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Site Characteristics More Than Vegetation Type Influence Food Web Structure of Intertidal Salt Marshes

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Salt marshes are under increasing anthropogenic pressures that have been reported to affect the diet of fish (e.g., change in prey composition and availability), eventually resulting in alterations in their nursery function. Most studies in Europe are based on fish gut content analysis, which only reflect a small proportion of pressures to salt marshes, and do not necessarily reflect long-term disturbances. In this study, we investigated the impact of salt-marsh vegetation type on trophic network structures (i.e., fish diet and trophic position). Primary producers (particulate organic matter, microphytobenthos, and dominant terrestrial plants), potential aquatic and terrestrial prey, and fish of two dominant species (sea bass and thinlip mullet) were sampled during the summer of 2010 in four creeks from two sites from Western France (the Mont-Saint-Michel Bay and the Seine Estuary). Analysis was undertaken using C and N stable-isotope compositions. Tested response variables (diet and trophic position) suggested a dominant site effect and a weaker effect of surrounding vegetation type. Site effect was attributed to differences in anthropogenic nitrogen inputs (with a steep increase in the Mont-Saint-Michel Bay) and tidal regime between the two bays, with more marine signatures associated with a higher frequency and duration of tidal flooding events in the Seine Estuary. A second hypothesis is that invasive *Elytrigia acuta*, which has recently replaced typical salt-marsh vegetation in Mont-Saint-Michel Bay, negatively impacted the native salt-marshes nursery function by modifying the access to terrestrial prey on this site. The trophic position of the sea bass and the thinlip mullet was unchanged by local salt-marsh vegetation, and considered consistent with their diet. This study highlights the relevance of stable-isotopes analyses for assessing long-term and integrative effects of changes in vegetation resulting from human disturbances in salt marshes.

Keywords: diet partitioning, trophic position, fish nursery, *Dicentrarchus labrax*, *Chelon ramada*, salt-marsh plants

INTRODUCTION

Mostly localized in the vicinity or within estuaries, salt marshes have typical ecotone functioning with fresh and salt water influences, and are subject to anthropic pressures from both marine and terrestrial ecosystems (McLusky and Elliott, 2004). This location explains their high primary production (up to 30 tonnes of dry matter per ha per year; Lefeuvre et al., 2000). Organic matter resulting from the decomposition of plant material is exported to the sea following high tides, as an outwelling process (Odum, 1980). In unaltered European macrotidal areas, salt-marsh vegetation is entirely submerged only once or twice a month. However, marine waters drill webs of drainage creeks, allowing aquatic fauna to temporarily access salt marshes resources during high tides. The high primary production of salt marshes supports high densities of arthropods and notably decomposers such as amphipods (Schrama et al., 2012). Some of these arthropods are in turn largely consumed by spiders and insectivorous birds (Foucreau et al., 2012; Geslin et al., 2006, respectively) and, when they fall into creeks during flooding (Laffaille et al., 1998; Joyeux et al., 2017), by juvenile fish. The complex created by salt marshes and their creeks thus plays a key role for the survival of many fish species during their first year, and can be qualified as a nursery (e.g., Cattrijsse et al., 1994; Kneib, 1997, the review of Cattrijsse and Hampel, 2006; Green et al., 2009, 2012; Nunn et al., 2016; Joyeux et al., 2017). Nursery habitat value has been described by Sheaves et al. (2015) as including (1) connectivity and population dynamic (2) ecological and ecophysiological factors and (3) resource dynamics. The nursery function of salt marshes can be modified by many disturbances, especially when salt-marsh vegetation is submitted to numerous pressures (e.g., invasive plant species). Evaluating in what extent nursery function changes along with vegetation changes is thus of primary importance to sustain fish populations.

Biological invasions can have huge consequences on ecosystems structure and functioning (see Grosholz, 2002 for an extensive review). Invasive plants are reported as a disturbing factor in several salt marshes. Most of these studies have focused on *Spartina spp.* (Ayres et al., 2004) that can change the habitat structure of salt marshes and have cascading effects on birds (Gan et al., 2010; Ma et al., 2011), arthropods (Wu et al., 2009), benthic macrofauna (Hedge and Kriwoken, 2000; Neira et al., 2006), deposit-feeding snails (Wang et al., 2014), and global carbon and nitrogen fluxes and stocking (Cheng et al., 2008; Chen et al., 2011; Yin et al., 2015; Yang et al., 2016; Davidson et al., 2018). Other examples include *Tamarix spp.* (Whitcraft et al., 2008) or *Phragmites australis* (Silliman and Bertness, 2004). An atypical case of invasion was also reported for the nitrophilous grass *Elytrigia acuta* (formerly *Elymus athericus*), which had spectacular effects in several sites of North-West Europe (Bockelmann and Neuhaus, 1999), particularly well characterized in the bay of Mont-Saint-Michel (Valéry et al., 2017). The species occupied only 3% of the total area of salt marshes in 1984 and spread up to 45% of their area in 2013. The invasion by *E. acuta* has been reported to drastically modify nesting bird (Geslin et al., 2006) and arthropod (Pétillon et al., 2005) communities.

Plant composition of salt marshes is first driven by salt-marsh inundation frequency and a resulting change in soil salinity gradient (e.g., Pétillon et al., 2010), but also depends largely on management practices such as grazing (Bouchard et al., 2003). Inundation frequency and management practices affect both ongoing processes and higher trophic levels. For example, management (grazing) reduces the dominance of *Atriplex portulacoides* or the invasive *E. acuta*, with lower arthropod densities (Pétillon et al., 2005), and less insectivorous birds (Geslin et al., 2006). The impact of salt-marsh management is important on potential prey of fish with generally lower abundances in managed areas (e.g., Pétillon et al., 2007; Ford et al., 2012; van Klink et al., 2014). Indeed, salt marshes are essential habitats for particular stages of life cycles for numerous species such as fish or invertebrates (Boesch and Turner, 1984; Rountree et al., 1992; Kneib, 1997; Laffaille et al., 2001). Their nursery function seems particularly impacted by habitat disturbance, and by changes in dominant vegetation as a result of management (Dionne et al., 1999; Laffaille et al., 2000, 2005; Warren et al., 2002; Joyeux et al., 2017). Laffaille et al. (2000) found sea bass juveniles relying less on terrestrial prey of the marsh in grazed areas than in unmanaged areas.

