatic digestion (single cell detritus, SCD). If studies presented absorbance efficiency (AE), the methodology used was recorded as AE, which is currently considered to be a measure of the immediate capability of the gut for digesting food and the availability of the organic content provided, rather than the assimilation efficiency, which is a measure of an organism's uptake of energy and nutrients into tissues when fed on a specific diet and after accounting for respiration and excretion loss [52]. Other metrics of health or growth in the studies included shell growth, rates of mortality/survival, condition index (CI), spawning rates, or live weight. Growth or health of the bivalves on macroalgal diets regardless of the specific metric that was used, was classified as positive, negative, or neutral in comparison to the referenced controls, which typically consisted of unfed or phytoplankton-only diets.

3 | Results

3.1 | Stable Isotope Studies

3.1.1 | Ecoregions and Seasons

Studies examining the trophic contribution of macroalgae to bivalves using SI only were heavily skewed toward the Temperate Northern Atlantic and Temperate Northern Pacific, making up 49% and 19% of the 67 studies that made SI measurements, respectively (Table 1). In all, macroalgal trophic contributions to bivalves in temperate locations accounted on average for $23\% \pm 20\%$ ($n=435$ data observations), while in Polar locations macroalgal contribution accounted for $38\% \pm 21\%$ ($n=25$) and Tropical locations $18\% \pm 6\%$ ($n=11$). Although global bivalve species richness is highest in tropical locations, bivalve species are utilized by humans in large numbers in both temperate and tropical coastlines, where upwelling and coastal mixing makes these locations ideal for bivalves in providing the conditions for growth, and thus exploitation and aquaculture [4, 120]. In contrast, global macroalgal primary production is highest in the temperate locations, which primarily consist of species in the Class Phaeophyceae as major primary producers in coastal waters [121, 122]. The net primary production in tropical coastal locations is dominated by phytoplankton, but there is a gradual shift toward greater contribution to production from macroalgae with increasing latitude, which is the dominant primary producer toward the poles [122]. Thus, the overlap between bivalve species and macroalgae is highest at temperate locations, which is also a location of interest due to harvesting and aquaculture of bivalve and macroalgal species. There was not a large variation in the trophic contributions of macroalgae to bivalves among the individual seasons (spring, summer, autumn, winter), which had a combined mean of $24\% \pm 20\%$ ($n=286$

observations) (Figure 1). In comparison, measures taken over a year were low at $14\% \pm 15\%$ ($n=63$ observations).

The majority of SI studies were for the purpose of investigating trophic food webs of different natural environments and species ($n=61$). Only six studies used SI to investigate relationships between organisms and their environment for the purpose of aquaculture [55–57, 68, 123–124]. One study used SI to determine competition and overlap between bivalve species [123], while four investigated the potential impacts of possible food sources near to existing bivalve farms [55–57, 69]. Only one study used SI to investigate potential food sources for the possibility of future aquaculture in a location [68].

3.1.2 | Bivalve Species

In all there were 72 species of suspension feeders studied or 13 taxonomic Superorders/orders of suspension feeders. Of those taxa, species in the order Mytilida made up 34% of all feeding studies, followed by order Cardiida (17%), Ostreida (14%), Venerida (8%), and Pectinida (8%), while the remaining eight orders each represented 1%–4% of all species studied. The estimate of macroalgal trophic contribution in the order Mytilida amounted to a mean of $24\% \pm 22\%$ ($n=195$ measures), while Ostreida and Cardiida accounted for $22\% \pm 19\%$ ($n=80$) and $22\% \pm 22\%$ ($n=98$), respectively. In the order Venerida macroalgal contribution accounted for $24\% \pm 19\%$ ($n=31$), while Pectinida and Carditida had a mean contribution of $46\% \pm 24\%$ ($n=12$) and $18\% \pm 18\%$ ($n=15$) (Figure 2).

The focus of studies on species in the orders Mytilida, Ostreida, Cardiida, and Pectinida is not unexpected, as numerous species

TABLE 1 | All studies that applied models using stable isotopes for determining the relative dietary contribution of macroalgae to bivalves as a mean macroalgal contribution with standard deviation (total studies $N=67$).

Ecoregion	Number of studies	Number of bivalve taxonomic orders	Number of bivalve species	Number of macroalgal species	Mean macroalgal contribution (%)	Sources
Arctic	2	6	7	9	51.6 ± 19.9	[53, 54]
Temperate Northern Pacific	13	7	18	42	22.6 ± 23.6	[55–67]
Temperate Northern Atlantic	32	10	23	86	20.9 ± 19.2	[34, 68–99]
Tropical Atlantic	1	1	1	1	15.5 ± 0.0	[100]
Central Indo-Pacific	3	3	6	8	19.4 ± 11.0	[101–103]
Temperate Southern Africa	2	3	5	10	29.3 ± 20.1	[104, 105]
Temperate South America	3	6	8	11	13.1 ± 10.9	[106–108]
Temperate Australasia	5	6	10	16	30.8 ± 23.5	[109–113]
Southern Ocean	6	5	5	15	26.1 ± 21.3	[99, 114–119]

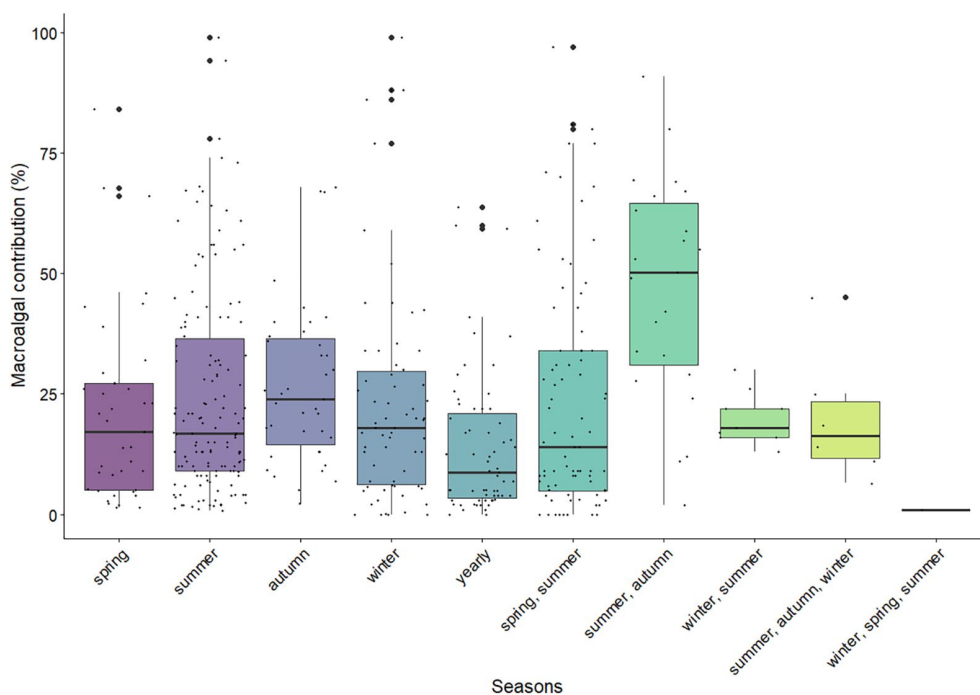


FIGURE 1 | Boxplot of the median percentage trophic contribution of macroalgae to different bivalve orders extracted from 67 published studies. Dark horizontal line represents the median and the solid boxes represent the interquartile range (IQR) and whiskers representing the $1.5 \times \text{IQR}$. Data outliers are bolded points outside of the $1.5 \times \text{IQR}$.

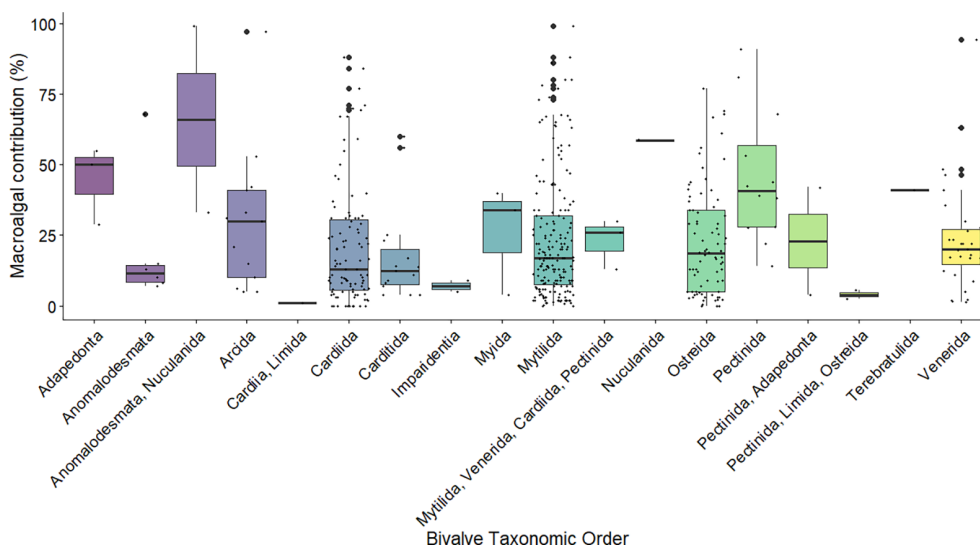


FIGURE 2 | Boxplot of the median macroalgal trophic contributions to bivalves, regardless of species, by seasons collated from a total of $n = 67$ published studies using stable isotopes to examine the trophic relationship. Results reported in studies from combined seasons as well as individual seasons are presented. Dark horizontal line represents the median and the solid boxes represent the interquartile range (IQR) and whiskers represent the $1.5 \times \text{IQR}$. Data outliers are bolded points outside of the $1.5 \times \text{IQR}$.

in these orders are harvested from the wild or cultured for human consumption, as well as recognized as ecosystem engineers [2, 8, 120, 125–126].

3.1.3 | Macroalgal Sources

For macroalgal sources of nutrition for suspension feeders included in all studies there was a total of 169 named macroalgal

species, three cases of only the Phylum being named and three unidentified as macroalgal turf mix. There were 258 individual specimens of macroalgae collected for analyses. When grouped by macroalgal Phylum/Class, individual species in the Class Phaeophyceae dominated those sampled in published studies, making up 42% of all species examined ($n = 69$) or 40% of individual samples (104 of 258), while species in the Phylum Rhodophyta made up 38% or 62 species that were sampled or 31% of individual samples (79 of 258). Species in the Phylum

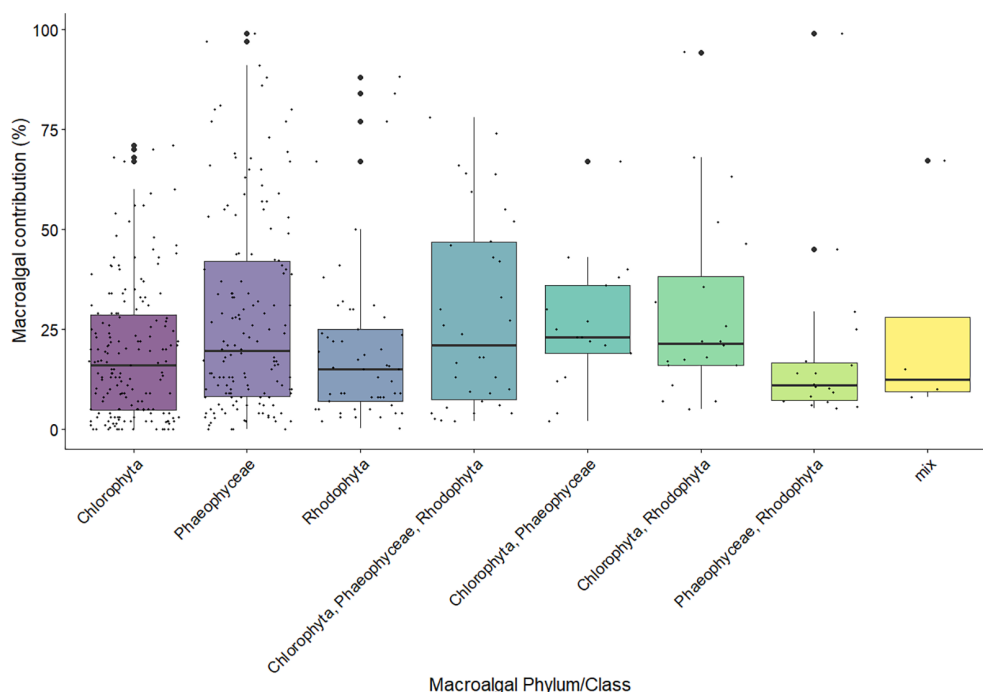


FIGURE 3 | Boxplot of the median macroalgal trophic contribution to individual bivalves as measured with SI when partitioned by the contributions of different Phylum/Class groupings of the macrophytes sampled in the studies. Dark horizontal line represents the median and the solid boxes represent the interquartile range (IQR) and whiskers representing the $1.5 \times \text{IQR}$. Data outliers are bolded points outside of the $1.5 \times \text{IQR}$.

Chlorophyta comprised 19% of all species or 28% of individual samples (72 of 258). Comparing the trophic contributions to bivalves as estimated by SI, macroalgae in the class Phaeophyceae contributed on average $29\% \pm 25\%$ ($n=154$ measures) compared to $19\% \pm 17\%$ ($n=175$) and $20\% \pm 21\%$ ($n=50$ estimates) for Chlorophyta and Rhodophyta, respectively (Figure 3). In studies that combined all macroalgal species, the measurements of the average macroalgal trophic contribution to bivalves for the sampled Chlorophyta, Rhodophyta, and Phaeophyceae was $29\% \pm 24\%$ ($n=33$) (Figure 3).

A total of 22 studies provided measurements of the trophic contribution to bivalves based on sampling of SI data from different components of the various macroalgal species, for example, parts of whole macroalgae in situ, detached or drift macroalgae, macroalgal detritus and so forth. Of those studies, six analysed detrital or drift macroalgae [53, 58, 70–72, 102]. The remaining 16 studies identified which part of the macroalgal tissue was sampled, that is, apical, basal, distal, thallus, or recent growth tissues [59, 73–74]. The remaining studies [45] did not specify which part of the macroalgae was sampled, mentioning only the species sampled and how it was treated prior to analyses (e.g., removal of epiphytes, rinsed with deionized water).

3.1.4 | Lipid Normalization and Trophic Enrichment Factors/Trophic Discrimination Factors

Trophic enrichment factors/trophic discrimination factors (TEFs/TDF) are used to represent the stepwise increases that occur as the trophic levels of organisms increase and these are used within SI mixing models to estimate trophic contributions to an organism [26]. In general, with each increasing trophic

level there is a 1% increase in $\delta^{13}\text{C}$ and 3.4% increase in $\delta^{15}\text{N}$ as determined by controlled feeding studies and meta-analyses [31–33, 44, 127]. The specific TEF/TDFs applied in a mixing model can have a significant effect on the estimated trophic contribution of a food source to an organism [75]. Carbon TEF/TDFs in the sampled publications ranged from 0% – 2.2% , with a 1% (28% of publications) and 0.8% (13% of publications) TEF representing the most common enrichment factors applied to $\delta^{13}\text{C}$ in models. Two studies did not report the enrichment factors they used [60, 115]. The most common nitrogen TEF/TDFs were 3.4% (25% of publications), 2.3% (8% of publications), and 3.8% (10% of publications), with a range from 1% – 4% and 10 of 67 publications not using/providing $\delta^{15}\text{N}$ TEF/TDFs in the mixing models, as some studies did not apply nitrogen isotopes. Trophic enrichment factors have only been calculated for a few species of suspension feeders (i.e., *Magallana gigas*, *Mytilus edulis*, *Mactra veneriformis*, and *Ruditapes philippinarum*) and involves controlled feeding experiments to establish an organism's baseline $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and how quickly these change with the provisioning of a specific food source over time (i.e., typically 1–3 months for bivalves) until reaching an asymptote for changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ [123, 128]. Trophic enrichment factors can be different depending upon the specific tissues that are sampled, as it is effectively a calculation of the tissue replacement/turnover [123, 127, 129]. For understanding species-specific utilization of carbon and nitrogen sources, a more precise TEF adds to the understanding of how much of an available food source is assimilated into tissues, and thus how different diet composition alters the rates of carbon and nitrogen turnover within the organism [128, 130–134].

As lipid is typically low in $\delta^{13}\text{C}$ compared to protein and carbohydrate, processes such as lipid extraction from tissues prior to SI

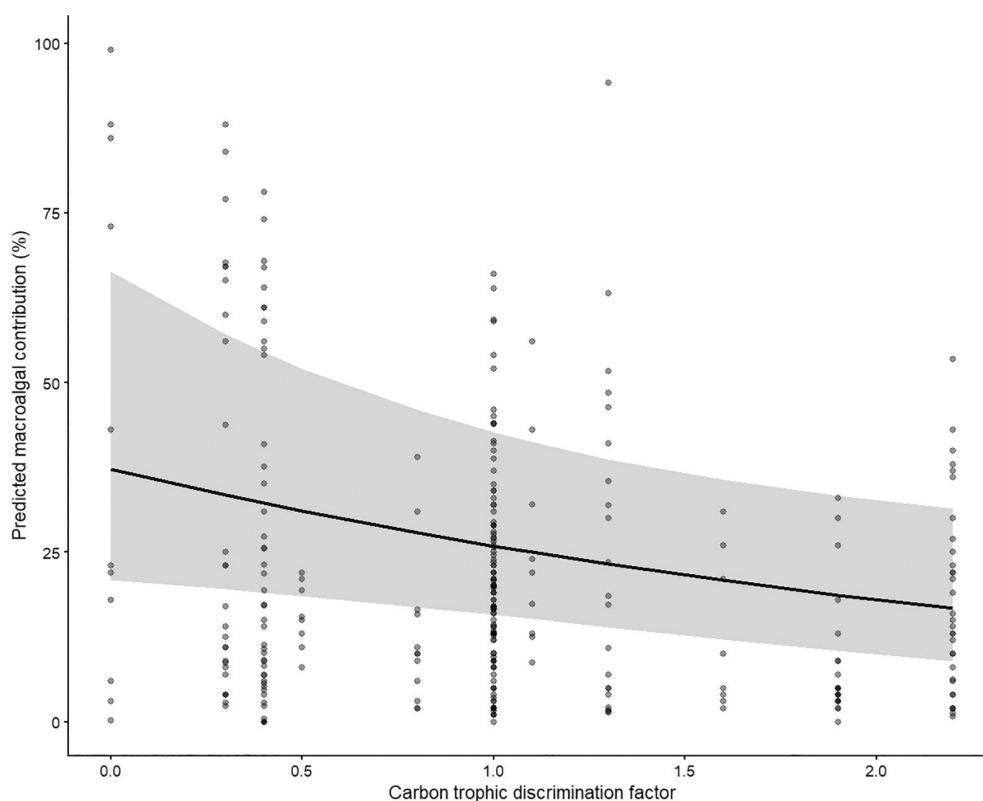


FIGURE 4 | Model of predicted macroalgal contribution to bivalves with increasing carbon trophic discrimination factor (TDF) plotted with 95% CI in gray and overlaid by carbon TDFs from studies.

analyses or mathematical corrections for the lipid content of an organism's tissues are sometimes applied in SI studies, depending upon the amount of lipid present in a sample (typically over 5%) [50, 127, 135]. Correction for tissue lipid content in SI studies was applied in the published studies more widely after 2006, although this was not consistent across all studies. The application of a lipid correction needs to account for the importance of lipid and carbohydrate in a specific organism's diet and for their catabolic reserves, as applying a correction based on lipid content or C:N ratios will change the $\delta^{13}\text{C}$ of the source and consumers used in mixing models and thus estimates of source contributions [50, 135–136]. The choice and application of TEFs and correction for lipid can significantly alter the estimated trophic contributors to an organism and therefore needs to be applied with careful consideration [76]. In the studies identified in this review, lipid or C:N corrections were only applied in a limited number of studies ($n = 10$) [53, 54, 75, 76, 106, 107, 109, 116, 117, 124]. Of those studies, four used mathematical C:N corrections from Post et al. (2007) [75, 76, 109, 116], four applied lipid corrections [106, 107, 117, 124], one applied both lipid and C:N corrections [54], and one study used lipid extracted samples for SI analyses [53].

3.1.5 | Macroalgal Phylum/Class $\times$ Order

The covariate carbon trophic discrimination factor had a significant effect on the estimated macroalgal contribution ($\chi^2 = 5.31$, $\text{df} = 1$, $p = 0.02$). The factor of Phylum/Class was marginally significant ($\chi^2 = 12.29$, $\text{df} = 6$, $p = 0.056$), as was the interaction of Phylum/Class $\times$ order ($\chi^2 = 16.60$, $\text{df} = 9$, $p = 0.055$). The

bivalve order ($\chi^2 = 6.09$, $\text{df} = 4$, $p = 0.19$) and covariate of seasons ($\chi^2 = 7.51$, $\text{df} = 4$, $p = 0.11$) had no significant effect on macroalgal contribution. The model accounted for some of the variance for the estimated macroalgae contribution (marginal $R^2 = 0.22$, conditional $R^2 = 0.54$), indicating that differences between studies accounted for 33% of the total variance. As the carbon trophic discrimination factor increased, there was a decrease in the estimated macroalgal contribution ($\beta = -0.36 \pm 0.16$, 95% CI $[-0.67, -0.05]$), at a rate that a 1-unit increase resulted in a 30% decrease in macroalgal contributions (Figure 4).

The bivalve order of Cardiida, Carditida, Venerida, and Ostreida had no differences for the estimates of the trophic contributions of different macroalgae, but there were some slight differences for the order Mytilida (Figure 5). The order Mytilida had the most estimates of macroalgal trophic contributions [61] and the largest differences between estimates of trophic contribution derived from among the macroalgal Phylum/Class groupings (Figure 5). In the estimates for the order Mytilida, the macroalgal group Phaeophyceae (18.5 ± 3.1 , 95% CI $[11.8, 29.0]$) ($p = 0.01$) and Chlorophyta, Phaeophyceae, and Rhodophyta (33.1 ± 10.7 , 95% CI $[13.1, 78.6]$) ($p < 0.01$) were larger than the estimates for Rhodophyta (3.4 ± 1.8 , 95% CI $[0.8, 14.1]$) (Figure 5). There were no other differences between the remaining macroalgal groupings.

3.2 | Fatty Acids and Essential Amino Acids

The number of studies that analysed FA contributions to bivalves was small (i.e., $n = 10$ out of a total of 75 studies that were

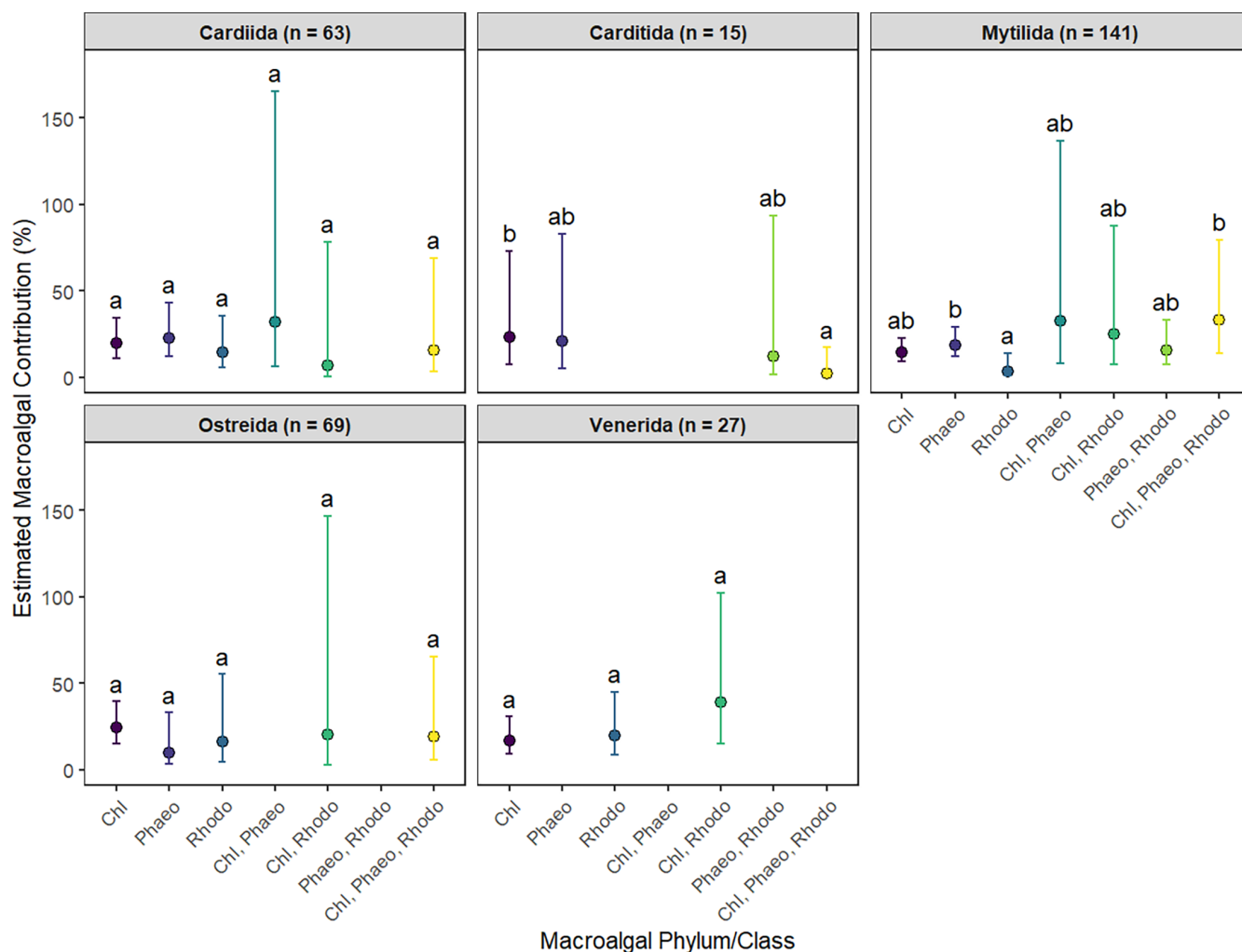


FIGURE 5 | Back-transformed Estimated Marginal Means (EMMs) for the most common bivalve orders from 42 published studies which used stable isotopes to examine the trophic relationship between macroalgae and bivalves and arranged by the most common groupings of macroalgal Phylum/Class. Different letters represent significant differences in macroalgal Phylum/Class contributions within bivalve orders.

reviewed) and of those 10 studies, only three provided separate analyses for both SI and FA [53, 68, 102] (Table 2). As most of the studies were on the trophic transfer of energy, the majority of analyses used multivariate analysis to compare the specific FAs ratios of the primary producers to those of the consumers to make estimates for the trophic contribution of FAs of macroalgae to bivalves. However, one study used mixing models that incorporated both FA and SI to make estimates of macroalgal trophic contributions [77]. Overall, the mean trophic contribution by macroalgae to bivalves as estimated by FA alone was $6.1\% \pm 6.2\%$ (range: 0.1%–28.3%) (Table 2) and there was no significant difference in trophic contributions by macroalgae among Phylum/Class, as the majority were estimated at under 10% overall contribution (Figure 6). Of the two studies that had at least one measurement above 10%, one was in a unique shallow water bight [137]; and the other considered multiple macrophytes for FA contribution, where the highest estimated contribution was from decaying vascular marine seagrasses and epiphytes, which due to bacterial colonization would be likely to result in different biochemical composition and digestibility of the material [77] (Figure 6). One study also incorporated essential amino acids (EAA) into the analysis, from which the estimated contribution of macroalgae to bivalves was $7.6\% \pm 5.2\%$. Although including

EAA is thought to provide greater capacity to trace the transfer of biochemical components through the ecosystem, the processing of samples is time consuming, more complex and expensive to undertake [138].

3.3 | Feeding Experiments

In total there were 30 feeding studies that utilized macroalgae diets, of which 12 used aged or bacterial degraded macroalgal tissue, 12 used dried/freeze-dried particles, and six used single cell detritus (SCD). The feeding studies accounted for 16 bivalve species in total covering some seven orders of bivalves. The bivalves *R. philippinarum* and *M. gigas* each accounted for 17% (5 studies) and 20% (6 studies), while *C. edule* accounted for 10% (3 studies). The bivalves *Abra segmentum*, *M. edulis*, *M. trossulus*, *Aulacomya atra*, and *Placopecten magellanicus* each represented 7% (2 studies each), while the remaining bivalve species represented less than 4% (1 study) each. For the feeding experiments there were 32 species of macroalgae, 6 vascular species, and 12 species of phytoplankton represented. Of the macroalgal species used, *Ulva* spp. was the most commonly used species at 34% (18 studies). Macroalgae in the phylum Chlorophyta and

Rhodophyta represented 19% (6 species) and 22% (7 species) each, while those in the class Phaeophyceae represented 59% (19 species). Diet preparations for dried/freeze-dried material involved drying fresh/cleaned material and grinding and sieving to less than 100 μm particles. A small number of studies added silt or diatomaceous earth to alter the inorganic content of the diets [139, 140]. Experimental SCD diets were prepared by enzymatic digestion, with the exception of one study that used freshwater to induce cell lysis [141]. Studies using aged or bacterial

particles to feed bivalves applied a variety of methods including aging whole sections of lamina and filtering the residual particles/bacterial biofilm [24, 142], aging the whole lamina and grinding [143, 144], or grinding and aging the particles in natural seawater/bacteria [145–147]. It should be noted that there are established estimates of ingestion and absorption efficiency of macrophytes/vascular marsh plants by bivalves in the literature; however, as this review was focused on the contribution by macroalgae, these studies were not included in this current analysis of the feeding studies [148–154].

TABLE 2 | Mean trophic contribution ($\pm$ SD) from macroalgae to bivalves as estimated by FAs for six ecoregions for 11 published studies examining the trophic relationship between macroalgae and bivalves.

Ecoregion	Number of studies	Number of measurements	Mean $\pm$ SD
Arctic	3	6	4.1 $\pm$ 2.1
Temperate Northern Pacific	3	7	6.8 $\pm$ 7.0
Temperate Northern Atlantic	2	5	11.8 $\pm$ 9.8
Central Indo-Pacific	1	4	2.8 $\pm$ 0.3
Temperate Southern Africa	1	1	3.3 $\pm$ 0.0
Temperate Australasia	1	3	4.2 $\pm$ 0.5

3.3.1 | Descriptive Feeding Studies

The metrics used in the 19 studies that classified growth in metrics other than AE ranged from ingestion, clearance rates (1h^{-1}), shell growth, condition index, mortality, survival, wet weight/live weight, dry weight, nitrogen incorporation, standard metabolic rate, and digestive gland dry weight (Supplementary Table 1). The time scales used ranged from minutes—hours (5 studies), days [1–30] (8 studies), and months [1–6] (6 studies). The majority of studies compared simply feeding macroalgae or phytoplankton alone [23, 130, 142–147, 155–157]. A smaller number of studies included mixed phytoplankton/macroalgae diets (dw/dw) at various concentrations of both [24, 141, 158–163]. The majority of the studies tested only solid macroalgal particles, but a small number of studies tested the effects of dissolved organic matter derived from macroalgal particles [24, 143–144]. There was one study that included the growth of oysters fed SCD from *Saccharina latissima*, as well as growth of oysters fed the feces of urchins that had been fed *S. latissima* [160].

Of the studies that included mixed phytoplankton/macroalgae, results that included a 25% replacement of phytoplankton with macroalgae typically had similar or slightly improved

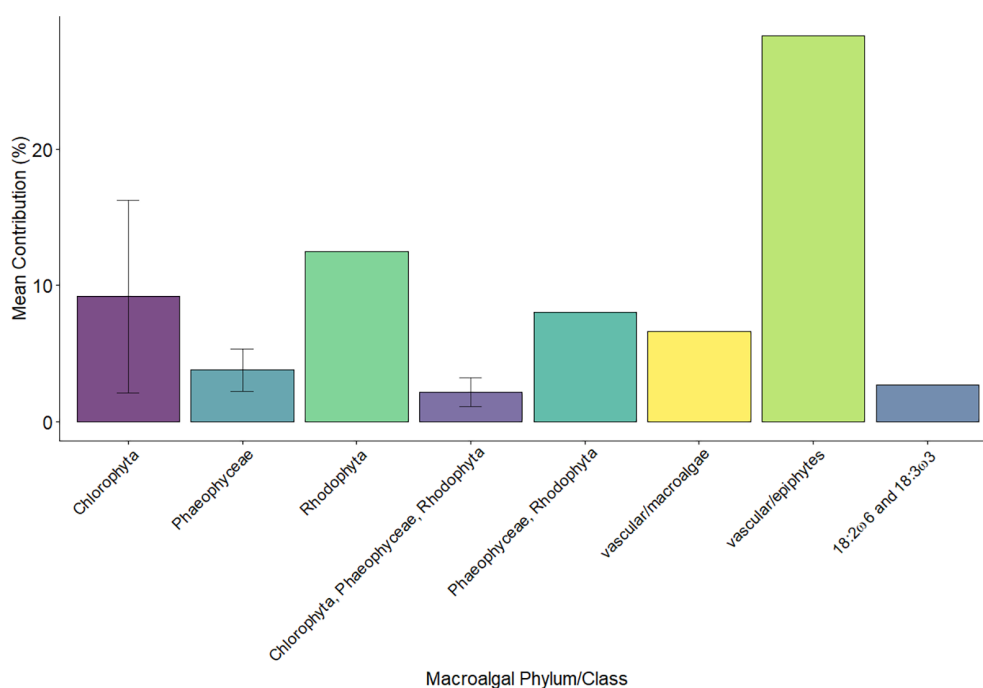


FIGURE 6 | Mean macroalgal trophic contributions to bivalves as estimated with FA (18:2 ω 6 and 18:3 ω 3) for individual and grouped macroalgal Phylum/Class for 11 published studies which examined the trophic relationship between macroalgae and bivalves using FA.

health metrics compared to a phytoplankton only diet (i.e., similar wet weight; 90% to 88% survival, or 60% to 70% spawning) [134, 141, 161]. For bivalves fed a 50:50 diet of phytoplankton:macroalgae, the growth of the bivalves was found to decline slightly, but not significantly from the 75:25 diet of phytoplankton:macroalgae, but on a 25:75 phytoplankton:macroalgae diet, bivalves typically experienced a dramatic decline in health and growth in comparison to the other diets (Table S1) [134, 141, 161–162]. There was only one study where the diet of only macroalgae resulted in a similar growth to the diet of only phytoplankton [156], while in all other studies a 100% macroalgal diet resulted in significantly lower growth/health metrics compared to the phytoplankton or mixed diets, although the diet preparation methods (fresh/aged/SCD) varied among the studies [134, 141, 146, 155, 158–163]. Rarely did growth on a mixed diet of phytoplankton and macroalgae exceed a diet of only phytoplankton, and in cases where it did, the macroalgae in the diet was an addition to a baseline phytoplankton diet, not as a replacement for any phytoplankton in the diet [159].