In salt marshes, plant communities are often dominated by a single or a few plant species that are considered as keystone species affecting other species and/or matter fluxes out of proportion to their abundance and through biotic mechanisms (Power et al., 1996). In this study, we tested the broad hypothesis that changes in salt-marsh plant composition cascade into aquatic food webs, including their consumers (e.g., Laffaille et al., 2005; Mantzouki et al., 2012). More precisely, the following expectations were tested: (i) a strong impact of vegetation type and a lesser site effect on fish diet and (ii) some changes in trophic position only visible for predatory species. These hypotheses were tested by comparing the C and N stable-isotope compositions of trophic networks from invasive and natural vegetation from two bays of Western France.

MATERIALS AND METHODS

Site Description

Two salt marshes located in northwest France were sampled: the Mont-Saint-Michel Bay and the Seine Estuary (**Figure 1**). The Mont-Saint-Michel Bay is located at the border between Brittany and Normandy at northwestern France (latitude 48°40′N, longitude 1°31′W). It is a macrotidal bay characterized by one of the highest tidal ranges in the world (15 m). The intertidal area covers 220 km^2, and is composed of 180 km^2 of mudflats (slikke) and 40 km^2 of salt marshes (schorre). The salt marsh is drained by a web of creeks filled by tidal waters when the tidal range exceeds 11.25 m (Lefeuvre et al., 2000) for a duration of 2–3 h according to the water level. Salinity range was the same in the two sampling locations: 17.4–35.1 (mean salinity: 32.5 ± 5.7) in 2010. Contrary to the Mont-Saint-Michel Bay, the morphology of the Seine Estuary (located in Normandy: latitude 49°27′N, longitude 0°16′E) has been heavily modified by humans, to reduce tidal influence on intertidal habitats. The

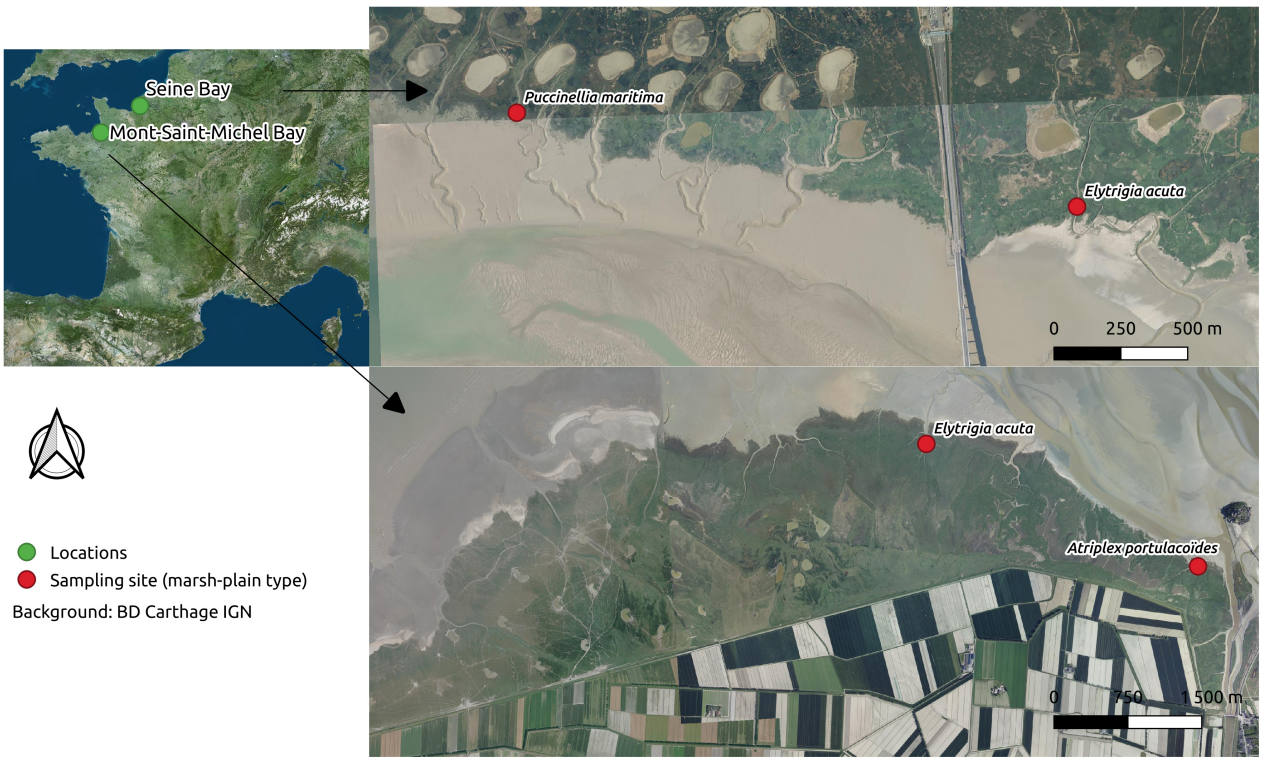

FIGURE 1 | Map of the sampling sites (green dots: Mont-Saint-Michel Bay and Seine Estuary) with sampling locations (red dots with dominant plant species name, referred as marsh-plain type in the body-text).

tidal range reaches 7 m, and the intertidal area covers 16 km^2 and is composed of 4 km^2 of mudflats (slikke) and 12 km^2 of salt marshes (schorre). Tidal waters fill the creeks when tidal range exceeds 3 m for a period of 5 h according to the water level. The salinity range was 9.8–28.8 (mean salinity: 22.7 ± 4.4) and 3.2–25.3 (mean salinity 16.6 ± 5.8) in each sampling site. Two vegetation types were sampled in the Seine Estuary: one was dominated by *Puccinellia maritima*, the other by *Elytrigia acuta* (which, in this site, is not considered as invasive by local managers based on vegetation mapping). The sampling sites (**Figure 1**) were located in the middle estuary. The Seine Estuary that is characterized by a strong salinity gradient.