The choice of macroalgae species used in the preparation of experimental diets for bivalves were generally native or naturally occurring wild species of macroalgae or vascular plants (i.e., seagrasses) that occur in similar locations as the bivalves species studied, but in some cases commercially available ground macroalgal material was used [130, 161–162]. Three studies with SCD macroalgal diets resulted in 100% mortality of the fed bivalves, two studies with bivalve larvae and juveniles fed *Pyropia* spp. and one study with larvae fed *S. latissima* [141, 155, 158]. Several other studies report feeding juvenile bivalves particles from a range of macroalgal species in the Phylum Rhodophyta (*Gracilaria* sp., *Chondrus* sp., *Corallina* sp., *Rissoella* sp.) with no increase in mortality or positive ingestion rate [140, 144, 163–164]. The complete mortality of the larval and juvenile bivalves on the *Pyropia* spp. could indicate that the mortality in the studies with *Pyropia* spp. is related to the specific biochemical components in the macroalgal or a lack of digestibility of the material, but as the studies involved different species of bivalves and macroalgae [141, 155] this is only speculative. The other study to focus only on larval bivalves, tested ingestion on a presence/absence basis, so it is unclear if the life stage used was a contributing factor to the increases in mortality [142]. Many macroalgae contain anti-grazer chemical compounds, such as polyphenols (Phaeophyceae) and halogenated compounds (Rhodophyta), that deter grazing by herbivores and can bind to proteins, thus potentially limiting the potential nutritional value of macroalgal material consumed by bivalves [165]. Polyphenol concentrations in macroalgae were only measured in two published studies, in which polyphenol concentrations displayed an exponential reduction over 8 days and did not affect ingestion of the macroalgal material by bivalves [145, 147]. Three out of the 19 studies measured changes in enzyme activity in the digestive gland and the alimentary canal of bivalves when fed macroalgal material or for seasonal changes for wild populations depending upon the diet (macroalgae:phytoplankton ratios). These findings indicate that bivalves are able to adjust their digestive processes to the available food sources, with the changes in the digestive enzymes appearing to reflect the different biochemical composition (i.e., lipids, proteins, carbohydrates) of the available macroalgae [23, 134, 155]. Some macroalgal diets were damaging to the bivalves, as shown in the histology of the digestive gland for

M. gigas fed on *U. clathrate* which showed tissue damage and atrophy [155].

3.3.2 | Absorbance Efficiency for Experimental Feeding

The 12 feeding studies that measured AE for bivalves that were experimentally fed a range of macroalgae and vascular plant material (i.e., seagrasses) produced varying estimates among species and diets (Table 3). This may be due in part to differences in the experimental arrangements among studies, which have included static feeding over varying timescales of hours to minutes to weeks (Table 3). The lowest macroalgal AE (3%–9% AE) from over 12 published studies which measured AE in bivalves fed macroalgal material, occurred in the species *A. segmentum*, in feeding studies that used ^{14}C radiolabelled macroalgal diets to measure the transfer of nutrients between diets and bivalve tissues [164, 166]. Radiolabelled macroalgal diets were also used in three other studies that resulted in moderate AE (25%–53%) for the bivalve species *A. ater* and *P. viridis*, indicating it may be a related to the species of bivalve or macroalgae used, but it is difficult to draw any conclusions without a phytoplankton AE baseline for comparison [164, 166–168, 170]. The one study using enriched isotopes found comparable AE between phytoplankton (54%) and macroalgae (54%–71%), but the number of bivalves that consumed the macroalgal material (25%–30%) was significantly lower than for the phytoplankton (75%) [157]. The methodology for measuring absorbance of nutrients from food by filter feeding organisms has changed over time. Originally, Conover's mass balance model was widely used, which accounted for the organic content of the food ingested compared to the egested feces. Increasingly, this model has been modified to also account for the production of pseudofeces and the metabolic cost of digestion that processing particulate organic matter can incur [20, 173–174]. For this reason, two studies only reported measurements of gross rates of absorption, as they were unable to account for losses in bivalve tissues during digestion of the ingested macroalgal material [171, 172]. Four of the 12 published studies reporting AE for bivalves feeding on macroalgal particles used either Conover's method or a variation on the method as detailed by Iglesias et al. (1998), which is the currently accepted standard method for measuring gross absorption efficiency in bivalves [23, 139, 140, 157, 169]. Only one study looked at AE in wild bivalve populations utilizing diets derived from naturally occurring macrophytes among seasons, and the results indicated that the AE of the different diets was related to changes in the digestive capabilities of the bivalves [140].

In the five published studies measuring AE in bivalves feeding on macroalgal material where there was a phytoplankton control diet, the corresponding mean AE for the phytoplankton diet (42%–77%) was not significantly different from the AE of the macroalgal diets (45%–80%) [140, 157, 167, 171]. In cases where vascular plant material was used (i.e., seagrasses), the mean AE for the plant material was typically slightly lower than that measured for the phytoplankton or macroalgae possibly indicating that there are components present in vascular plant material, such as lignocellulose, that are indigestible by bivalves [23, 140, 164, 166, 169]. The dietary material used in these feeding experiments was fresh freeze dried plants or macroalgae which could be expected to have a different biochemical

TABLE 3 | Compilation of published studies ($n=12$) that calculated absorbance efficiency (AE) of bivalves fed on different experimental diets incorporating phytoplankton, macroalgal, or vascular plant material. Means are grouped by bivalve species, diet macroalgal classification, and diet preparation. Means and SD are collated from individual measurements.

Bivalve species	Diet preparation	Diet classification	n	Mean AE ($\pm$ SD)	Author and feeding duration
<i>Abra segmentum</i>	Freeze dried/ ground	Chlorophyta	2	8.3 ± 1.7	Charles et al. [164] (4–48 h)
		Phaeophyceae	7	5.0 ± 3.7	Charles [166], Charles et al. [164] (2 h) (4–48 h)
		Rhodophyta	2	9.2 ± 3.5	Charles et al. [164] (4–48 h)
		vascular	2	2.8 ± 0.4	Charles [166], Charles et al. [164] (2 h) (4–48 h)
<i>Aulacomya ater</i>	Aged particles/ bacterial growth	Phaeophyceae	34	52.6 ± 8.7	Stuart et al. [167, 168] (4 h)
		phytoplankton	4	48.8 ± 10.3	Stuart et al. [168] (4 h)
<i>Cerastoderma edule</i>	Freeze dried/ ground	Chlorophyta	14	54.3 ± 12.1	Arambalza et al. [23, 140, 169] (3–10 days)
		phytoplankton	3	42.3 ± 12.5	Arambalza et al. [140] (3 days)
		Rhodophyta	3	45.3 ± 31.5	Arambalza et al. [140] (3 days)
		vascular	12	33.0 ± 21.7	Arambalza et al. [23, 140, 169] (3–10 days)
<i>Mercenaria mercenaria</i>	Freeze dried/ ground	Benthic microalgae	2	46.6 ± 1.8	Secrist [157] (2–3 h)
		Chlorophyta	2	54.0 ± 6.3	
		phytoplankton	2	54.5 ± 17.3	
		Rhodophyta	2	70.9 ± 9.6	
<i>Laternula elliptica</i>	Freeze dried/ ground	Phaeophyceae	4	41.5 ± 11.4	Tatián et al. [139] (30 min)
<i>Perna viridis</i>	Aged particles/ bacterial growth	Chlorophyta	1	25.3 ± 0.0	Pan & Wen-Xiong [170] (3 days)
		Chlorophyta DOM	1	0.01 ± 0.0	
<i>Placopecten magellanicus</i>	Aged particles/ bacterial growth	Phaeophyceae (C, N)	4	80.5 ± 13.6	Cranford & Grant [171], Grant & Cranford [172] (8 weeks, 52 days)
		phytoplankton (C, N)	5	77.0 ± 10.4	

and microbial composition compared to eroding/decaying material [23, 140, 164, 166, 169, 175–177]. Typically macroalgal and vascular marine plant material has a higher C:N ratio than phytoplankton, which can be used as a proxy measurement of nutritional suitability, and is altered by aging/bacterial colonization of particulates [147, 177–179]. Overall, the mean AE measured for bivalves feeding on phytoplankton and macroalgal material ranged greatly among the 12 studies (5%–80% AE), but there was no clear pattern among the species of bivalve or macroalgae, and/or diet preparation (Table 3).

4 | Discussion

4.1 | Feeding Studies and SI Studies

The majority of the SI studies reviewed were focused on mapping the transfer of energy for natural populations of organisms, rather than for organisms in an aquaculture setting, although

there were six studies that used SI and/or FA for determining contributions of macroalgae to bivalves in an aquaculture setting in the field [55–57, 68, 69, 78]. The feeding studies were primarily focused on understanding consumption of detritus by bivalves or determining methods for the production of alternative food sources for raising bivalve larvae and juveniles. The results of the studies of experimental feeding of bivalves with macroalgal material are consistent with the SI studies of ambient diets in natural environments, with both sets of studies confirming that bivalves can generally consume and assimilate macroalgal detritus [23, 53–55, 58, 61–63, 70, 76, 79–83, 109–111, 134, 140, 141, 145, 155, 157, 158, 160–163, 169]. However, the collective growth metrics from these feeding studies suggest macroalgal trophic contributions to growth are typically inferior when compared to a phytoplankton diet. This is in line with some trophic studies that have found differences in the SI of bivalves between areas with and without kelp, but find that bivalve growth is primarily tied to phytoplankton abundance [110, 180]. The short term AE studies would indicate that bivalves have the capacity to ingest

and make some use of macroalgal material, which in some instances can be comparable to AE of a phytoplankton diet, but the long-term feeding studies indicate that macroalgal material is inferior for supporting growth in bivalves in the same manner as phytoplankton [130, 134, 146, 160, 161, 163]. The widely applied AE measurements provide a useful snapshot measure of the consumption of material and even though material is ingested, it does not mean it is assimilated at the same efficiency over longer time periods [173, 174, 181–182]. The lack of alignment between the results of short-term AE measurement and long-term feeding experiments for bivalves fed with macroalgal material indicate that research is yet to fully understand the ability of bivalves to derive nutrition from detrital organic material from sources other than phytoplankton [23, 134, 145, 146, 161, 163, 168]. The reason for the indigestibility of the macroalgal material could be due to several reasons, either the biochemical makeup of the macroalgal material limits the availability of the material to bivalves or the macroalgal material contains compounds that actively inhibit bivalve growth [165, 178]. Feeding studies that deliver enzymatically digested macroalgal material created through the use of hydrochloric acid, cellulose and endoglucanase enzymes or the addition of bacteria would have altered the polysaccharides of the macroalgae, potentially making them more digestible to bivalves [24, 134, 142, 145, 146, 155, 158–160]. In some cases, this degraded macroalgal material resulted in higher ingestion rates or better growth in the bivalves, but this was not consistent among macroalgal species likely due to differences in biochemical composition among macroalgal species and the varying capacity of bivalve species to digest the material [24, 134, 142, 145, 146, 155, 159]. In the small number of studies where bivalve growth was comparable or greater on macroalgal material than phytoplankton, the amount of macroalgal material needed was often a magnitude or more than the amount of phytoplankton required to achieve the same growth [24, 159].

4.2 | Stable Isotopes and Macroalgal Contributions

The total average macroalgal contribution to the diets of bivalves as estimated by SI from all the field studies combined was $23.7\% \pm 21.6\%$, but with a range of 0%–99% depending upon the seasons and location of the measurements [61, 62, 74, 183]. For the bivalve orders where it was possible to use the data in a model, the covariates of the macroalgal Phylum/Class, season, and carbon TEF/TDF only accounted for 22% of the model variation, whereas the random factor of study ID was responsible for another 33%, suggesting that differences among individual studies had a strong influence on the estimated macroalgal contribution to bivalves. Overall, there are still variables that cannot be explained by the model. There was a strong relationship between the decline in macroalgal contribution to bivalves with increasing carbon TDF. The large influence that the TDFs had on determining estimates of macroalgal utilization by bivalves emphasizes that the mixing models have inherent biases depending upon the parameters chosen [184, 185]. Indeed, some authors are clear that there can be significant differences based on the TDFs chosen, and that understanding how much of specific food sources are available in an environment and how an organism feeds can help to determine which TDFs are best applied for the organisms in question [70, 76, 123, 186]. The TDFs determined for bivalves are typically based on specific TDFs

determined for a few specific bivalve species fed phytoplankton diets or based on general TDFs determined for organisms based on their metabolism (poikilotherms vs. homeotherms) and environment (aquatic vs. terrestrial) [31, 32, 123, 127, 128, 184].

For the majority of the bivalve orders, there was no clear difference in the trophic contributions among the various Phylum/Classes of the macroalgae. Only the order Mytilida had greater trophic contributions from among different macroalgal Phylum/Classes. This could be expected as the order Mytilida accounted for 34% [187] of estimates in total and is among the most studied of the different bivalve orders [4, 120]. The higher trophic contributions for the combination of macroalgal Phylum/Class over individual Phylum/Classes may relate to the potential for a mix of macroalgae to provide a more diverse diet nutritionally, potentially overcoming any deficiencies from relying on feeding on a single macroalga and also more realistic in terms of the mix of particles from different macroalgae that would be present in the seston in situ. This lack of difference could be related either to aspects of the bivalve physiology/feeding methods, the macroalgal biochemical composition or degradation state, and the general availability of the detritus in the water column among different locations in which it has been measured for these published studies.

There is evidence that the parts of macroalgae sampled will have different SI signatures [147, 188–189]. The SI signatures of macroalgal meristematic or growing tissues are affected by environmental characteristics (i.e., nutrients, light, temperature, carbon availability), and longer-lived perennial species can have different SI signatures for growing and eroding tissues [190, 191]. Additionally, as different macroalgal species have different growth morphology (i.e., basal or apical meristematic growth) the sections of macroalgae sampled for SI analyses can have an impact on the SI signature when used in mixing models to assess the utilization of macroalgal material by bivalves if it is assumed that material available to the bivalves is coming from the eroding sections rather than the fresh material [175, 189]. For annual macroalgal species, such as some species of *Ulva* (Chlorophyceae) and *Undaria pinnatifida* and *Nereocystis lutekeana* (Phaeophyceae), the trophic contributions to bivalves would be expected to be higher during their senescence, but there was not enough evidence to distinguish a difference between seasonal estimated consumption of these macroalgae to bivalves from the published studies [57, 61, 62, 70, 84, 112, 123].

The degradation of kelp and other macroalgal material is an aspect of trophic studies that can be difficult to capture and define due to the changing composition of detrital matter in coastal ecosystems [21, 25, 36, 192]. Often there are changes in macroalgal and phytoplankton contribution to particulate organic matter (POM) that result in gradients of the macroalgal contributions along coastal areas or create seasonal differences as measured by SI methods in bivalves [21, 25, 35, 193–194]. In SI trophic studies, the practice of using the SI of offshore phytoplankton as a baseline for adjusting samples from coastal waters which contain contributions from both phytoplankton and other organic sources has been criticized as it can artificially inflate the contribution from macroalgae and other sources due to fundamental biological differences between coastal and oceanic phytoplankton [36, 37, 195]. Some research has tried to clarify

the differences in macroalgal/phytoplankton contributions to bivalves and has found spatial differences in contributions due to weather and upwelling/downwelling effects altering SOM/POM composition [21, 73–76, 113]. Other techniques have been developed to separate organic detritus and phytoplankton in seston so their SI contribution can be measured separately, for example microscopically [192], via density fractionation [196], staining [197], or flow cytometry [198] but these techniques can be difficult and time consuming to implement, and therefore not always feasible. As such, the focus has turned toward implementing complementary techniques such as FA analysis or EAA tracing of specific biochemical components in an effort to more accurately elucidate the trophic contributions of macroalgae to bivalves [25, 199–200]. Additional methods such as the addition of enriched isotopes or radioactive tracers added to environments are useful in accounting for the role that bacterial organisms have in recycling materials [201]. Collectively, these techniques allow further investigation into how POM and dissolved organic matter (DOM) breaks down in coastal environments, and how bacteria and detrital processes alter the biochemical composition of POM that cannot always be elucidated with SI alone [202–205]. Research on the decay processes and microbial colonization of macroalgal material (POM and DOM) shows clear changes in the amount and types of microbes, as well as the changes in C:N ratios that occur as the macroalgae decays, although the exact biochemical changes are not well described [145, 175–177, 179, 206–207].

4.3 | Feeding Experiments and Macroalgal Composition

As macroalgae usually have high amounts of complex carbohydrates (i.e., polysaccharides) in comparison to phytoplankton, changes in their biochemical composition (i.e., carbohydrates, proteins, lipids) may serve to make the macroalgal particles digestible to the bivalves either through the addition of bacteria or the breakdown of the various polysaccharides by the bacteria from the kelp material [178, 208–210]. For the optimal growth and survival of larval and juvenile bivalves, the optimal diet typically consists of multiple species of phytoplankton to completely meet their nutritional needs (lipid, carbohydrate, and protein) as the biochemical composition of different phytoplankton will differ significantly between species [211, 212]. The general biochemical composition of macroalgae as a whole (i.e., lipid: 3%, protein: 10%, carbohydrate: 49%) [178] is very different from phytoplankton which tend to have a higher lipid and protein content (i.e., lipid: 17%, protein: 32%, carbohydrate: 15%) and a lower C:N ratio [211, 213–214]. Lipid, especially the essential FAs of docosahexaenoic acid, eicosapentaenoic acid and arachidonic acid, are crucial in bivalve diets, and without good dietary sources, growth can be limited, especially in early developmental stages [211, 212, 215]. Bivalve feeding studies that have compared the biochemical composition of available phytoplankton to macroalgae have consistently found they are very different [23, 134, 155, 161–162]. These differences would explain the reduced growth for bivalves in long term feeding experiments after a certain percentage of replacement (50%–100%) of phytoplankton with macroalgae in the diet, despite the often similar rates of AE for bivalves fed macroalgae and phytoplankton, indicating that the biochemical composition of

the macroalgal material does not support the same growth rates as the phytoplankton material [23, 134, 141, 160, 161, 168]. In addition, the biochemical composition of the polysaccharides in macroalgae are very diverse and can sometimes affect the digestion and gut microbial composition of organisms that consume some macroalgae [210, 216–219]. Based on the changes in digestive enzymes of bivalves fed on different diets, clearly some bivalves have the ability to adjust their capacity to digest different food sources [23, 140, 155]. However, the results of the long term feeding experiments suggest there is reduced growth due to incomplete nutrition or interference to the digestive system of the bivalves when consuming most macroalgal material [23, 134, 155, 169]. With the application of microbial and enzyme degradation of macroalgal material to simulate the natural decay process or make particles more palatable or more bioavailable for bivalves, it would be expected that the biochemical differences would affect ingestion or absorption by the bivalves [134, 140, 144, 175, 179, 206, 220]. However, bivalve feeding studies comparing diets of fresh and aged particles have generally produced mixed results with differences appearing to result more from the macroalgal species that are used. This would indicate that biochemical differences among macroalgal species, including after degradation, are probably an important factor affecting the capacity of bivalves to digest the material [145, 146]. Whichever metrics are used to measure consumption, digestion, or growth in the feeding experiments, it is clear that the species of macroalgae from which the particles are derived have a large effect on the ability of bivalves to utilize them. Several feeding studies have tested multiple macroalgal species, and even for the same genus of macroalgae, have found differences in the measured characteristics [143–146, 155, 157, 163].