In the Mont-Saint-Michel Bay, two vegetation types were also sampled: one dominated by *E. acuta* (which is considered as invasive in this site, see Valéry et al., 2017 for a review) and the other by native *Atriplex portulacoides*. The dominant vegetation types in which sampling took place is from here on referred to "marsh-plain type."

Food Web Sampling and Stable Isotopes Preparation

Sampling took place during summer 2010. A fyke net (4 mm mesh size) was set across one representative creek within each site in both salt marshes to catch fish leaving sites after the ebb (see Joyeux et al., 2017 for more details on a similar design). All fish captured were identified and measured (fork length) to get a proxy of individual age. Only the most abundant species, i.e., juvenile sea bass (*Dicentrarchus labrax*) and juvenile thinlip mullet (*Chelon ramada*), were kept for isotope analyses. Size ranges were 30.8 ± 8.4 mm and 26.5 ± 5.3 mm for *D. labrax*, 55.60 ± 11.1 mm and 72.5 ± 12.6 mm for *C. ramada*, in Mont-Saint-Michel Bay and Seine Estuary, respectively. White muscle tissues were collected from each individual at the laboratory.

Potential preys were collected by hand or caught in the fyke net when sampling fish. A minimum of 10 sample individuals per site and vegetation type and per predator was collected. For potential prey species (based on previous studies using gut content identification, e.g., Laffaille et al., 2001, 2002, 2005), a minimum of six samples per site was collected. Crustaceans (*Carcinus maenas*, *Lekanesphaera rugicauda*, *Mysida*, *Orchestia gammarellus*, and *Palaemonetes varians*) samples were subjected to a rapid acid wash to reduce inorganic carbon content. For these species, an extra sample (not submitted to acid washing) was collected to check for the possible impact of the decarbonation treatment on δ15N values (Pinnegar and Polunin, 1999). No significant differences were found, so only decarbonated samples were used.

Particulate organic matter (POM), microphytobenthos (MPB), and terrestrial plants were sampled as different primary producers. Terrestrial plants were collected by hand. For the Mont-Saint-Michel Bay, POM came from 1 L of water collected in the creek during the ebb. The water was filtered on decarbonated (4 h at 550°C) GF-F filters (47 mm diameter

Whatman). For the Seine Estuary, as analyses of field samples failed, POM data were extracted from the SOMLIT[1] long-term database (9 values for 2010). MPB was extracted from the superficial layer (5 mm) of scraped muddy sediment by exposing it to light during 2 h. The sediment was then covered with a 100 μm nylon filter and sand previously sieved (63 and 250 μm) and decarbonated (5 h, 550°C). After waiting several hours for MPB to migrate to the surface through the nylon filter, the superficial layer (2 mm) was scraped and sieved through seawater on a 45 μm filter. The content of the filter was then filtered again under decarbonated GF-F filters (4 h, 550°C).

All samples (except for the filters -POM and MPB) were then frozen before being lyophilized and crushed into a fine powder, then dried for 24 h at 50°C in a drying oven. No delipidation was performed on lyophilized samples since the C/N threshold of 3.5 proposed by Post et al. (2007) for aquatic animal samples has never been reached.

Stable Isotopes Analyses

The nitrogen and carbon isotopic compositions were determined using EA- IRMS (Isoprime, Micromass, United Kingdom). The carbon and nitrogen isotope ratios are expressed in the delta notation $\delta^{13}C$ and $\delta^{15}N$ where: $\delta^X = [(RSample / RReference) - 1] \times 1000$, where $X = \delta^{13}C$ or $\delta^{15}N$ and R is the ratio $^{13}C:^{12}C$ or $^{15}N:^{14}N$ in the sample and in the reference material. Results are referred to Vienna Pee Dee Belemnite (VPDB) for C and to atmospheric nitrogen for N and expressed in units of ‰ ± standard deviation (sd). The analytical precision (standard deviation for repeated measurements of internal standards) was ±0.2‰ and ±0.3‰ for $\delta^{13}C$ or $\delta^{15}N$, respectively.

Statistical Analyses

Isotopic signatures of fish, prey and baselines were compared between sites and marsh-plain types using multivariate analysis of variance (MANOVA) with site, marsh-plain type and site/marsh-plain type interaction as fixed factors. Normality of the $\delta^{15}N$ and $\delta^{13}C$ values was evaluated using Kolmogorov–Smirnov test. As both variables had a normal distribution, parametric tests were used.

Fish diet partitioning was achieved using Bayesian mixing model performed with package MixSIAR 3.1.10 (Stock and Semmens, 2013) in R 3.6.1 (R Core Team, 2020) with two tracers: $\delta^{13}C$ and $\delta^{15}N$.

As a first step, models were built for each fish species with POM, MPB and terrestrial plant as potential primary producers. We used primary producers rather than potential prey as we were interested in studying the effect of terrestrial plants changes in the overall contribution of salt-marsh components. For *D. labrax*, we also built models with potential prey, inferred from stomach contents obtained from previous studies and stable isotope signatures. Given the close isotopic signatures of *Carcinus maenas*, *Mysida sp.*, *Palaemonetes varians*, and *Hediste diversicolor* (**Figure 2**), the four prey were grouped altogether (further referred as "marine preys") for diet modeling. *Chelon ramada* juveniles being grazers (Lebreton et al., 2011), no diet mixing model based on prey was built. For each fish species, a null model and models including different combinations of random (site) and fixed (marsh-plain type) effects were tested with the following settings: three chains with 300,000 iterations and burn-in of 200,000 to allow for adequate model convergence. Site was included as a random factor for both fish species and primary producer signatures. Model convergence was checked using Gelman-Rubin and Geweke diagnostics. Candidate models were then compared using leave-one-out cross-validation (LOO). Input values for each model were the raw isotopic values for fish and mean and standard deviation of each primary producer. To compare the relative contribution of factors included in the best model, a new model with both factors included as random variables was run. Trophic enrichment factor values were derived from Kostecki et al. (2012) and Selleslagh et al. (2015). Two sets of values were used according to fish species trophic guilds. Values for predator (*D. labrax*) were 2 ± 0.6% and 5.6 ± 1.5% for $\delta^{13}C$ and $\delta^{15}N$, respectively. Values for grazer (*C. ramada*) were 1 ± 0.6% and 3.4 ± 1.5% for $\delta^{13}C$ and $\delta^{15}N$, respectively (Carpentier et al., 2014; Como et al., 2018).

The fish trophic position was estimated using a two-sources Bayesian model. The two sources included were the ones contributing most to the fish's diet according to the previous mixing models. Estimation was performed using the tRophicPosition 0.7.7 package (Quezada-Romegialli et al., 2019). Input values for each model were the raw isotopic values for fish and primary producers. The grouping variable was marsh-plain type.

RESULTS

Overall Stable Isotope Composition of Salt-Marsh Food Web

The MANOVA on fish isotopic signatures (**Figure 2**, **Table 1**, and **Supplementary Table 1**) demonstrated a significant effect of fish species ($F = 49.23$, df = 4, $p < 0.001$), site ($F = 220.86$, df = 2, $p < 0.001$) and marsh-plain type ($F = 9.07$, df = 4, $p < 0.001$), but no interaction between site and marsh-plain type ($F = 2.48$, df = 2, $p = 0.087$). The MANOVA on primary producers (MPB, POM, and terrestrial plants) isotopic signatures (**Table 1**) demonstrated significant differences between primary producers ($F = 11.21$, df = 4, $p < 0.001$), sites ($F = 27.32$, df = 2, $p < 0.001$), but no effect of marsh-plain type ($F = 2.03$, df = 4,z $p = 0.094$), and no interaction between site and marsh-plain type ($F = 0.05$, df = 2, $p = 0.943$).

The MANOVA on potential prey isotopic signature demonstrated a significant effect of prey species ($F = 32.04$, df = 42, $p < 0.001$), site ($F = 87.06$, df = 2, $p < 0.001$) and marsh-plain type ($F = 5.10$, df = 4, $p < 0.001$), but no interaction between site and marsh-plain type ($F = 0.234$, df = 2, $p = 0.790$).

Fish Diet Partitioning

Diets of the two fish species were better explained by models based on primary producers (MPB, POM, and terrestrial plants) including both site and marsh-plain type (**Table 2**). Similar

[1]www.somlit.fr

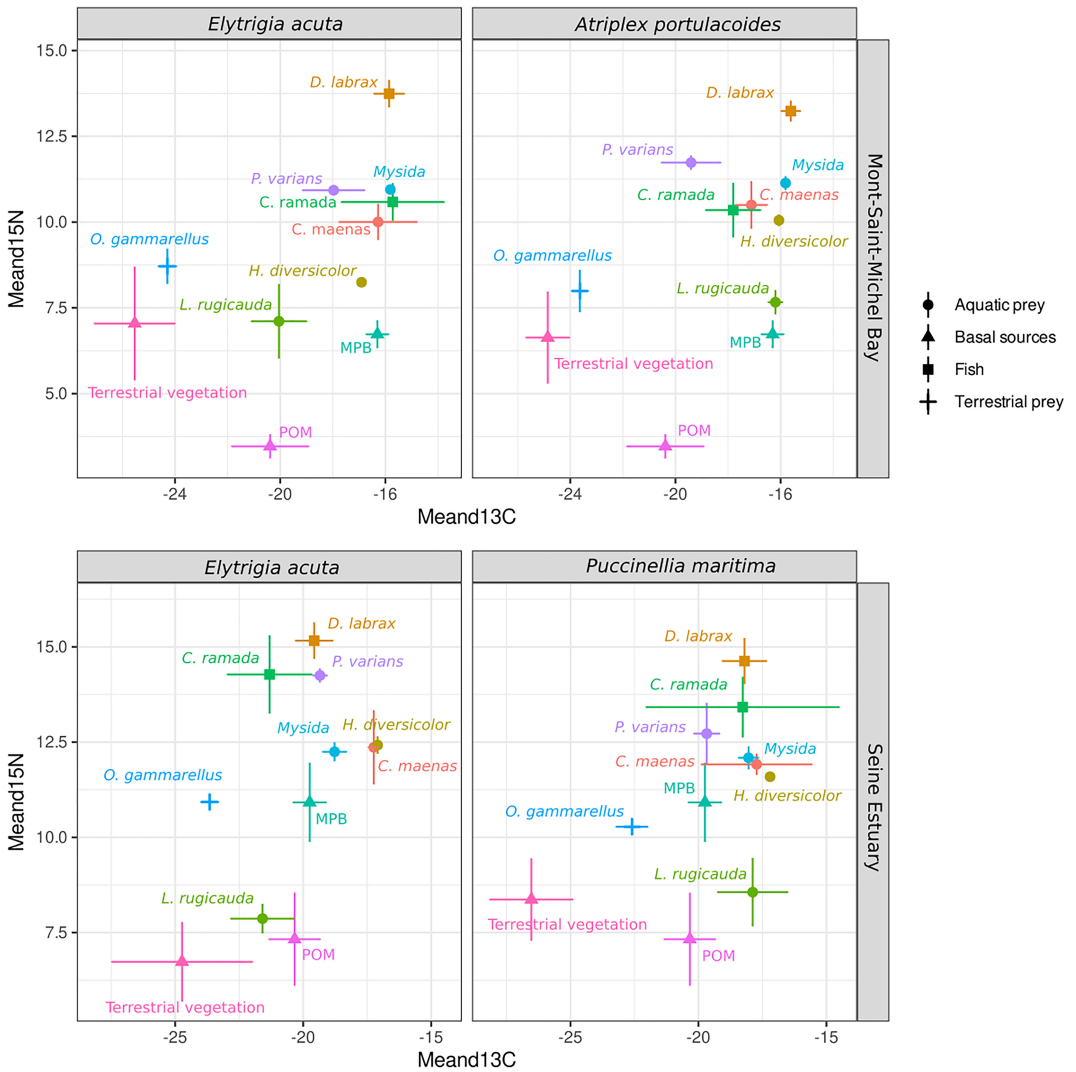

FIGURE 2 | Biplots presenting the mean and standard deviation of isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of fish, their prey and basal resources for each site and marsh-plain type (*Elytrigia acuta*, *Atriplex portulacoides*, *Puccinellia maritima*). Note, the prey and basal resources in the models are without marsh-plain type effects, the values presented are means per site.

results were found for *D. labrax* models based on potential prey (**Table 3**).