The mortality of some bivalves in feeding experiments suggest that damage by ingesting macroalgae is dependent on the species of macroalgae used in the diet and while the majority of the macroalgae species appear to be digestible by bivalves at lower rates than phytoplankton, some macroalgal species (*Pyropia* spp.) may contain compounds that are actively harmful to bivalves when consumed [141, 155]. Macroalgae produce a number of secondary metabolites (i.e., phlorotannins, halogenated compounds, etc.), which serve a wide variety of purposes, such as UV protection and wound healing [187, 221–222] as well as impacting grazers [165, 223]. While only two studies measured and noted a decline in concentrations of one type of metabolite (i.e., phlorotannins) in macroalgal particles over time, which was correlated with a slight increase in CR of one macroalgal species, there is not currently enough evidence to determine what effect phlorotannins have on bivalve feeding and digestion [145, 147]. Additional research on the effects of secondary metabolites on bivalve feeding could determine which macroalgal species and compounds are harmful to bivalves.

4.4 | Fatty Acids

The degree to which FAs from macroalgae are estimated to contribute nutritionally to bivalves was relatively low (Table 3). As macroalgae typically have relatively low lipid (3%) content compared to most phytoplankton (17.3%), it is not surprising that the estimated contributions of macroalgae FAs to bivalves are low as well [40, 178, 214, 224]. Additionally, the FA content of bivalves

varies with species, age, and reproductive stage; thus, contributions from macroalgae would be expected to change depending upon the individuals sampled and the time of year sampled [40, 178, 225]. Although FA tracers provide another useful tool for understanding complex trophic relationships, the dominance of carbohydrates/polysaccharides in macroalgae greatly limits the effectiveness of these methods for tracking trophic contributions from macroalgae in comparison to phytoplankton, which generally have higher lipid content [40, 41, 178, 212, 226]. Therefore, to create a complete picture of macroalgal utilization by bivalves in the wild, it is desirable to use SI in conjunction with FA or AA tracers to provide a more complete understanding of the food sources utilized by bivalves based on the biochemical composition of different food sources [25, 178].

4.5 | Implications for Aquaculture

The determination of the nutrition of organisms in natural food webs relies extensively on SI methods, but these methods are also used in aquaculture to determine how organisms assimilate different formulated feeds and interact with their environment [26, 227]. Successful examples of co-culture have used SI to monitor how the inputs from some organisms affect the composition of the co-cultured organisms when compared to each of the species grown alone [228–230]. The SI studies that were reviewed were rarely targeted primarily for aquaculture, and if they were, the majority focused on the different available food sources in an environment and the contribution they made to the farmed bivalves [55, 57, 68, 123]. One study looked at the impacts of cultivated kelp on the diets of wild populations of bivalves, and there was only one study that made estimates for the dietary contribution of farmed macroalgae to farmed bivalves in a specific co-culture setting [56, 69]. Research has advocated for co-culture in aquaculture based on the potential positive effects through taking advantage of the ability of bivalves to filter feed on different organic sources, as well as the ability of macroalgae to absorb dissolved nutrients derived from co-cultured animals [1]. There may be other benefits derived from co-cultivation, such as improving water clarity for macroalgal growth and potential amelioration of ocean acidification impacts under certain hydrodynamic conditions [19, 231]. While there may be growth benefits to aquaculture organisms when co-culturing fed and extractive species, this review of SI and feeding studies demonstrates that there is likely to be a limited growth benefit to bivalves when co-cultured with macroalgae if macroalgal detritus is considered as an additional food source to the bivalves [2, 232–233]. The hydrodynamic conditions within a location are important when considering aquaculture, as currents within an area would impact the availability of detrital material to bivalves, especially the amount of kelp particulates available to bivalves and thus their contribution to bivalve diets [55–57, 68, 69, 78]. Examples of successful co-culture in aquaculture frequently involve either fed species and extractive species or take place in an enclosed or semi-enclosed environment where water or nutrient exchange is limited [232, 234–237]. While some research has demonstrated a benefit from bivalves to macroalgae, with increased growth for macroalgae placed near or on shellfish farms, potentially due to increases in light or increases in nutrients, this depends greatly upon the hydrodynamics of an aquaculture location and the overlap in suitable locations and environmental conditions to

promote growth for the species involved [18, 19, 238–239]. Based on the review of stable isotope studies alone, it could be presumed that macroalgal carbon is readily consumed by different bivalve species when available. The feeding studies have more mixed results, as in the short term bivalves can digest some macroalgae at the same level as phytoplankton, but as demonstrated in long-term studies, macroalgal can only replace phytoplankton up to a limited amount and mostly does not result in higher growth rates for bivalves [134, 158, 160, 169].

5 | Conclusions

Based on this literature review, the potential for bivalves to benefit from consuming macroalgal material in a multi-trophic aquaculture environment appears to be limited. Stable isotope and AE studies show that bivalves will consume the macroalgal material when it is available and that typically some portion of the material is digestible and assimilated, but feeding studies indicate that it does not necessarily improve the growth of the bivalves. The estimates of consumption of macroalgal material of wild bivalve populations appears to be more influenced by TDF chosen in mixing models rather than factors related to macroalgal species and season. The disconnect between the relatively high absorbance efficiencies measured in short-term feeding experiments with bivalves fed on macroalgal material and the reduction in growth or increased mortality of the bivalves fed on macroalgal material in the long-term would signify that the nutritional composition of the macroalgal material limits the ability of the bivalves to digest and utilize the material in the same manner as phytoplankton. Whether this is due to the high carbohydrate (i.e., polysaccharides) content of the macroalgae, or potentially harmful compounds (i.e., polyphenols, halogenated compounds), or the presence of materials that are physically harmful to the digestive tract is unclear and requires further investigation [165, 178]. Determining which species of macroalgae and the aspects of the material are harmful to bivalves would be possible to undertake in the laboratory, but there needs to be consideration of how the decay and microbial colonization affects the biochemical composition of the macroalgal and how this will affect bivalve consumption and digestion [145, 175, 240]. Laboratory feeding and digestion experiments can determine if there are harmful effects due to the consumption and digestion of macroalgae by bivalves. Even if the digestibility of macroalgal particles by bivalves is limited, site locations and water turnover of an aquaculture setting has significant influence on the growth of bivalve species in aquaculture and may limit any harmful effects from the co-culture of macroalgae with bivalves [3, 241–242].

Author Contributions

Fiona P. MacKechnie: conceptualization, investigation, methodology, writing – original draft (lead), formal analysis, data curation, writing – review and editing. **Andrew G. Jeffs:** conceptualization, investigation, writing – original draft, funding acquisition, writing – review and editing, methodology, formal analysis, resources.

Acknowledgments

This research was supported by the Endeavor Fund administered by the Ministry of Business, Innovation and Employment in New Zealand through contract RJGHT1901 to Blue Carbon Services Ltd. The

research was also supported by The Nature Conservancy. We are grateful to Robert Hickson for his relentless support for all aspects of blue carbon research and development. Open access publishing facilitated by The University of Auckland, as part of the Wiley - The University of Auckland agreement via the Council of Australasian University Librarians.

Funding

This work was supported by the Ministry of Business, Innovation and Employment in New Zealand, RJGHT1901; Nature Conservancy; Blue Carbon Services Ltd.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

References

1. M. Troell, A. Joyce, T. Chopin, A. Neori, A. H. Buschmann, and J. G. Fang, "Ecological Engineering in Aquaculture — Potential for Integrated Multi-Trophic Aquaculture (IMTA) in Marine Offshore Systems," *Aquaculture* 297, no. 1–4 (2009): 1–9, <https://doi.org/10.1016/j.aquaculture.2009.09.010>.
2. R. L. Naylor, R. W. Hardy, A. H. Buschmann, et al., "A 20-Year Retrospective Review of Global Aquaculture," *Nature* 591, no. 7851 (2021): 551–563, <https://doi.org/10.1038/s41586-021-03308-6>.
3. C. R. Newell, A. J. S. Hawkins, K. Morris, et al., "Using High-Resolution Remote Sensing to Characterize Suspended Particulate Organic Matter as Bivalve Food for Aquaculture Site Selection," *Journal of Shellfish Research* 40, no. 1 (2021): 113–118, <https://doi.org/10.2983/035.040.0110>.
4. P. J. Cranford, J. E. Ward, and S. E. Shumway, "Bivalve Filter Feeding: Variability and Limits of the Aquaculture Biofilter," in *Shellfish Aquaculture and the Environment*, ed. S. E. Shumway (Wiley-Blackwell, 2011), 81–124, <https://doi.org/10.1002/9780470960967.ch4>.
5. B. H. Buck, M. W. Ebeling, and T. Michler-Cieluch, "Mussel Cultivation as a co-Use in Offshore Wind Farms: Potential and Economic Feasibility," *Aquaculture Economics & Management* 14, no. 4 (2010): 255–281, <https://doi.org/10.1080/13657305.2010.526018>.
6. R. M. Tullberg, H. P. Nguyen, and C. M. Wang, "Review of the Status and Developments in Seaweed Farming Infrastructure," *Journal of Marine Science and Engineering* 10, no. 10 (2022): 1447, <https://doi.org/10.3390/jmse10101447>.
7. S. J. Theuerkauf, L. T. Barrett, H. K. Alleway, B. A. Costa-Pierce, A. St. Gelais, and R. C. Jones, "Habitat Value of Bivalve Shellfish and Seaweed Aquaculture for Fish and Invertebrates: Pathways, Synthesis and Next Steps," *Reviews in Aquaculture* 14, no. 1 (2022): 54–72, <https://doi.org/10.1111/raq.12584>.
8. A. C. Smaal, J. G. Ferreira, J. Grant, J. K. Petersen, and Ø. Strand, eds., *Goods and Services of Marine Bivalves* (Springer International Publishing, 2019), <https://doi.org/10.1007/978-3-319-96776-9>.
9. J. K. Kim, C. Yarish, E. K. Hwang, M. Park, and Y. Kim, "Seaweed Aquaculture: Cultivation Technologies, Challenges and Its Ecosystem Services," *Algae* 32, no. 1 (2017): 1–13, <https://doi.org/10.4490/algae.2017.32.3.3>.
10. P. G. Beninger, A. Valdizan, P. Decottignies, and B. Cognie, "Impact of Seston Characteristics on Qualitative Particle Selection Sites and Efficiencies in the Pseudolamellibranch Bivalve *Crassostrea gigas*," *Journal of Experimental Marine Biology and Ecology* 360, no. 1 (2008): 9–14, <https://doi.org/10.1016/j.jembe.2008.03.003>.
11. M. Rosa, J. E. Ward, and S. E. Shumway, "Selective Capture and Ingestion of Particles by Suspension-Feeding Bivalve Molluscs: A Review," *Journal of Shellfish Research* 37, no. 4 (2018): 727–746, <https://doi.org/10.2983/035.037.0405>.
12. J. R. Zeldis, K. Robinson, A. Ross, and B. Hayden, "First Observations of Predation by New Zealand Greenshell Mussels (*Perna canaliculus*) on Zooplankton," *Journal of Experimental Marine Biology and Ecology* 311, no. 2 (2004): 287–299, <https://doi.org/10.1016/j.jembe.2004.05.019>.
13. T. Chopin, J. A. Cooper, G. K. Reid, S. Cross, and C. Moore, "Open-Water Integrated Multi-Trophic Aquaculture: Environmental Bioremediation and Economic Diversification of Fed Aquaculture by Extractive Aquaculture," *Reviews in Aquaculture* 4, no. 4 (2012): 209–220, <https://doi.org/10.1111/j.1753-5131.2012.01074.x>.
14. K. A. Krumhansl and R. E. Scheibling, "Production and Fate of Kelp Detritus," *Marine Ecology Progress Series* 467 (2012): 281–302, <https://doi.org/10.3354/meps09940>.
15. M. S. Hargrave, A. Ekelund, G. M. Nylund, and H. Pavia, "Filtration and Fertilisation Effects of the Bivalves *Mytilus edulis* and *Magallana gigas* on the Kelp *Saccharina latissima* in Tank Culture," *Journal of Applied Phycology* 33 (2021): 3927–3938, <https://doi.org/10.1007/s10811-021-02553-6>.
16. C. Sanz-Lazaro and P. Sanchez-Jerez, "Regional Integrated Multi-Trophic Aquaculture (RIMTA): Spatially Separated, Ecologically Linked," *Journal of Environmental Management* 271 (2020): 110921, <https://doi.org/10.1016/j.jenvman.2020.110921>.
17. E. Dugeny, J. de Lorigeril, B. Petton, E. Toulza, Y. Gueguen, and F. Pernet, "Seaweeds Influence Oyster Microbiota and Disease Susceptibility," *Journal of Animal Ecology* 91, no. 4 (2022): 805–818, <https://doi.org/10.1111/1365-2656.13662>.
18. J. R. C. Freitas, J. M. Salinas Morrondo, and U. J. Cremades, "Saccharina latissima (Laminariales, Ochrophyta) Farming in an Industrial IMTA System in Galicia (Spain)," *Journal of Applied Phycology* 28, no. 1 (2016): 377–385, <https://doi.org/10.1007/s10811-015-0526-4>.
19. M. S. Hargrave, G. M. Nylund, S. Enge, and H. Pavia, "Co-Cultivation With Blue Mussels Increases Yield and Biomass Quality of Kelp," *Aquaculture* 550 (2022): 737832, <https://doi.org/10.1016/j.aquaculture.2021.737832>.
20. A. J. S. Hawkins, P. L. Pascoe, H. Parry, et al., "Comparative Feeding on Chlorophyll-Rich Versus Remaining Organic Matter in Bivalve Shellfish," *Journal of Shellfish Research* 32, no. 3 (2013): 883–897, <https://doi.org/10.2983/035.032.0332>.
21. D. C. Dyer, M. J. Butler, A. J. Smit, R. J. Anderson, and J. J. Bolton, "Kelp Forest POM During Upwelling and Downwelling Conditions: Using Stable Isotopes to Differentiate Between Detritus and Phytoplankton," *Marine Ecology Progress Series* 619 (2019): 17–34, <https://doi.org/10.3354/meps12941>.
22. C. Liénart, N. Savoye, Y. Bozec, et al., "Dynamics of Particulate Organic Matter Composition in Coastal Systems: A Spatio-Temporal Study at Multi-Systems Scale," *Progress in Oceanography* 156 (2017): 221–239, <https://doi.org/10.1016/j.pocean.2017.03.001>.
23. U. Arambalza, I. Ibarrola, E. Navarro, I. Urrutxurtu, and M. B. Urrutia, "How to Handle 'Poor' Foodstuffs: Acclimation of the Common Cockle (*Cerastoderma edule*) to Detrital Diets," *Journal of Sea Research* 134 (2018): 16–25, <https://doi.org/10.1016/j.seares.2018.01.001>.
24. M. Uchida, T. Miyoshi, M. Kanematsu, and Y. Kobayashi, "Inhibition of Growth in Juvenile Asari Clams *Ruditapes philippinarum* Fed *Ulva* spp. Marine Silage," *Fisheries Science* 86, no. 3 (2020): 519–530, <https://doi.org/10.1007/s12562-020-01424-2>.