The posterior estimates of diet proportions demonstrated that MPB and POM were the main sources of organic matter contributing to *D. labrax* diet (**Figure 3**). Site and marsh-plain type equally contributed to variations in *D. labrax* diet [site median standard deviation = 8.17 (95% CI = 1.65–17.86), marsh-plain type median standard deviation: 6.21 (95% CI = 1.16–16.24)]. For sampling locations from the Mont-Saint-Michel Bay, no terrestrial primary producer contribution was observed in *D. labrax* diet, whichever marsh-plain type the individuals were sampled in (**Figure 3** and **Supplementary Table 2**). In the Seine Estuary, the contribution of terrestrial primary producers to *D. labrax* diet was 0.274 (95% CI = 0.190–0.346) for individuals collected in *E. acuta*-dominated marsh-plain areas, and 0.049 (95% CI = 0.009–0.098) in *P. maritima* areas. MPB was the main source of aquatic primary producers for *D. labrax* (>0.975) in the Mont-Saint-Michel Bay, whichever marsh-plain type the individuals were sampled in (**Figure 3** and **Supplementary Table 2**). In the Seine Estuary, POM and MPB both contributed to *D. labrax* diet in similar proportions (0.427 and 0.525), except in *E. acuta* areas where POM was lower (0.185 and 0.541) (**Figure 3** and **Supplementary Table 2**).

The posterior estimates of diet proportions based on prey signatures showed that marine species (*Carcinus maenas*, *Mysida sp.*, *Palaemonetes varians*, and *Hediste diversicolor*) were the main prey of *D. labrax* in the Mont-Saint-Michel Bay (contribution >0.5 in all cases, **Figure 4** and **Supplementary Table 3**). Nevertheless the contribution of *Lekanesphaera rugicauda* and *Orchestia gammarellus* were also important, especially in *E. acuta*-dominated areas of the Seine Estuary (**Figure 4** and **Supplementary Table 3**).

TABLE 1 | Number of samples collected (per marsh-plain type and site for predators and per site for primary producers and prey).

Marsh plain type	Species	Common name	MSMB	SE
E. acuta	*Dicentrarchus labrax*	Sea bass	14	20
E. acuta	*Chelon ramada*	Thinlip mullet	14	10
Native vegetation	*Dicentrarchus labrax*	Sea bass	21	25
Native vegetation	*Chelon ramada*	Thinlip mullet	13	10
	Carcinus maenas	Shore crab	7	7
	Chorthippus albomarginatus	Lesser marsh grasshopper	3	3
	Hediste diversicolor	Ragworm	6	5
	Lekanesphaera rugicauda	Sea slater	6	5
	Lycosidae	Wolf spiders	6	2
	Microphytobenthos		6	6
	Mysida	Opossum shrimp	6	6
	Orchestia gammarellus	Sea flea	5	5
	Palaemonetes varians	Common ditch shrimp	6	6
	Particulate organic matter		6	3
	Terrestrial vegetation		24	18

SE, Seine Estuary; MSMB, Mont-Saint-Michel Bay. "Native vegetation" refers to Atriplex portulacoides in the MSMB and to Puccinellia maritima in the SE.

TABLE 2 | LOOic values of each mixing model tested with primary producers (microphytobenthos, particulate organic matter, and terrestrial vegetation).

Fish species	Common name	Model	LOOic	Std error LOOic	Weight
Dicentrarchus labrax	Sea bass	Site + marsh-plain type	−126.2	25.9	1.0
		Site	−103.4	22.6	0.0
		Marsh-plain type	−19.0	25.0	0.0
		Null	92.5	14.1	0.0
Chelon ramada	Thinlip mullet	Site + marsh-plain type	99.7	0.0	0.852
		Site	103.2	13.8	0.148
		Marsh-plain type	173.9	74.2	0.0
		Null	195.9	96.2	0.0

Weights closer to 1 indicate an increased probability that the model explains diet partitioning.

The posterior estimates of overall diet proportions showed that *C. ramada*'s main source of carbon was MPB in both sites and for all marsh-plain types (**Figure 5** and **Supplementary Table 2**). In the Mont-Saint-Michel Bay, terrestrial plants also contributed to *C. ramada* diet in areas dominated by *A. portulacoides* (up to 0.148, see **Figure 5** and **Supplementary Table 2**).

Fish Trophic Position

Fish trophic position did not vary with marsh-plain types, since probabilities of significant differences of posterior estimates were consistently inferior to 0.5 (**Supplementary Tables 4, 5** and **Figure 6**). On the other hand, fish trophic position varied systematically with fish species, with high probabilities of difference observed when comparing sites and fish species trophic position between each other (indicating that fish species have different trophic position and that the latter is varying with site) (**Supplementary Tables 4, 5** and **Figure 6**).

TABLE 3 | LOOic values of each mixing model tested with potential prey as sources for *Dicentrarchus labrax*.

Model	LOOic	Std error LOOic	Weight
Site + marsh-plain type	25.0	27.3	1.0
Site	59.7	22.7	0.0
Marsh-plain type	156.2	23.5	0.0
Null	278.5	14.1	0.0

High weight indicates high probability the model is the best explaining diet partitioning.

DISCUSSION

To the best of our knowledge, this study is the first to investigate the effect of terrestrial vegetation type on salt-marsh nursery function for juvenile fish using stable isotopes. We found a clear difference in the contribution of main primary producers to sea bass (*D. labrax*) and thinlip mullet (*C. ramada*) diets. Nevertheless, vegetation type had an influence on the contribution of primary producers and prey only to *D. labrax* diet and only in the Seine Estuary. In the Seine Estuary, however, terrestrial primary producers had a significant contribution to *D. labrax* diet. The most striking and unexpected result of our study was the very low contribution of terrestrial carbon to *D. labrax* diet provided by salt marshes in the Mont-Saint-Michel Bay (MSMB) which strongly contrasts with the conclusions of previous studies (e.g., Laffaille et al., 2001, 2005). Interestingly, we could not find any difference of trophic position between the different marsh-plain types (i.e., types of vegetation surrounding the creek) nor for *D. labrax* nor for *C. ramada*.

Results of Bayesian mixing models suggest that the contribution of primary producers to juvenile *D. labrax* did not vary with marsh-plain type where fish are foraging [i.e., >90% microphytobenthos (MPB)] in the MSMB. MPB was the dominant source in the Seine Estuary but other primary producers (POM and terrestrial vegetation) significantly contributed to *D. labrax* diet, in proportions differing according to the marsh-plain type. The mixing model based on prey revealed that marine species (*Carcinus maenas*, *Mysida*, *Palaemonetes varians*, and *Hediste diversicolor*) appeared to be the main prey of juvenile *D. labrax* in both sites, but *O. gammarellus* and *Lekanesphaera rugicauda* significantly contributed to *D. labrax* diet in areas dominated, respectively, by *E. acuta* and *P. maritima* in the Seine Estuary.

From these results, one can state that in the Seine Estuary, terrestrial primary producers have a significant contribution to the diet of *D. labrax* juveniles, of up to 30% in areas

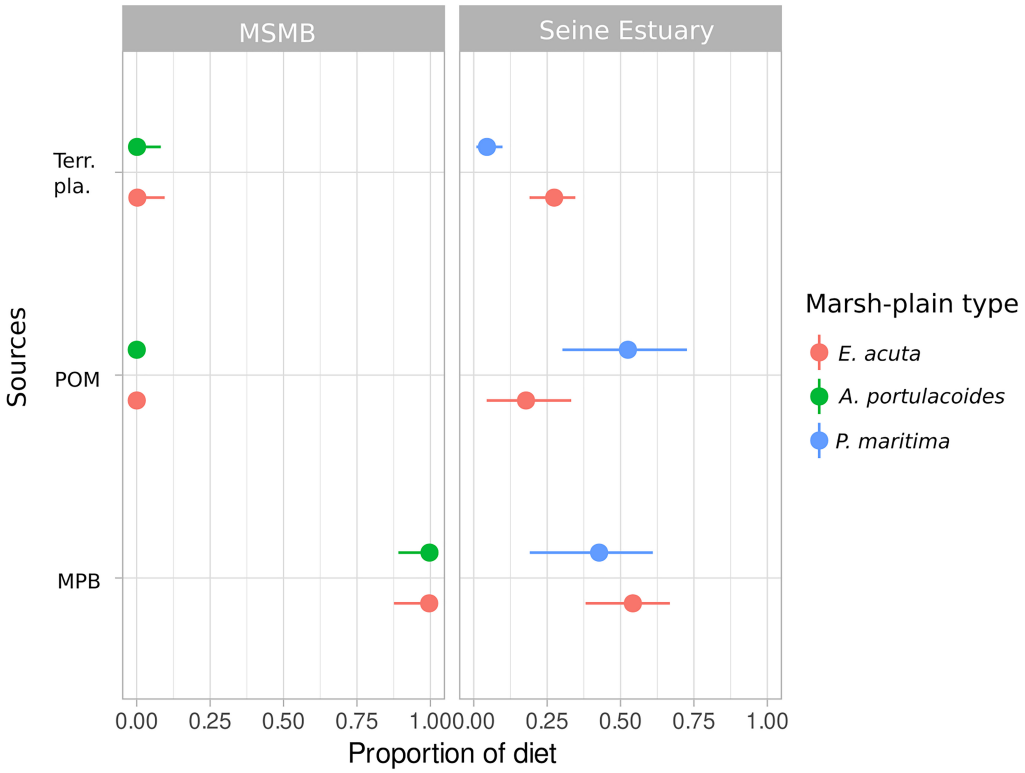

FIGURE 3 | Posterior median (points) with 90% (horizontal lines) confidence intervals for contribution of each primary producer (MPB, microphytobenthos; POM, particulate organic matter; Terr. pla., terrestrial vegetation) according to marsh-plain type in the sampling area for *D. labrax*. MSMB, Mont-Saint-Michel Bay.