25. E. A. Elliott Smith and M. D. Fox, "Characterizing Energy Flow in Kelp Forest Food Webs: A Geochemical Review and Call for Additional Research," *Ecography* 2022, no. 6 (2021): ecog.05566, <https://doi.org/10.1111/ecog.05566>.
26. B. Fry, *Stable Isotope Ecology*, 1st ed. (Springer, 2006), <https://doi.org/10.1007/0-387-33745-8>.
27. D. M. Post, "Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions," *Ecology* 83, no. 3 (2002): 703–718, [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2).
28. R. H. Michener and K. Lajtha, "Compound-Specific Stable Isotope Analysis in Ecology and Paleoecology," in *Stable Isotopes in Ecology and Environmental Science: Second Edition*, 2nd ed. (Blackwell Publishing Ltd, 2008), 480–540, <https://doi.org/10.1002/9780470691854.ch14>.
29. C. K. Kang, E. J. Choy, Y. Son, et al., "Food Web Structure of a Restored Macroalgal Bed in the Eastern Korean Peninsula Determined by C and N Stable Isotope Analyses," *Marine Biology* 153, no. 6 (2008): 1181–1198, <https://doi.org/10.1007/s00227-007-0890-y>.
30. K. Iken, C. Amsler, K. Gorman, et al., "Macroalgal Input Into the Coastal Food Web Along a Gradient of Seasonal Sea Ice Cover Along the Western Antarctic Peninsula," *Marine Ecology Progress Series* 718 (2023): 1–22, <https://doi.org/10.3354/meps14388>.
31. M. J. DeNiro and S. Epstein, "Influence of Diet on the Distribution of Carbon Isotopes in Animals," *Geochimica et Cosmochimica Acta* 42, no. 5 (1978): 495–506, [https://doi.org/10.1016/0016-7037\(78\)90199-0](https://doi.org/10.1016/0016-7037(78)90199-0).
32. M. J. DeNiro and S. Epstein, "Influence of Diet on the Distribution of Nitrogen Isotopes in Animals," *Geochimica et Cosmochimica Acta* 45, no. 3 (1981): 341–351, [https://doi.org/10.1016/0016-7037\(81\)90244-1](https://doi.org/10.1016/0016-7037(81)90244-1).
33. M. Minagawa and E. Wada, "Stepwise Enrichment of ^{15}N Along Food Chains: Further Evidence and the Relation Between $\delta^{15}\text{N}$ and Animal Age," *Geochimica et Cosmochimica Acta* 48, no. 5 (1984): 1135–1140, [https://doi.org/10.1016/0016-7037\(84\)90204-7](https://doi.org/10.1016/0016-7037(84)90204-7).
34. S. Fredriksen, "Food Web Studies in a Norwegian Kelp Forest Based on Stable Isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) Analysis," *Marine Ecology Progress Series* 260 (2003): 71–81, <https://doi.org/10.3354/meps260071>.
35. J. M. Hill, C. D. McQuaid, and S. Kaehler, "Temporal and Spatial Variability in Stable Isotope Ratios of SPM Link to Local Hydrography and Longer Term SPM Averages Suggest Heavy Dependence of Mussels on Nearshore Production," *Marine Biology* 154, no. 5 (2008): 899–909, <https://doi.org/10.1007/s00227-008-0983-2>.
36. R. J. Miller and H. M. Page, "Kelp as a Trophic Resource for Marine Suspension Feeders: A Review of Isotope-Based Evidence," *Marine Biology* 159, no. 7 (2012): 1391–1402, <https://doi.org/10.1007/s00227-012-1929-2>.
37. M. O. Nadon and J. H. Himmelman, "Stable Isotopes in Subtidal Food Webs: Have Enriched Carbon Ratios in Benthic Consumers Been Misinterpreted?," *Limnology and Oceanography* 51, no. 6 (2006): 2828–2836, <https://doi.org/10.4319/lo.2006.51.6.2828>.
38. J. Dalsgaard, M. John, G. Kattner, D. Müller-Navarra, and W. Hagen, "Fatty Acid Trophic Markers in the Pelagic Marine Environment," *Advances in Marine Biology* 46 (2003): 225–340, [https://doi.org/10.1016/S0065-2881\(03\)46005-7](https://doi.org/10.1016/S0065-2881(03)46005-7).
39. S. M. Budge, S. J. Iverson, and H. N. Koopman, "Studying Trophic Ecology in Marine Ecosystems Using Fatty Acids: A Primer on Analysis and Interpretation," *Marine Mammal Science* 22, no. 4 (2006): 759–801, <https://doi.org/10.1111/j.1748-7692.2006.00079.x>.
40. C. E. Hanson, G. A. Hyndes, and S. F. Wang, "Differentiation of Benthic Marine Primary Producers Using Stable Isotopes and Fatty Acids: Implications to Food Web Studies," *Aquatic Botany* 93, no. 2 (2010): 114–122, <https://doi.org/10.1016/j.aquabot.2010.04.004>.
41. J. R. Kelly and R. E. Scheibling, "Fatty Acids as Dietary Tracers in Benthic Food Webs," *Marine Ecology Progress Series* 446 (2012): 1–22, <https://doi.org/10.3354/meps09559>.
42. A. W. E. Galloway, M. T. Brett, G. W. Holtgrieve, et al., "A Fatty Acid Based Bayesian Approach for Inferring Diet in Aquatic Consumers," *PLoS One* 10, no. 6 (2015): e0129723, <https://doi.org/10.1371/journal.pone.0129723>.
43. R. Whippo, K. Iken, C. D. Amsler, et al., "Fatty Acid Profiles and Stable Isotope Composition of Antarctic Macroalgae: A Baseline for a Combined Biomarker Approach in Food Web Studies," *Polar Biology* 47 (2024): 367–386, <https://doi.org/10.1007/s00300-024-03234-z>.
44. S. Caut, E. Angulo, and F. Courchamp, "Variation in Discrimination Factors ($\Delta^{15}\text{N}$ and $\Delta^{13}\text{C}$): The Effect of Diet Isotopic Values and Applications for Diet Reconstruction," *Journal of Applied Ecology* 46, no. 2 (2009): 443–453.
45. B. C. Stock, A. L. Jackson, E. J. Ward, A. C. Parnell, D. L. Phillips, and B. X. Semmens, "Analyzing Mixing Systems Using a New Generation of Bayesian Tracer Mixing Models," *PeerJ* 6 (2018): e5096, <https://doi.org/10.7717/peerj.5096>.
46. P. Decottignies, P. G. Beninger, Y. Rincé, and P. Riera, "Trophic Interactions Between Two Introduced Suspension-Feeders, *Crepidula fornicata* and *Crassostrea gigas*, Are Influenced by Seasonal Effects and Qualitative Selection Capacity," *Journal of Experimental Marine Biology and Ecology* 342, no. 2 (2007): 231–241, <https://doi.org/10.1016/j.jembe.2006.10.005>.
47. J. Rosa, M. F. L. Lemos, D. Crespo, et al., "Integrated Multitrophic Aquaculture Systems – Potential Risks for Food Safety," *Trends in Food Science & Technology* 96 (2020): 79–90, <https://doi.org/10.1016/j.tifs.2019.12.008>.
48. H. Luo, Y. Yang, and S. Xie, "The Ecological Effect of Large-Scale Coastal Natural and Cultivated Seaweed Litter Decay Processes: An Overview and Perspective," *Journal of Environmental Management* 341 (2023): 118091, <https://doi.org/10.1016/j.jenvman.2023.118091>.
49. M. D. Spalding, H. E. Fox, G. R. Allen, et al., "Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas," *Bioscience* 57, no. 7 (2007): 573–583, <https://doi.org/10.1641/B570707>.
50. D. M. Post, C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montaña, "Getting to the Fat of the Matter: Models, Methods and Assumptions for Dealing With Lipids in Stable Isotope Analyses," *Oecologia* 152, no. 1 (2007): 179–189, <https://doi.org/10.1007/s00442-006-0630-x>.
51. B. C. Ramshaw, E. A. Pakhomov, R. W. Markel, and S. Kaehler, "Quantifying Spatial and Temporal Variations in Phytoplankton and Kelp Isotopic Signatures to Estimate the Distribution of Kelp-Derived Detritus Off the West Coast of Vancouver Island, Canada," *Limnology and Oceanography* 62, no. 5 (2017): 2133–2153, <https://doi.org/10.1002/lno.10555>.
52. R. J. Conover, "Factors Affecting the Assimilation of Organic Matter by Zooplankton and the Question of Superfluous Feeding," *Limnology and Oceanography* 11, no. 3 (1966): 346–354, <https://doi.org/10.4319/lo.1966.11.3.0346>.
53. B. C. McMeans, N. Rooney, M. T. Arts, and A. T. Fisk, "Food Web Structure of a Coastal Arctic Marine Ecosystem and Implications for Stability," *Marine Ecology Progress Series* 482 (2013): 17–28, <https://doi.org/10.3354/meps10278>.
54. P. E. Renaud, T. S. Løkken, L. L. Jørgensen, J. Berge, and B. J. Johnson, "Macroalgal Detritus and Food-Web Subsidies Along an Arctic Fjord Depth-Gradient," *Frontiers in Marine Science* 2 (2015): 31, <https://doi.org/10.3389/fmars.2015.00031>.
55. K. A. Emery, G. M. Wilkinson, V. F. Camacho-Ibar, et al., "Resource Use of an Aquacultured Oyster (*Crassostrea gigas*) in the Reverse Estuary Bahía San Quintín, Baja California, México," *Estuaries and Coasts* 39, no. 3 (2016): 866–874, <https://doi.org/10.1007/s12237-015-0021-9>.
56. Q. Xu, F. Gao, and H. Yang, "Importance of Kelp-Derived Organic Carbon to the Scallop *Chlamys farreri* in an Integrated Multi-Trophic

- Aquaculture System," *Chinese Journal of Oceanology and Limnology* 34, no. 2 (2016): 322–329, <https://doi.org/10.1007/s00343-015-4332-2>.
57. Q. Xu and H. Yang, "Food Sources of Three Bivalves Living in Two Habitats of Jiaozhou Bay (Qingdao, China): Indicated by Lipid Biomarker and Stable Isotope Analysis," *Journal of Shellfish Research* 26, no. 2 (2007): 561–567.
58. K. Kon, Y. Hoshino, K. Kanou, D. Okazaki, S. Nakayama, and H. Kohno, "Importance of Allochthonous Material in Benthic Macrofaunal Community Functioning in Estuarine Salt Marshes," *Estuarine, Coastal and Shelf Science* 96 (2012): 236–244, <https://doi.org/10.1016/j.ecss.2011.11.015>.
59. E. Howe and C. A. Simenstad, "Using Isotopic Measures of Connectivity and Ecosystem Capacity to Compare Restoring and Natural Marshes in the Skokomish River Estuary, WA, USA," *Estuaries and Coasts* 38, no. 2 (2015): 639–658, <https://doi.org/10.1007/s12237-014-9831-4>.
60. D. O. Duggins, C. A. Simenstad, and J. A. Estes, "Magnification of Secondary Production by Kelp Detritus in Coastal Marine Ecosystems," *Science* 245, no. 4914 (1989): 170–173, <https://doi.org/10.1126/science.245.4914.170>.
61. H. Tallis, "Kelp and Rivers Subsidize Rocky Intertidal Communities in the Pacific Northwest (USA)," *Marine Ecology Progress Series* 389 (2009): 85–96, <https://doi.org/10.3354/meps08138>.
62. E. Howe, C. A. Simenstad, and A. Ogston, "Detrital Shadows: Estuarine Food Web Connectivity Depends on Fluvial Influence and Consumer Feeding Mode," *Ecological Applications* 27, no. 7 (2017): 2170–2193, <https://doi.org/10.1002/eap.1600>.
63. K. Corliss, V. Von Biela, H. Coletti, J. Bodkin, D. Esler, and K. Iken, "Relative Importance of Macroalgae and Phytoplankton to Nearshore Consumers and Growth Across Climatic Conditions in the Northern Gulf of Alaska," *Estuaries and Coasts* 47, no. 6 (2024): 1579–1597, <https://doi.org/10.1007/s12237-024-01371-6>.
64. S. Ha, W. K. Min, D. S. Kim, and K. H. Shin, "Trophic Importance of Meiofauna to Polychaetes in a Seagrass (*Zostera marina*) Bed as Traced by Stable Isotopes," *Journal of the Marine Biological Association of the United Kingdom* 94, no. 1 (2014): 121–127, <https://doi.org/10.1017/S0025315413001148>.
65. S. S. Gabara, "Trophic Structure and Potential Carbon and Nitrogen Flow of a Rhodolith Bed at Santa Catalina Island Inferred From Stable Isotopes," *Marine Biology* 167, no. 3 (2020): 30, <https://doi.org/10.1007/s00227-019-3635-9>.
66. H. J. Park, E. Han, Y.-J. Lee, and C.-K. Kang, "Trophic Linkage of a Temperate Intertidal Macrobenthic Food Web Under Opportunistic Macroalgal Blooms: A Stable Isotope Approach," *Marine Pollution Bulletin* 111, no. 1–2 (2016): 86–94, <https://doi.org/10.1016/j.marpolbul.2016.07.026>.
67. C. J. Reddin, F. Docmac, N. E. O'Connor, J. H. Bothwell, and C. Harrod, "Coastal Upwelling Drives Intertidal Assemblage Structure and Trophic Ecology," *PLoS One* 10, no. 7 (2015): e0130789, <https://doi.org/10.1371/journal.pone.0130789>.
68. A. C. Both, C. J. Byron, B. A. Costa-Pierce, C. C. Parrish, and D. C. Brady, "Detrital Subsidies in the Diet of *Mytilus edulis*: Macroalgal Detritus Likely Supplements Essential Fatty Acids," *Frontiers in Marine Science* 7 (2020): 7, <https://doi.org/10.3389/fmars.2020.561073>.
69. A. W. Walls, *Ecosystem Services and Environmental Impacts Associated With Commercial Kelp Aquaculture* (National University of Ireland, 2017), <https://aran.library.nuigalway.ie/bitstream/handle/10379/6913/2017WallsPhD.pdf?sequence=1#page=155>.
70. J. C. Marín Leal, S. F. Dubois, F. Orvain, et al., "Stable Isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and Modelling as Tools to Estimate the Trophic Ecology of Cultivated Oysters in Two Contrasting Environments," *Marine Biology* 153, no. 4 (2008): 673–688, <https://doi.org/10.1007/s00227-007-0841-7>.
71. G. Schaal, P. Riera, and C. Leroux, "Trophic Ecology in a Northern Brittany (Batz Island, France) Kelp (*Laminaria digitata*) Forest, as Investigated Through Stable Isotopes and Chemical Assays," *Journal of Sea Research* 63, no. 1 (2010): 24–35, <https://doi.org/10.1016/j.seares.2009.09.002>.
72. F. Rossi, A. Baeta, and J. C. Marques, "Stable Isotopes Reveal Habitat-Related Diet Shifts in Facultative Deposit-Feeders," *Journal of Sea Research* 95 (2015): 172–179, <https://doi.org/10.1016/j.seares.2014.07.004>.
73. V. Marchais, G. Schaal, J. Grall, et al., "Spatial Variability of Stable Isotope Ratios in Oysters (*Crassostrea gigas*) and Primary Producers Along an Estuarine Gradient (Bay of Brest, France)," *Estuaries and Coasts* 36, no. 4 (2013): 808–819, <https://doi.org/10.1007/s12237-012-9584-x>.
74. T. I. Kahma, A. Norkko, and I. F. Rodil, "Macrofauna Community Dynamics and Food Webs in the Canopy-Forming Macroalgae and the Associated Detrital Subsidies," *Estuaries and Coasts* 46, no. 5 (2023): 1345–1362, <https://doi.org/10.1007/s12237-023-01196-9>.
75. T. I. Kahma, A. M. L. Karlson, C. Liénart, et al., "Food-Web Comparisons Between Two Shallow Vegetated Habitat Types in the Baltic Sea," *Marine Environmental Research* 169 (2021): 105402, <https://doi.org/10.1016/j.marenvres.2021.105402>.
76. T. I. Kahma, A. M. L. Karlson, X. Sun, et al., "Macroalgae Fuels Coastal Soft-Sediment Macrofauna: A Triple-Isotope Approach Across Spatial Scales," *Marine Environmental Research* 162 (2020): 105163, <https://doi.org/10.1016/j.marenvres.2020.105163>.
77. S. Dubois, H. Blanchet, A. Garcia, et al., "Trophic Resource Use by Macrozoobenthic Primary Consumers Within a Semi-Enclosed Coastal Ecosystem: Stable Isotope and Fatty Acid Assessment," *Journal of Sea Research* 88 (2014): 87–99, <https://doi.org/10.1016/j.seares.2014.01.004>.
78. S. F. Dubois, F. Orvain, J. Marin-Léal, M. Ropert, and S. Lefebvre, "Small-Scale Spatial Variability of Food Partitioning Between Cultivated Oysters and Associated Suspension-Feeding Species, as Revealed by Stable Isotopes," *Marine Ecology Progress Series* 336 (2007): 151–160, <https://doi.org/10.3354/meps336151>.
79. D. Davoult, G. Surget, V. Stiger-Pouvreau, et al., "Multiple Effects of a *Gracilaria vermiculophylla* Invasion on Estuarine Mudflat Functioning and Diversity," *Marine Environmental Research* 131 (2017): 227–235, <https://doi.org/10.1016/j.marenvres.2017.09.020>.
80. M. E. M. Walton, R. Browne, J. N. Griffiths, et al., "Kelp Detritus: Unutilized Productivity or an Unacknowledged Trophic Resource," *Science of the Total Environment* 820 (2022): 12, <https://doi.org/10.1016/j.scitotenv.2022.153191>.
81. T. D. Daggers, *Quantifying the Role of Microphytobenthos in Temperate Intertidal Ecosystems Using Optical Remote Sensing* (University of Twente, 2021), <https://doi.org/10.3990/1.9789036551243>.
82. E. Jankowska, L. N. Michel, G. Lepoint, and M. Włodarska-Kowalczyk, "Stabilizing Effects of Seagrass Meadows on Coastal Water Benthic Food Webs," *Journal of Experimental Marine Biology and Ecology* 510 (2019): 54–63, <https://doi.org/10.1016/j.jembe.2018.10.004>.
83. S. Deudero, A. Box, M. Vázquez-Luis, and N. L. Arroyo, "Benthic Community Responses to Macroalgae Invasions in Seagrass Beds: Diversity, Isotopic Niche and Food Web Structure at Community Level," *Estuarine, Coastal and Shelf Science* 142 (2014): 12–22, <https://doi.org/10.1016/j.ecss.2014.03.006>.
84. A. Jones, *Effect of an Engineer Species on the Diversity and Functioning of Benthic Communities: The Sabellaria alveolata Reef Habitat* (Université de Bretagne Occidentale, 2017), <https://hal.science/tel-01801202/>.
85. A. B. V. Baeta, *Food Webs in Intertidal Ecosystems: A Stable Isotope Approach and Trophic Network Analysis* (Université de La Rochelle;

- Universidade de Coimbra, 2010), <https://theses.hal.science/tel-00579775v1>.
86. N. Mavraki, I. De Mesel, S. Degraer, T. Moens, and J. Vanaverbeke, "Resource Niches of Co-Occurring Invertebrate Species at an Offshore Wind Turbine Indicate a Substantial Degree of Trophic Plasticity," *Frontiers in Marine Science* 7 (2020): 7, <https://doi.org/10.3389/fmars.2020.00379>.
 87. K. Hondula and M. Pace, "Macroalgal Support of Cultured Hard Clams in a Low Nitrogen Coastal Lagoon," *Marine Ecology Progress Series* 498 (2014): 187–201, <https://doi.org/10.3354/meps10644>.
 88. P. Dauby, "The Stable Carbon Isotope Ratios in Benthic Food Webs of the Gulf of Calvi, Corsica," *Continental Shelf Research* 9, no. 2 (1989): 181–195, [https://doi.org/10.1016/0278-4343\(89\)90091-5](https://doi.org/10.1016/0278-4343(89)90091-5).
 89. F. Colombo, V. Costa, S. F. Dubois, P. Gianguzza, A. Mazzola, and S. Vizzini, "Trophic Structure of Vermetid Reef Community: High Trophic Diversity at Small Spatial Scales," *Journal of Sea Research* 77 (2013): 93–99, <https://doi.org/10.1016/j.seares.2012.10.005>.
 90. G. Schaal, P. Riera, and C. Leroux, "Trophic Coupling Between Two Adjacent Benthic Food Webs Within a Man-Made Intertidal Area: A Stable Isotopes Evidence," *Estuarine, Coastal and Shelf Science* 77, no. 3 (2008): 523–534, <https://doi.org/10.1016/j.ecss.2007.10.008>.
 91. W. L. Wiedemeyer and R. Schwamborn, "Detritus Derived From Eelgrass and Macroalgae as Potential Carbon Source for *Mytilus edulis* in Kiel Fjord, Germany: A Preliminary Carbon Isotopic Study," *Helgoländer Wissenschaftliche Meeresuntersuchungen* 50, no. 3 (1996): 409–413, <https://doi.org/10.1007/BF02367112>.
 92. M. Cabanellas-Reboredo, A. Blanco, S. Deudero, and S. Tejada, "Effects of the Invasive Macroalga *Lophocladia lallemandii* on the Diet and Trophism of *Pinna nobilis* (Mollusca: Bivalvia) and Its Guests *Pontonia pinnophylax* and *Nepinnotheres pinnotheres* (Crustacea: Decapoda)," *Scientia Marina* 74, no. 1 (2010): 1–110, <https://doi.org/10.3989/scimar.2010.74n1101>.
 93. P. Cresson, S. Ruitton, and M. Harmelin-Vivien, "Feeding Strategies of Co-Occurring Suspension Feeders in an Oligotrophic Environment," *Food Webs* 6 (2016): 19–28, <https://doi.org/10.1016/j.fooweb.2015.12.002>.
 94. G. Sarà, "Sedimentary and Particulate Organic Matter: Mixed Sources for Cockle *Cerastoderma glaucum* in a Shallow Pond, Western Mediterranean," *Aquatic Living Resources* 20, no. 3 (2007): 271–277, <https://doi.org/10.1051/alr:2007040>.
 95. S. Deudero, A. Box, J. Alós, N. L. Arroyo, and N. Marbà, "Functional Changes due to Invasive Species: Food Web Shifts at Shallow *Posidonia Oceanica* Seagrass Beds Colonized by the Alien Macroalga *Caulerpa Racemosa*," *Estuarine, Coastal and Shelf Science* 93, no. 2 (2011): 106–116, <https://doi.org/10.1016/j.ecss.2011.03.017>.
 96. N. Zwierschke, H. van Rein, C. Harrod, et al., "Competition Between Co-Occurring Invasive and Native Consumers Switches Between Habitats," *Functional Ecology* 32, no. 12 (2018): 2717–2729, <https://doi.org/10.1111/1365-2435.13211>.
 97. S. Lefebvre, J. C. M. Leal, S. F. Dubois, et al., "Seasonal Dynamics of Trophic Relationships Among Co-Occurring Suspension-Feeders in Two Shellfish Culture Dominated Ecosystems," *Estuarine, Coastal and Shelf Science* 82, no. 3 (2009): 415–425, <https://doi.org/10.1016/j.ecss.2009.02.002>.
 98. S. F. Dubois and F. Colombo, "How Picky Can You Be? Temporal Variations in Trophic Niches of Co-Occurring Suspension-Feeding Species," *Food Webs* 1, no. 1–4 (2014): 1–9, <https://doi.org/10.1016/j.fooweb.2014.07.001>.
 99. E. Jankowska, M. De Troch, L. N. Michel, G. Lepoint, and M. Włodarska-Kowalczyk, "Modification of Benthic Food Web Structure by Recovering Seagrass Meadows, as Revealed by Trophic Markers and Mixing Models," *Ecological Indicators* 90 (2018): 28–37, <https://doi.org/10.1016/j.ecolind.2018.02.054>.
 100. S. T. Daigle, J. W. Fleeger, J. H. Cowan, and P. Y. Pascal, "What Is the Relative Importance of Phytoplankton and Attached Macroalgae and Epiphytes to Food Webs on Offshore Oil Platforms?," *Marine and Coastal Fisheries* 5, no. 1 (2013): 53–64, <https://doi.org/10.1080/19425120.2013.774301>.
 101. S. Lai, L. H. L. Loke, T. J. Bouma, and P. A. Todd, "Biodiversity Surveys and Stable Isotope Analyses Reveal Key Differences in Intertidal Assemblages Between Tropical Seawalls and Rocky Shores," *Marine Ecology Progress Series* 587 (2018): 41–53, <https://doi.org/10.3354/meps12409>.
 102. T. C. Wai, J. S. S. Ng, K. M. Y. Leung, D. Dudgeon, and G. A. Williams, "The Source and Fate of Organic Matter and the Significance of Detrital Pathways in a Tropical Coastal Ecosystem," *Limnology and Oceanography* 53, no. 4 (2008): 1479–1492, <https://doi.org/10.4319/lo.2008.53.4.1479>.
 103. J. Ning, F. Du, X. Wang, L. Wang, and Y. Li, "Trophic Connectivity Between Intertidal and Offshore Food Webs in Miers Bay, China," *Oceanologia* 61, no. 2 (2019): 208–217, <https://doi.org/10.1016/j.oceano.2018.10.001>.
 104. K. Bezuidenhout, *Sandy Beach Food Webs and Trophic Linkages With Estuaries: A Stable Light Isotope Approach* (Nelson Mandela Metropolitan University, 2010), <http://hdl.handle.net/10948/1269>.
 105. R. H. Bustamante and G. M. Branch, "The Dependence of Intertidal Consumers on Kelp-Derived Organic Matter on the West Coast of South Africa," *Journal of Experimental Marine Biology and Ecology* 196, no. 1–2 (1996): 1–28, [https://doi.org/10.1016/0022-0981\(95\)00093-3](https://doi.org/10.1016/0022-0981(95)00093-3).
 106. L. Zenteno, L. Cárdenas, N. Valdivia, et al., "Unraveling the Multiple Bottom-Up Supplies of an Antarctic Nearshore Benthic Community," *Progress in Oceanography* 174 (2019): 55–63, <https://doi.org/10.1016/j.pocean.2018.10.016>.
 107. P. Ortiz, E. Quiroga, P. Montero, M. Hamame, and F. Betti, "Trophic Structure of Benthic Communities in a Chilean Fjord (45°S) Influenced by Salmon Aquaculture: Insights From Stable Isotopic Signatures," *Marine Pollution Bulletin* 173 (2021): 113149, <https://doi.org/10.1016/j.marpolbul.2021.113149>.
 108. M. E. Becherucci, M. F. Alvarez, O. Iribarne, and P. Martinetto, "Eutrophication in a Semi-Desert Coastal Ecosystem Promotes Increases in N and C Isotopic Signatures and Changes in Primary Sources," *Marine Environmental Research* 146 (2019): 71–79, <https://doi.org/10.1016/j.marenvres.2019.03.004>.
 109. C. D. Schlieman, S. R. Wing, S. A. O'Connell-Milne, et al., "Catchment Modifications Influence the Composition of Basal Organic Matter Supporting Suspension-Feeding Bivalves," *Estuarine, Coastal and Shelf Science* 275, no. 3 (2022): 107989, <https://doi.org/10.1016/j.ecss.2022.107989>.
 110. A. K. Salomon, N. T. Shears, T. J. Langlois, and R. C. Babcock, "Cascading Effects of Fishing Can Alter Carbon Flow Through a Temperate Coastal Ecosystem," *Ecological Applications* 18, no. 8 (2008): 1874–1887, <https://doi.org/10.1890/07-1777.1>.
 111. S. R. Wing and L. Jack, "Resource Specialisation Among Suspension-Feeding Invertebrates on Rock Walls in Fiordland, New Zealand, Is Driven by Water Column Structure and Feeding Mode," *Marine Ecology Progress Series* 452 (2012): 109–118, <https://doi.org/10.3354/meps09588>.
 112. J. C. Tam, *Intertidal Community Differences Between the Cook Strait and Wellington Harbour* (Victoria University, 2012), <https://doi.org/10.26686/wgtn.17003704.v1>.
 113. D. Leduc, P. K. Probert, R. D. Frew, and C. L. Hurd, "Macroinvertebrate Diet in Intertidal Seagrass and Sandflat Communities: A Study Using C, N, and S Stable Isotopes," *New Zealand Journal of Marine and Freshwater Research* 40, no. 4 (2006): 615–629, <https://doi.org/10.1080/00288330.2006.9517450>.

114. S. Kaehler, E. Pakhomov, R. Kalin, and S. Davis, "Trophic Importance of Kelp-Derived Suspended Particulate Matter in a Through-Flow Sub-Antarctic System," *Marine Ecology Progress Series* 316 (2006): 17–22, <https://doi.org/10.3354/meps316017>.
115. A. Norkko, S. F. Thrush, V. J. Cummings, et al., "Trophic Structure of Coastal Antarctic Food Webs Associated With Changes in Sea Ice and Food Supply," *Ecology* 88, no. 11 (2007): 2810–2820, <https://doi.org/10.1890/06-1396.1>.
116. E. Calizza, G. Careddu, S. S. Caputi, L. Rossi, and M. L. Costantini, "Time- and Depth-Wise Trophic Niche Shifts in Antarctic Benthos," *PLoS One* 13, no. 5 (2018): e0197009, <https://doi.org/10.1371/journal.pone.0194796>.
117. G. Alurralde, V. L. Fuentes, M. De Troch, and M. Tatián, "Suspension Feeders as Natural Sentinels of the Spatial Variability in Food Sources in an Antarctic Fjord: A Stable Isotope Approach," *Ecological Indicators* 115 (2020): 106378, <https://doi.org/10.1016/j.ecolind.2020.106378>.
118. K. H. Dunton, " $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ Measurements of Antarctic Peninsula Fauna: Trophic Relationships and Assimilation of Benthic Seaweeds," *American Zoologist* 41 (2001): 14–112.
119. B. Le Bourg, T. Saucède, A. Charpentier, G. Lepoint, and L. N. Michel, "What Is the Menu Today in a Subantarctic Kelp Food Web From the Kerguelen Islands? Phytodetritus, Phytoplankton and Phytobenthos; Not Living Kelp," *Marine Biology* 169, no. 9 (2022): 118, <https://doi.org/10.1007/s00227-022-04105-z>.
120. S. Huang, S. M. Edie, K. S. Collins, N. M. A. Crouch, K. Roy, and D. Jablonski, "Diversity, Distribution and Intrinsic Extinction Vulnerability of Exploited Marine Bivalves," *Nature Communications* 14, no. 1 (2023): 4639, <https://doi.org/10.1038/s41467-023-40053-y>.
121. C. M. Duarte, J. Gattuso, K. Hancke, et al., "Global Estimates of the Extent and Production of Macroalgal Forests," *Global Ecology and Biogeography* 31, no. 7 (2022): geb.13515, <https://doi.org/10.1111/geb.13515>.
122. A. Pessarrodona, K. Filbee-Dexter, K. A. Krumhansl, M. F. Pedersen, P. J. Moore, and T. Wernberg, "A Global Dataset of Seaweed Net Primary Productivity," *Scientific Data* 9, no. 1 (2022): 1, <https://doi.org/10.1038/s41597-022-01554-5>.
123. S. F. Dubois, B. Jean-Louis, B. Bertrand, and S. Lefebvre, "Isotope Trophic-Step Fractionation of Suspension-Feeding Species: Implications for Food Partitioning in Coastal Ecosystems," *Journal of Experimental Marine Biology and Ecology* 351, no. 1 (2007): 121–128, <https://doi.org/10.1016/j.jembe.2007.06.020>.
124. A. W. Walls, R. Kennedy, M. D. Edwards, and M. P. Johnson, "Impact of Kelp Cultivation on the Ecological Status of Benthic Habitats and *Zostera marina* Seagrass Biomass," *Marine Pollution Bulletin* 123, no. 1 (2017): 19–27, <https://doi.org/10.1016/j.marpolbul.2017.07.048>.
125. A. van der Schatte Olivier, L. Jones, L. L. Vay, M. Christie, J. Wilson, and S. K. Malham, "A Global Review of the Ecosystem Services Provided by Bivalve Aquaculture," *Reviews in Aquaculture* 12, no. 1 (2020): 3–25, <https://doi.org/10.1111/raq.12301>.
126. FAO, *The State of World Fisheries and Aquaculture 2022* (FAO, 2022), <https://doi.org/10.4060/cc0461en>.
127. J. H. McCutchan, W. M. Lewis, C. Kendall, and C. C. McGrath, "Variation in Trophic Shift for Stable Isotope Ratios of Carbon, Nitrogen, and Sulfur," *Oikos* 102, no. 2 (2003): 378–390, <https://doi.org/10.1034/j.1600-0706.2003.12098.x>.
128. H. Yokoyama and Y. Ishihi, "Variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Among Different Tissues of Three Estuarine Bivalves: Implications for Dietary Reconstructions," *Plankton and Benthos Research* 4 (2006): 6–182, <https://doi.org/10.3800/pbr.1.178>.
129. H. Yokoyama, A. Tamaki, K. Harada, K. Shimoda, K. Koyama, and Y. Ishihi, "Variability of Diet-Tissue Isotopic Fractionation in Estuarine Macrobenthos," *Marine Ecology Progress Series* 296 (2005): 115–128, <https://doi.org/10.3354/meps296115>.
130. J. M. Hill and C. D. McQuaid, "Effects of Food Quality on Tissue-Specific Isotope Ratios in the Mussel *Perna perna*," *Hydrobiologia* 635, no. 1 (2009): 81–94, <https://doi.org/10.1007/s10750-009-9865-y>.
131. A. Blanchet-Aurigny, M. Guillou, F. Pernet, J. D. Gaffet, and S. F. Dubois, "Tissue-Diet Discrimination Factors of Isotopic Ratios ($\Delta\delta^{13}\text{C}$ and $\Delta\delta^{15}\text{N}$) in Two Brittle Star Species: Effect of Reproductive State, Diet and Tissue Composition," *Journal of Experimental Marine Biology and Ecology* 426, no. 427 (2012): 68–77, <https://doi.org/10.1016/j.jembe.2012.05.013>.
132. N. Wolf, S. D. Newsome, J. Peters, and M. L. Fogel, "Variability in the Routing of Dietary Proteins and Lipids to Consumer Tissues Influences Tissue-Specific Isotopic Discrimination," *Rapid Communications in Mass Spectrometry* 29, no. 15 (2015): 1448–1456, <https://doi.org/10.1002/rcm.7239>.
133. E. S. Antonio and N. B. Richoux, "Influence of Diet on the Metabolic Turnover of Stable Isotope Ratios and Fatty Acids in the Omnivorous Shrimp *Palaemon Peringueyi*," *Marine Biology* 163, no. 7 (2016): 154, <https://doi.org/10.1007/s00227-016-2930-y>.
134. A. Omont, C. Py, J. Gamboa-Delgado, H. Nolasco-Soria, M. Spanopoulos-Zarco, and A. Peña-Rodríguez, "Nutritional Contribution of Seaweed *Ulva lactuca* Single-Cell Detritus and Microalgae *Chaetoceros calcitrans* to the Growth of the Pacific Oyster *Crassostrea gigas*," *Aquaculture* 541 (2021): 736835, <https://doi.org/10.1016/j.aquaculture.2021.736835>.
135. M. Kiljunen, J. Grey, T. Sinisalo, C. Harrod, H. Immonen, and R. I. Jones, "A Revised Model for Lipid-Normalizing $\delta^{13}\text{C}$ Values From Aquatic Organisms, With Implications for Isotope Mixing Models," *Journal of Applied Ecology* 43, no. 6 (2006): 1213–1222, <https://doi.org/10.1111/j.1365-2664.2006.01224.x>.
136. M. C. Arostegui, D. E. Schindler, and G. W. Holtgrieve, "Does Lipid-Correction Introduce Biases Into Isotopic Mixing Models? Implications for Diet Reconstruction Studies," *Oecologia* 191, no. 4 (2019): 745–755, <https://doi.org/10.1007/s00442-019-04525-7>.
137. V. I. Kharlamenko, S. I. Kiyashko, A. B. Imbs, and D. I. Vyshkvartzev, "Identification of Food Sources of Invertebrates From the Seagrass *Zostera marina* Community Using Carbon and Sulfur Stable Isotope Ratio and Fatty Acid Analyses," *Marine Ecology Progress Series* 220 (2001): 103–117, <https://doi.org/10.3354/meps220103>.
138. A. G. Rowe, K. Iken, A. L. Blanchard, et al., "Sources of Primary Production to Arctic Bivalves Identified Using Amino Acid Stable Carbon Isotope Fingerprinting," *Isotopes in Environmental and Health Studies* 55, no. 4 (2019): 366–384, <https://doi.org/10.1080/10256016.2019.1620742>.
139. M. Tatián, R. Sahade, G. Mercuri, et al., "Feeding Ecology of Benthic Filter-Feeders at Potter Cove, an Antarctic Coastal Ecosystem," *Polar Biology* 31, no. 4 (2008): 509–517, <https://doi.org/10.1007/s00300-0-007-0379-7>.
140. U. Arambalza, M. B. Urrutia, E. Navarro, and I. Ibarrola, "Ingestion, Enzymatic Digestion and Absorption of Particles Derived From Different Vegetal Sources by the Cockle *Cerastoderma edule*," *Journal of Sea Research* 64, no. 3 (2010): 408–416, <https://doi.org/10.1016/j.seares.2010.06.003>.
141. S. Tanyaros and S. Chuseingjaw, "A Partial Substitution of Microalgae With Single Cell Detritus Produced From Seaweed (*Porphyra haitanensis*) for the Nursery Culture of Tropical Oyster (*Crassostrea belcheri*)," *Aquaculture Research* 47, no. 7 (2016): 2080–2088, <https://doi.org/10.1111/are.12662>.
142. M. Uchida and K. Numaguchi, "Formation of Protoplasmic Detritus With Characteristics Favorable as Food for Secondary Animals During Microbial Decomposition of *Ulva pertusa* (Chlorophyta) Frond,"