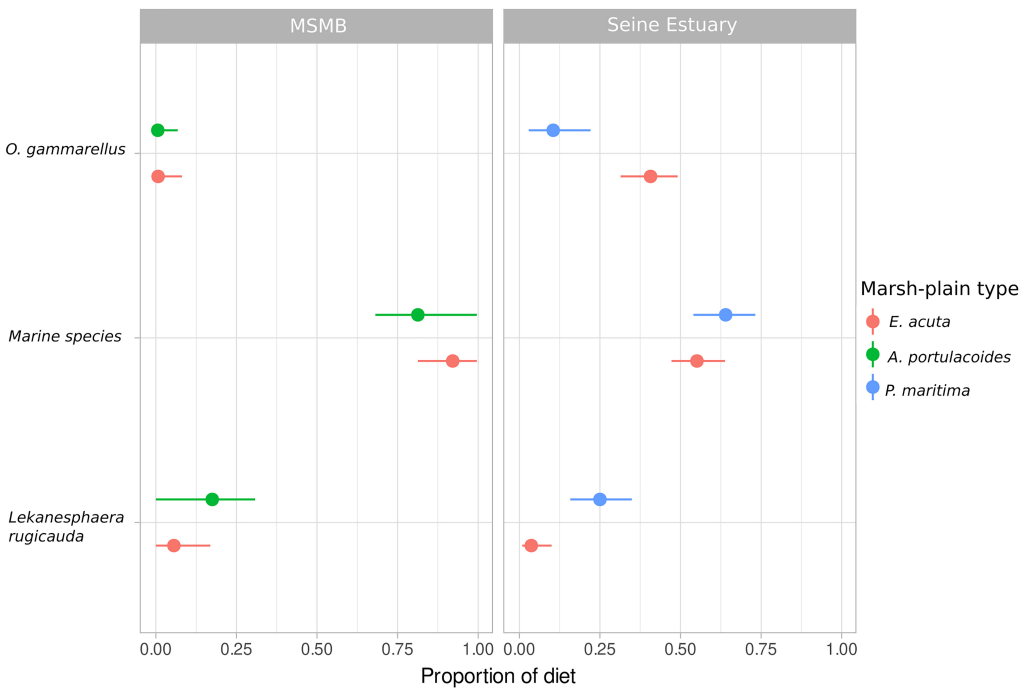

FIGURE 4 | Posterior median (points) with 90% (horizontal lines) confidence intervals for the contribution of each prey according to marsh-plain type in the sampling area for *Dicentrarchus labrax*. MSMB, Mont-Saint-Michel Bay. Marine species refers to the group: *Carcinus maenas*, *Mysida sp.*, *Palaemonetes varians*, and *Hediste diversicolor*.

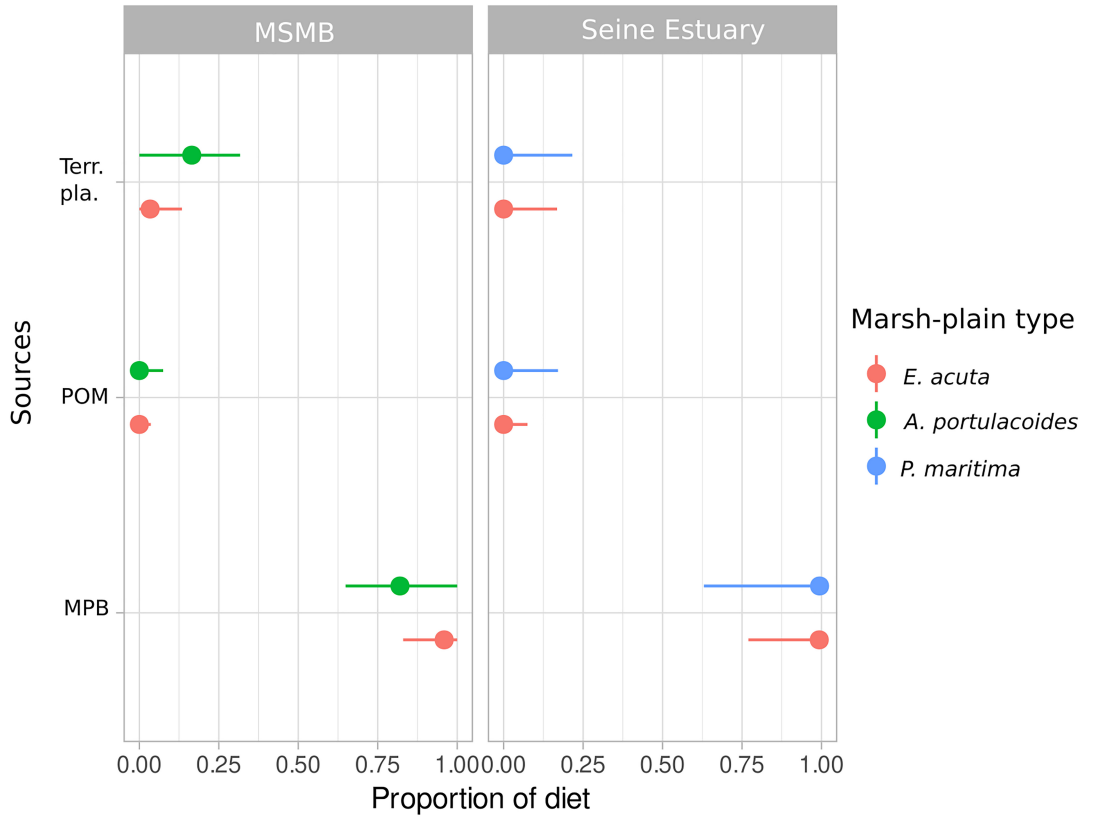

FIGURE 5 | Posterior median (points) with 90% (horizontal lines) confidence intervals for contribution of each primary producer (MPB, microphytobenthos; POM, particulate organic matter; Terr. pla., terrestrial plants) according to marsh-plain type in the sampling area for *Chelon ramada*. MSMB, Mont-Saint-Michel Bay.

dominated by *E. acuta*. Conversely, the terrestrial contribution of salt-marsh sources to *D. labrax* diet was almost inexistent in the MSMB. In the MSMB, Laffaille et al. (2001) identified *Mysida* as the main prey of *D. labrax* juveniles entering salt marshes but *O. gammarellus* was the main prey in the stomach of individuals leaving salt marshes during ebb. In Laffaille et al. (2005) demonstrated, based on stomach content analyses, that in the MSMB, *D. labrax* juveniles were consuming less *O. gammarellus* in areas invaded by *E. acuta*. In the same study, they estimated the numerical contribution of *O. gammarellus* to the diet of *D. labrax* juveniles as 58% (73% in biomass) in uninvaded areas and 28% (40% in biomass) in invaded areas. They hypothesized that such change in diet was due to a decrease in accessibility of terrestrial prey (here *O. gammarellus*) because of changes in vegetation structure (increased stem density may have been a physical obstruction for fish preying on amphipods). Laffaille et al. (2005) indeed observed a reduced prey availability due to the *E. acuta* invasion, but considered it was still high enough to not act a limiting factor on fish feeding behavior.

Our results suggest that, about 15 years after Laffaille et al. (2005) study, the contribution of terrestrial primary producers to *D. labrax* diet decreased to close to zero in the MSMB, both in creeks invaded by *E. acuta* and natural ones. We also found no significant difference in *O. gammarellus* contribution between marsh-plain types in the Seine Estuary, suggesting that vegetation is not the main factor explaining the contribution of terrestrial prey to *D. labrax* diet.