- Journal of Marine Biotechnology* 4, no. 4 (1996): 200–206, <https://www.scopus.com/inward/record.uri?eid=2-s2.0-0001203602&partnerID=40&md5=3089ae45e187d8082b655781a679d8d1>.
143. M. Alber and I. Valiela, “Incorporation of Organic Aggregates by Marine Mussels,” *Marine Biology* 121, no. 2 (1994): 259–265, <https://doi.org/10.1007/BF00346734>.
144. M. Alber and I. Valiela, “Organic Aggregates in Detrital Food Webs: Incorporation by Bay Scallops *Argopecten irradians*,” *Marine Ecology Progress Series* 121, no. 1/3 (1995): 117–124.
145. J. S. Levinton, J. E. Ward, and S. E. Shumway, “Feeding Responses of the Bivalves *Crassostrea gigas* and *Mytilus trossulus* to Chemical Composition of Fresh and Aged Kelp Detritus,” *Marine Biology* 142, no. 4 (2003): 825, <https://doi.org/10.1007/s00227-003-1025-8>.
146. D. O. Duggins and J. E. Eckman, “Is Kelp Detritus a Good Food for Suspension Feeders? Effects of Kelp Species, Age and Secondary Metabolites,” *Marine Biology* 128, no. 3 (1997): 489–495, <https://doi.org/10.1007/s002270050115>.
147. C. M. Buchholz and C. Wiencke, “Working on a Baseline for the Kongsfjorden Food Web: Production and Properties of Macroalgal Particulate Organic Matter (POM),” *Polar Biology* 39, no. 11 (2016): 2053–2064, <https://doi.org/10.1007/s00300-015-1828-3>.
148. R. I. E. Newell and C. Langdon, “Digestion and Absorption of Refractory Carbon From the Plant *Spartina alterniflora* by the Oyster *Crassostrea virginica*,” *Marine Ecology Progress Series* 34 (1986): 105–115, <https://doi.org/10.3354/meps034105>.
149. D. A. Kreeger, C. J. Langdon, and R. I. E. Newell, “Utilization of Refractory Cellulosic Carbon Derived From *Spartina alterniflora* by the Ribbed Mussel *Geukensia demissa*,” *Marine Ecology Progress Series* 42, no. 2 (1988): 171–179.
150. M. P. Crosby, C. J. Langdon, and R. I. E. Newell, “Importance of Refractory Plant Material to the Carbon Budget of the Oyster *Crassostrea virginica*,” *Marine Biology* 100, no. 3 (1989): 343–352, <https://doi.org/10.1007/BF00391150>.
151. F. Charles and R. I. E. Newell, “Digestive Physiology of the Ribbed Mussel *Geukensia demissa* (Dillwyn) Held at Different Tidal Heights,” *Journal of Experimental Marine Biology and Ecology* 209, no. 1–2 (1997): 201–213, [https://doi.org/10.1016/S0022-0981\(96\)02694-9](https://doi.org/10.1016/S0022-0981(96)02694-9).
152. D. A. Kreeger and R. I. E. Newell, “Seasonal Utilization of Different Seston Carbon Sources by the Ribbed Mussel, *Geukensia demissa* (Dillwyn) in a Mid-Atlantic Salt Marsh,” *Journal of Experimental Marine Biology and Ecology* 260, no. 1 (2001): 71–91, [https://doi.org/10.1016/S0022-0981\(01\)00242-8](https://doi.org/10.1016/S0022-0981(01)00242-8).
153. K. L. Bushaw-Newton, D. A. Kreeger, S. Doaty, and D. J. Velinsky, “Utilization of *Spartina*- and *Phragmites*-Derived Dissolved Organic Matter by Bacteria and Ribbed Mussels (*Geukensia demissa*) From Delaware Bay Salt Marshes,” *Estuaries and Coasts* 31, no. 4 (2008): 694–703, <https://doi.org/10.1007/s12237-008-9061-8>.
154. E. Navarro, S. Méndez, I. Ibarrola, and M. B. Urrutia, “Comparative Utilization of Phytoplankton and Vascular Plant Detritus by the Cockle *Cerastoderma edule*: Digestive Responses During Diet Acclimation,” *Aquatic Biology* 6 (2009): 247–262, <https://doi.org/10.3354/ab00127>.
155. A. Peña-Rodríguez, G. Morales-Alvarado, R. Elizondo-González, G. Mendoza-Carrión, D. Tovar-Ramírez, and C. Escobedo-Fregoso, “Seaweed Single Cell Detritus Effects on the Digestive Enzymes Activity and Microbiota of the Oyster *Crassostrea gigas*,” *Journal of Applied Phycology* 32, no. 5 (2020): 3481–3493, <https://doi.org/10.1007/s10811-020-02167-4>.
156. J. M. Diamond, *The Effect of Laminaria Hyperborea Detritus on the Growth of Key Filter Feeding Species in the Littoral Zone* (University of Oslo, 2018), <http://urn.nb.no/URN:NBN:no-67983>.
157. R. Secrist, Food Availability and Utilization for Cultured Hard Clams. College of William and Mary – Virginia Institute of Marine Science (2013), <http://scholarworks.wm.edu/etd/1539617932>.
158. A. Pérez Camacho, J. M. Salinas, C. Fuertes, and M. Delgado, “Preparation of Single Cell Detritus From *Laminaria saccharina* as a Hatchery Diet for Bivalve Mollusks,” *Marine Biotechnology* 6, no. 6 (2004): 642–649, <https://doi.org/10.1007/s10126-004-2901-z>.
159. A. Pérez-Camacho, J. M. Salinas, M. Delgado, and C. Fuertes, “Use of Single Cell Detritus (SCD) Produced From *Laminaria saccharina* in the Feeding of the Clam *Ruditapes Decussatus* (Linnaeus, 1758),” *Aquaculture* 266, no. 1 (2007): 211–218, <https://doi.org/10.1016/j.aquaculture.2006.12.033>.
160. S. Carboni, S. H. Clegg, and A. D. Hughes, “The Use of Biorefinery By-Products and Natural Detritus as Feed Sources for Oysters (*Crassostrea gigas*) Juveniles,” *Aquaculture* 464 (2016): 392–398, <https://doi.org/10.1016/j.aquaculture.2016.07.021>.
161. A. Rato, S. Joaquim, T. G. Tavares, et al., “Viability of Dietary Substitution of Live Microalgae With Dry *Ulva rigida* in Broodstock Conditioning of the Pacific Oyster (*Crassostrea gigas*),” *Biology Open* 7, no. 9 (2018): bio035923, <https://doi.org/10.1242/bio.035923>.
162. A. Rato, L. F. Pereira, S. Joaquim, et al., “Fatty Acid Profile of Pacific Oyster, *Crassostrea gigas*, Fed Different Ratios of Dietary Seaweed and Microalgae During Broodstock Conditioning,” *Lipids* 54, no. 9 (2019): 531–542, <https://doi.org/10.1002/lipd.12177>.
163. X. Yin, J. Wang, M. Yang, and X. Xie, “Evaluation of Macroalgal Detritus as Food Source for Juvenile Manila Clam, *Ruditapes philippinarum*: Effects on Growth, Amino Acid Content and Fatty Acid Composition,” *Aquaculture Research* 50, no. 12 (2019): 3579–3588, <https://doi.org/10.1111/are.14313>.
164. F. Charles, A. Grémare, and J. M. Amouroux, “Ingestion Rates and Absorption Efficiencies of *Abra ovata* (Mollusca: Bivalvia) Fed on Macrophytobenthic Detritus,” *Estuarine, Coastal and Shelf Science* 42, no. 1 (1996): 83–102, <https://doi.org/10.1006/ecss.1996.0007>.
165. C. D. Amsler, *Algal Chemical Ecology*, 1st ed. (Springer, 2008), <https://doi.org/10.1007/978-3-540-74181-7>.
166. F. Charles, “Utilization of Fresh Detritus Derived From *Cystoseira mediterranea* and *Posidonia oceanica* by the Deposit-Feeding Bivalve *Abra ovata*,” *Journal of Experimental Marine Biology and Ecology* 174, no. 1 (1993): 22–64, [https://doi.org/10.1016/0022-0981\(93\)90250-R](https://doi.org/10.1016/0022-0981(93)90250-R).
167. V. Stuart, “Absorbed Ration, Respiratory Costs and Resultant Scope for Growth in the Mussel *Aulacomya ater* (Molina) Fed on a Diet of Kelp Detritus of Different Ages,” *Marine Biology Letters* 3 (1982): 289–306.
168. V. Stuart, J. G. Field, and R. C. Newell, “Evidence for Absorption of Kelp Detritus by the Ribbed Mussel *Aulacomya ater* Using a New ⁵¹Cr-Labelled Microsphere Technique,” *Marine Ecology Progress Series* 9 (1982): 263–271.
169. U. Arambalza, I. Ibarrola, E. Navarro, and M. B. Urrutia, “Ingestion and Absorption of Particles Derived From Different Macrophyta in the Cockle *Cerastoderma edule*: Effects of Food Ration,” *Journal of Comparative Physiology. B* 184, no. 2 (2014): 179–192, <https://doi.org/10.1007/s00360-013-0789-5>.
170. J. F. Pan and W. Wen-Xiong, “Differential Uptake of Dissolved and Particulate Organic Carbon by the Marine Mussel *Perna viridis*,” *Limnology and Oceanography* 49, no. 6 (2004): 1980–1991, <https://doi.org/10.4319/lo.2004.49.6.1980>.
171. P. J. Cranford and J. Grant, “Particle Clearance and Absorption of Phytoplankton and Detritus by the Sea Scallop *Placopecten magellanicus* (Gmelin),” *Journal of Experimental Marine Biology and Ecology* 137, no. 2 (1990): 105–121, [https://doi.org/10.1016/0022-0981\(90\)90064-J](https://doi.org/10.1016/0022-0981(90)90064-J).
172. J. Grant and P. J. Cranford, “Carbon and Nitrogen Scope for Growth as a Function of Diet in the Sea Scallop *Placopecten magellanicus*,” *Journal of the Marine Biological Association of the United Kingdom* 71, no. 2 (1991): 437–450, <https://doi.org/10.1017/S0025315400051699>.

173. R. J. Conover, "Assimilation of Organic Matter by Zooplankton," *Limnology and Oceanography* 11, no. 3 (1966): 338–345, <https://doi.org/10.4319/lo.1966.11.3.0338>.
174. J. I. P. Iglesias, M. B. Urrutia, E. Navarro, and I. Ibarrola, "Measuring Feeding and Absorption in Suspension-Feeding Bivalves: An Appraisal of the Biodeposition Method," *Journal of Experimental Marine Biology and Ecology* 219, no. 1–2 (1998): 71–86, [https://doi.org/10.1016/S0022-0981\(97\)00175-5](https://doi.org/10.1016/S0022-0981(97)00175-5).
175. E. A. Sosik and C. A. Simenstad, "Isotopic Evidence and Consequences of the Role of Microbes in Macroalgae Detritus-Based Food Webs," *Marine Ecology Progress Series* 494 (2013): 107–119, <https://doi.org/10.3354/meps10544>.
176. M. I. Lucas, R. C. Newell, and B. Velimirov, "Heterotrophic Utilisation of Mucilage Released During Fragmentation of Kelp (*Ecklonia maxima* and *Laminaria pallida*). II. Differential Utilisation of Dissolved Organic Components From Kelp Mucilage," *Marine Ecology Progress Series* 4 (1981): 43–55, <https://doi.org/10.3354/meps004043>.
177. R. C. Newell, E. A. S. Linley, and M. I. Lucas, "Bacterial Production and Carbon Conversion Based on Saltmarsh Plant Debris," *Estuarine, Coastal and Shelf Science* 17, no. 4 (1983): 405–419, [https://doi.org/10.1016/0272-7714\(83\)90126-9](https://doi.org/10.1016/0272-7714(83)90126-9).
178. C. Fiset, A. J. Irwin, and Z. V. Finkel, "The Macromolecular Composition of Noncalcified Marine Macroalgae," *Journal of Phycology* 55, no. 6 (2019): 1361–1369, <https://doi.org/10.1111/jpy.12913>.
179. K. Koop, R. C. Newell, and M. I. Lucas, "Biodegradation and Carbon Flow Based on Kelp (*Ecklonia maxima*) Debris in a Sandy Beach Microcosm," *Marine Ecology Progress Series* 7, no. 3 (1982): 315–326.
180. S. C. Hansen, *The Erosion of Kelp Forest Resilience in an Increasingly Turbid Environment* (University of Auckland, 2019), https://auckland.primo.exlibrisgroup.com/permalink/64UAUCK_INST/13vfdcn/alma99265158814002091.
181. B. L. Bayne, A. J. S. Hawkins, and E. Navarro, "Feeding and Digestion by the Mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in Mixtures of Silt and Algal Cells at Low Concentrations," *Journal of Experimental Marine Biology and Ecology* 111, no. 1 (1987): 1–22, [https://doi.org/10.1016/0022-0981\(87\)90017-7](https://doi.org/10.1016/0022-0981(87)90017-7).
182. J. P. A. Gardner, "Effects of Seston Variability on the Clearance Rate and Absorption Efficiency of the Mussels *Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus* From New Zealand," *Journal of Experimental Marine Biology and Ecology* 268, no. 1 (2002): 83–101, [https://doi.org/10.1016/S0022-0981\(01\)00378-1](https://doi.org/10.1016/S0022-0981(01)00378-1).
183. P. Cresson, S. Ruitton, and M. Harmelin-Vivien, "Artificial Reefs Do Increase Secondary Biomass Production: Mechanisms Evidenced by Stable Isotopes," *Marine Ecology Progress Series* 509 (2014): 15–26, <https://doi.org/10.3354/meps10866>.
184. R. B. Stephens, O. N. Shipley, and R. J. Moll, "Meta-Analysis and Critical Review of Trophic Discrimination Factors ($\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$): Importance of Tissue, Trophic Level and Diet Source," *Functional Ecology* 37, no. 9 (2023): 2535–2548, <https://doi.org/10.1111/1365-2435.14403>.
185. R. F. Bastos, F. Corrêa, K. O. Winemiller, and A. M. Garcia, "Are You What You Eat? Effects of Trophic Discrimination Factors on Estimates of Food Assimilation and Trophic Position With a New Estimation Method," *Ecological Indicators* 75 (2017): 234–241, <https://doi.org/10.1016/j.ecolind.2016.12.007>.
186. R. García-Seoane, I. G. Viana, and A. Bode, "Using MixSIAR to Quantify Mixed Contributions of Primary Producers From Amino Acid $\delta^{15}\text{N}$ of Marine Consumers," *Marine Environmental Research* 183 (2023): 105792, <https://doi.org/10.1016/j.marenvres.2022.105792>.
187. U. H. Lüder and M. N. Clayton, "Induction of Phlorotannins in the Brown Macroalga *Ecklonia radiata* (Laminariales, Phaeophyta) in Response to Simulated Herbivory? The First Microscopic Study," *Planta* 218, no. 6 (2004): 928–937, <https://doi.org/10.1007/s00425-003-1176-3>.
188. R. L. Stephenson, F. C. Tan, and K. H. Mann, "Stable Carbon Isotope Variability in Marine Macrophytes and Its Implications for Food Web Studies," *Marine Biology* 81, no. 3 (1984): 223–230, <https://doi.org/10.1007/BF00393216>.
189. C. M. Buchholz, B. Lebreton, I. Bartsch, and C. Wiencke, "Variation of Isotope Composition in Kelps From Kongsfjorden (Svalbard)," *Marine Biology* 166, no. 6 (2019): 71, <https://doi.org/10.1007/s00227-019-3513-5>.
190. J. A. Raven, A. M. Johnston, J. E. Kübler, et al., "Mechanistic Interpretation of Carbon Isotope Discrimination by Marine Macroalgae and Seagrasses," *Australian Journal of Plant Physiology* 29, no. 3 (2002): 355–378, <https://doi.org/10.1071/PP01201>.
191. J. A. Raven, M. Giordano, J. Beardall, and S. C. Maberly, "Algal Evolution in Relation to Atmospheric CO_2 : Carboxylases, Carbon-Concentrating Mechanisms and Carbon Oxidation Cycles," *Philosophical Transactions of the Royal Society B* 367, no. 1588 (2012): 493–507, <https://doi.org/10.1098/rstb.2011.0212>.
192. P. G. Verity, T. Beatty, and S. C. Williams, "Visualization and Quantification of Plankton and Detritus Using Digital Confocal Microscopy," *Aquatic Microbial Ecology* 10, no. 1 (1996): 55–67, <https://doi.org/10.3354/ame010055>.
193. J. M. Hill, C. D. McQuaid, and S. Kaehler, "Biogeographic and Nearshore–Offshore Trends in Isotope Ratios of Intertidal Mussels and Their Food Sources Around the Coast of Southern Africa," *Marine Ecology Progress Series* 318 (2006): 63–73, <https://doi.org/10.3354/meps318063>.
194. D. Bearham, M. A. Vanderklift, R. A. Downie, D. P. Thomson, and L. A. Clementson, "Macrophyte-Derived Detritus in Shallow Coastal Waters Contributes to Suspended Particulate Organic Matter and Increases Growth Rates of *Mytilus edulis*," *Marine Ecology Progress Series* 644 (2020): 91–103, <https://doi.org/10.3354/meps13314>.
195. H. M. Page, D. C. Reed, M. A. Brzezinski, J. M. Melack, and J. E. Dugan, "Assessing the Importance of Land and Marine Sources of Organic Matter to Kelp Forest Food Webs," *Marine Ecology Progress Series* 360 (2008): 47–62, <https://doi.org/10.3354/meps07382>.
196. S. K. Hamilton, S. J. Sippel, and S. E. Bunn, "Separation of Algae From Detritus for Stable Isotope or Ecological Stoichiometry Studies Using Density Fractionation in Colloidal Silica," *Limnology and Oceanography: Methods* 3, no. 3 (2005): 149–157, <https://doi.org/10.4319/lom.2005.3.149>.
197. S. C. Williams, P. G. Verity, and T. Beatty, "A New Staining Technique for Dual Identification of Plankton and Detritus in Seawater," *Journal of Plankton Research* 17, no. 11 (1995): 2037–2047, <https://doi.org/10.1093/plankt/17.11.2037>.
198. R. L. Hansman and A. L. Sessions, "Measuring the *in Situ* Carbon Isotopic Composition of Distinct Marine Plankton Populations Sorted by Flow Cytometry: Measurement of *in Situ* Plankton $\delta^{13}\text{C}$," *Limnology and Oceanography: Methods* 14, no. 2 (2016): 87–99, <https://doi.org/10.1002/lom3.10073>.
199. E. A. Elliott Smith, M. D. Fox, M. L. Fogel, and S. D. Newsome, "Amino Acid $\delta^{13}\text{C}$ Fingerprints of Nearshore Marine Autotrophs Are Consistent Across Broad Spatiotemporal Scales: An Intercontinental Isotopic Dataset and Likely Biochemical Drivers," *Functional Ecology* 36 (2022): 1191–1203, <https://doi.org/10.1111/1365-2435.14017>.
200. C. Liénart, M. Tedengren, A. Garbaras, et al., "Diet Quality Determines Blue Mussel Physiological Status: A Long-Term Experimental Multi-Biomarker Approach," *Journal of Experimental Marine Biology and Ecology* 563 (2023): 151894, <https://doi.org/10.1016/j.jembe.2023.151894>.
201. J. J. Middelburg, "Stable Isotopes Dissect Aquatic Food Webs From the Top to the Bottom," *Biogeosciences* 11, no. 8 (2014): 2357–2371, <https://doi.org/10.5194/bg-11-2357-2014>.
202. J. J. Middelburg, C. Barranguet, H. T. S. Boschker, P. M. J. Herman, T. Moens, and C. H. R. Heip, "The Fate of Intertidal

- Microphytobenthos Carbon: An in Situ ^{13}C -Labeling Study," *Limnology and Oceanography* 45, no. 6 (2000): 1224–1234, <https://doi.org/10.4319/lo.2000.45.6.1224>.
203. P. L. M. Cook, B. Veuger, S. Böer, and J. J. Middelburg, "Effect of Nutrient Availability on Carbon and Nitrogen Incorporation and Flows Through Benthic Algae and Bacteria in Near-Shore Sandy Sediment," *Aquatic Microbial Ecology* 49 (2007): 165–180, <https://doi.org/10.3354/ame01142>.
204. S. R. Maier, T. Kutti, R. J. Bannister, et al., "Recycling Pathways in Cold-Water Coral Reefs: Use of Dissolved Organic Matter and Bacteria by Key Suspension Feeding Taxa," *Scientific Reports* 10, no. 1 (2020): 9942, <https://doi.org/10.1038/s41598-020-66463-2>.
205. C. Liénart, N. Savoye, P. Conan, et al., "Relationship Between Bacterial Compartment and Particulate Organic Matter (POM) in Coastal Systems: An Assessment Using Fatty Acids and Stable Isotopes," *Estuarine, Coastal and Shelf Science* 239 (2020): 106720, <https://doi.org/10.1016/j.ecss.2020.106720>.
206. E. A. S. Linley, R. C. Newell, and M. I. Lucas, "Quantitative Relationships Between Phytoplankton, bacteria and Heterotrophic Microflagellates in Shelf Waters," *Marine Ecology Progress Series* 12 (1983): 77–89, <https://doi.org/10.3354/meps012077>.
207. F. Thomas, N. L. Duff, C. Leroux, L. Darteville, and P. Riera, "Isotopic Labeling of Cultured Macroalgae and Isolation of ^{13}C -Labeled Cell Wall Polysaccharides for Trophic Investigations," in *Advances in Botanical Research*, vol. 95 (Elsevier, 2020), 1–17, <https://doi.org/10.1016/bs.abr.2019.11.005>.
208. Z. A. Popper, G. Michel, C. Hervé, et al., "Evolution and Diversity of Plant Cell Walls: From Algae to Flowering Plants," *Annual Review of Plant Biology* 62, no. 1 (2011): 567–590, <https://doi.org/10.1146/annurev-arplant-042110-103809>.
209. M. Martin, D. Portetelle, G. Michel, and M. Vandenbol, "Microorganisms Living on Macroalgae: Diversity, Interactions, and Biotechnological Applications," *Applied Microbiology and Biotechnology* 98, no. 7 (2014): 2917–2935, <https://doi.org/10.1007/s00253-014-5557-2>.
210. M. Barbato, V. Vacchini, A. H. Engelen, et al., "What Lies on Macroalgal Surface: Diversity of Polysaccharide Degradation in Culturable Epiphytic bacteria," *AMB Express* 12, no. 1 (2022): 98, <https://doi.org/10.1186/s13568-022-01440-8>.
211. R. Marshall, S. McKinley, and C. M. Pearce, "Effects of Nutrition on Larval Growth and Survival in Bivalves," *Reviews in Aquaculture* 2, no. 1 (2010): 33–55, <https://doi.org/10.1111/j.1753-5131.2010.01022.x>.
212. P. Cheng, C. Zhou, R. Chu, et al., "Effect of Microalgae Diet and Culture System on the Rearing of Bivalve Mollusks: Nutritional Properties and Potential Cost Improvements," *Algal Research* 51 (2020): 102076, <https://doi.org/10.1016/j.algal.2020.102076>.
213. J. N. C. Whyte, "Biochemical Composition and Energy Content of Six Species of Phytoplankton Used in Mariculture of Bivalves," *Aquaculture* 60, no. 3–4 (1987): 231–241, [https://doi.org/10.1016/0044-8486\(87\)90290-0](https://doi.org/10.1016/0044-8486(87)90290-0).
214. Z. V. Finkel, M. J. Follows, J. D. Liefer, C. M. Brown, I. Benner, and A. J. Irwin, "Phylogenetic Diversity in the Macromolecular Composition of Microalgae," *PLoS One* 11, no. 5 (2016): e0155977, <https://doi.org/10.1371/journal.pone.0155977>.
215. N. V. Zhukova, "Fatty Acids of Marine Mollusks: Impact of Diet, Bacterial Symbiosis and Biosynthetic Potential," *Biomolecules* 9, no. 12 (2019): 12, <https://doi.org/10.3390/biom9120857>.
216. M. Garcia-Vaquero, G. Rajauria, J. V. O'Doherty, and T. Sweeney, "Polysaccharides From Macroalgae: Recent Advances, Innovative Technologies and Challenges in Extraction and Purification," *Food Research International* 99 (2017): 1011–1020, <https://doi.org/10.1016/j.foodres.2016.11.016>.
217. V. V. Agarkova, T. N. Krupnova, S. P. Ermakova, N. M. Shevchenko, and T. N. Zvyagintseva, "The Action of *Laminaria japonica* Extractives on 1,3- β -D-Glucanase, a Digestive Enzyme of the *Strongylocentrotus intermedius* Sea Urchin," *Applied Biochemistry and Microbiology* 43, no. 4 (2007): 459–464, <https://doi.org/10.1134/S0003683807040187>.
218. S. A. Lynch, R. Breslin, B. Bookelaar, T. Rudtanatip, K. Wongprasert, and S. C. Culloty, "Immunomodulatory and Antiviral Effects of Macroalgae Sulphated Polysaccharides: Case Studies Extend Knowledge on Their Importance in Enhancing Shellfish Health, and the Control of a Global Viral Pathogen Ostreid Herpesvirus-1 micro-Var," *Polysaccharides* 2, no. 2 (2021): 202–217, <https://doi.org/10.3390/polysaccharides2020014>.
219. Y. Zheng, F. Wang, Y. Jiang, et al., "The Multifaceted Role of Gut Microbiota in Sea Urchin Digestion: Diversity, Function, Symbiosis, and Carbohydrate Degradation," *Aquaculture Research* 2024, no. 1 (2024): 7363987, <https://doi.org/10.1155/2024/7363987>.
220. M. Uchida, *Microbial Conversion of Macroalgae Into a Detrital Hatchery Diet* (JPN AGR Res Q, 1999), 295–301.
221. A. K. Swanson and L. D. Druehl, "Induction, Exudation and the UV Protective Role of Kelp Phlorotannins," *Aquatic Botany* 73, no. 3 (2002): 241–253, [https://doi.org/10.1016/S0304-3770\(02\)00035-9](https://doi.org/10.1016/S0304-3770(02)00035-9).
222. E. Cruces, R. Rautenberger, Y. Rojas-Lillo, et al., "Physiological Acclimation of *Lessonia spicata* to Diurnal Changing PAR and UV Radiation: Differential Regulation Among Down-Regulation of Photochemistry, ROS Scavenging Activity and Phlorotannins as Major Photoprotective Mechanisms," *Photosynthesis Research* 131, no. 2 (2017): 145–157, <https://doi.org/10.1007/s11120-016-0304-4>.
223. K. L. Van Alstyne, S. L. Whitman, and J. M. Ehlig, "Differences in Herbivore Preferences, Phlorotannin Production, and Nutritional Quality Between Juvenile and Adult Tissues From Marine Brown Algae," *Marine Biology* 139, no. 1 (2001): 201–210, <https://doi.org/10.1007/s002270000507>.
224. H. Chen, D. Zhou, G. Luo, S. Zhang, and J. Chen, "Macroalgae for Biofuels Production: Progress and Perspectives," *Renewable and Sustainable Energy Reviews* 47 (2015): 427–437, <https://doi.org/10.1016/j.rser.2015.03.086>.
225. J. Nepper-Davidsen, C. R. K. Glasson, R. J. Lawton, and M. Magnusson, "High Spatial and Temporal Variation in Biomass Composition of the Novel Aquaculture Target *Ecklonia radiata*," *Journal of Applied Phycology* 35, no. 4 (2023): 1755–1768, <https://doi.org/10.1007/s10811-023-02969-2>.
226. Y. Yang, L. Du, M. Hosokawa, and K. Miyashita, "Total Lipids Content, Lipid Class and Fatty Acid Composition of Ten Species of Microalgae," *Journal of Oleo Science* 69, no. 10 (2020): 1181–1189, <https://doi.org/10.5650/jos.ess20140>.
227. J. Gamboa-Delgado, "Isotopic Techniques in Aquaculture Nutrition: State of the Art and Future Perspectives," *Reviews in Aquaculture* 14, no. 1 (2021): 456–476, <https://doi.org/10.1111/raq.12609>.
228. K. Cutajar, L. Falconer, A. Massa-Gallucci, et al., "Stable Isotope and Fatty Acid Analysis Reveal the Ability of Sea Cucumbers to Use Fish Farm Waste in Integrated Multi-Trophic Aquaculture," *Journal of Environmental Management* 318 (2022): 115511, <https://doi.org/10.1016/j.jenvman.2022.115511>.
229. S. Nahon, G. V. de Brito, H. Quental-Ferreira, et al., "Food Web in Mediterranean Coastal Integrated Multi-Trophic Aquaculture Ponds: Learnings From Fatty Acids and Stable Isotope Tracers," *Aquaculture* 567 (2023): 739292, <https://doi.org/10.1016/j.aquaculture.2023.739292>.
230. M. S. Park, J. K. Kim, S. Shin, B. H. Min, and P. Samanta, "Trophic Fractionation in an Integrated Multi-Trophic Aquaculture Off Tongyoung Coast: A Stable Isotope Approach," *Aquaculture* 536 (2021): 736454, <https://doi.org/10.1016/j.aquaculture.2021.736454>.
231. C. L. Hurd, "Slow-Flow Habitats as Refugia for Coastal Calcifiers From Ocean Acidification," *Journal of Phycology* 51, no. 4 (2015): 599–605, <https://doi.org/10.1111/jpy.12307>.

232. D. Chatzivasilieou, P. D. Dimitriou, J. Theodorou, et al., "An IMTA in Greece: Co-Culture of Fish, Bivalves, and Holothurians," *Journal of Marine Science and Engineering* 10, no. 6 (2022): 6, <https://doi.org/10.3390/jmse10060776>.
233. J. Irisarri, M. J. Fernández-Reiriz, U. Labarta, P. J. Cranford, and S. M. C. Robinson, "Availability and Utilization of Waste Fish Feed by Mussels *Mytilus edulis* in a Commercial Integrated Multi-Trophic Aquaculture (IMTA) System: A Multi-Indicator Assessment Approach," *Ecological Indicators* 48 (2015): 673–686, <https://doi.org/10.1016/j.ecoli.2014.09.030>.
234. N. T. N. Anh, N. H. Vinh, D. T. Doan, L. M. Lan, A. Kurihara, and T. N. Hai, "Co-Culture of Red Seaweed *Gracilaria tenuistipitata* and Black Tiger Shrimp *Penaeus monodon* in an Improved Extensive Pond at Various Stocking Densities With Partially Reduced Feed Rations: A Pilot-Scale Study," *Journal of Applied Phycology* 34, no. 2 (2022): 1109–1121, <https://doi.org/10.1007/s10811-021-02661-3>.
235. G. T. Dobson, N. D. Q. Duy, N. A. Paul, and P. C. Southgate, "Assessing Potential for Integrating Sea Grape (*Caulerpa lentillifera*) Culture With Sandfish (*Holothuria scabra*) and Babylon Snail (*Babylonia areolata*) co-Culture," *Aquaculture* 522 (2020): 735153, <https://doi.org/10.1016/j.aquaculture.2020.735153>.
236. J. X. Feng, Q. F. Gao, S. L. Dong, Z. L. Sun, and K. Zhang, "Trophic Relationships in a Polyculture Pond Based on Carbon and Nitrogen Stable Isotope Analyses: A Case Study in Jinghai Bay, China," *Aquaculture* 428–429 (2014): 258–264, <https://doi.org/10.1016/j.aquaculture.2014.03.008>.
237. J. Fossberg, S. Forbord, O. J. Broch, et al., "The Potential for Upscaling Kelp (*Saccharina latissima*) Cultivation in Salmon-Driven Integrated Multi-Trophic Aquaculture (IMTA)," *Frontiers in Marine Science* 5 (2018): 5, <https://doi.org/10.3389/fmars.2018.00418>.
238. L. A. Green-Gavrielidis, C. S. Thornber, and A. Oczkowski, "Integrated Multi-Trophic Aquaculture With Sugar Kelp and Oysters in a Shallow Coastal Salt Pond and Open Estuary Site. *Frontiers*," *Aquaculture* 2 (2023): 2–14, <https://doi.org/10.3389/faq.2023.1147524>.
239. G. S. Marinho, S. L. Holdt, M. J. Birkeland, and I. Angelidaki, "Commercial Cultivation and Bioremediation Potential of Sugar Kelp, *Saccharina latissima* Danish Waters," *Journal of Applied Phycology* 27, no. 5 (2015): 1963–1973, <https://doi.org/10.1007/s10811-014-0519-8>.
240. G. J. McCarthy and S. R. Wing, "Removal of Macroalgal-Derived Organic Matter From Suspension by Green-Lipped Mussels (*Perna canaliculus*): Potential Influence of Phlorotannin Concentrations and Nutritional Profiles," *Journal of Shellfish Research* 44, no. 2 (2025): 197–209, <https://doi.org/10.2983/035.044.0203>.
241. M. Pinkerton, M. Gall, S. Wood, and J. R. Zeldis, "Measuring the Effects of Bivalve Mariculture on Water Quality in Northern New Zealand Using 15 Years of MODIS-Aqua Satellite Observations," *Aquaculture Environment Interactions* 10 (2018): 529–545, <https://doi.org/10.3354/aei00288>.
242. D. R. Plew, "Shellfish Farm-Induced Changes to Tidal Circulation in an Embayment, and Implications for Seston Depletion," *Aquaculture Environment Interactions* 1, no. 3 (2011): 201–214, <https://doi.org/10.3354/aei00020>.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Supplementary Table 1** Descriptive feeding studies which fed macroalgal material to bivalves. Data are separated by diet preparation methods (Aged/bacterial, fresh/freeze dried, or single cell detritus). Details of how each diet was prepared, bivalve species used, macroalgal species, duration and amount of feeding, and bivalve health/growth metric. The effect of each diet was classified based upon the control diet used (•), with diets having a similar effect to the control marked as (○), while positive effects compared to control (+), and negative effects compared to control (– or —).