We hypothesize that, in the MSMB, the access to prey was altered by changes in halophylic vegetation, resulting from increasing nitrogen inputs (the main factor explaining the spread of *E. acuta* in the Saint-Michel Bay: Valéry et al., 2017). Nelson et al. (2019) demonstrated that the nutrient enrichment of waters entering salt marshes triggers a cascade of effects, resulting in geomorphological changes (creek deepening and enlargement with cliff-like banks: Deegan et al., 2012) and decoupling the high-marsh ecosystem from the creek ecosystem. Similarly to our results on *D. labrax* in the MSMB, Nelson et al. (2019) observed a lower contribution of terrestrial prey to mummichog (*Fundulus heteroclitus*) diet. Our hypothesis is reinforced by the situation in the Seine Estuary where *E. acuta* is not invasive and where *D. labrax* juveniles appear more dependent on salt-marsh sources (*O. gammarellus* contributed up to 40% in diet partitioning). In the Seine Estuary, the contribution of terrestrial prey to *D. labrax* diet varied with vegetation type. We are aware that our interpretation implies that site fidelity exists for juveniles of *D. labrax*. Despite several studies demonstrating that *D. labrax* are site (and even creek) dependent (Vinagre et al., 2011; Green et al., 2012; Joyeux et al., 2017), evidence is still lacking, and should be the focus of further studies.

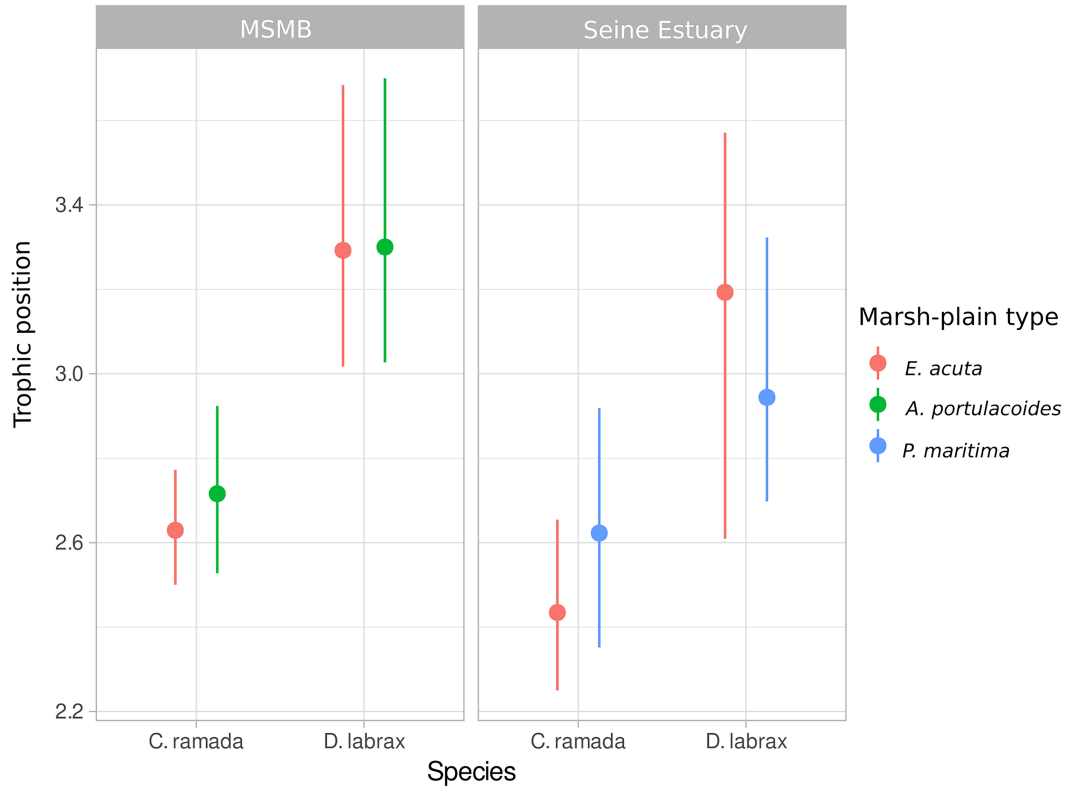

FIGURE 6 | Median and 95% CI of posterior trophic position for each fish species according to marsh-plain type. MSMB, Mont-Saint-Michel Bay, C. ramada, *Chelon ramada*; D. labrax, *Dicentrarchus labrax*.

Differences in the contributions of terrestrial primary producers between the two sites may be the result of different frequencies of access to salt marshes for fish. The two sites strongly differ in tidal amplitude (15 m in the MSMB vs. 7 m in the Seine Estuary) and high water slack duration (zero in the MSMB vs. ±3 h in the Seine Estuary because of the existence in the channel of two asynchronic tides entering the estuary). Because of this differing tidal amplitude, the percent of tides during which fish are able to enter into salt-marsh creeks are estimated to be 43% per year in the MSMB (Laffaille et al., 2001) and up to 60% in the Seine Estuary (Duhamel comm.pers.). Finally, the huge difference in the total surface of sites, with 220, 180, and 40 km^2 in MSMB and 16, 4, and 12 km^2 in the Seine Estuary for intertidal area, mudflats and salt marsh areas, respectively, could also lead to contrasting accessibility and attractivity for fish. One can thus hypothesize that such a difference in the ability for fish to exploit salt-marsh creeks for feeding, would have a significant effect on their isotopic signature.

As expected, juveniles of *C. ramada* derived most of their carbon from benthic primary producers, and particularly MPB. Similar results were reported by Lebreton et al. (2011) using stable isotopes. These authors confirmed that *C. ramada* juveniles exploiting salt marshes are limno-benthophagous. Nevertheless, the uncertainty regarding the contribution of each primary producer was very high in our study. Such a result suggests that this species probably uses several salt marshes with different isotopic signatures to forage. This hypothesis tends to be confirmed by the telemetry results obtained by Trancart et al. (2012) and by several studies on other species highlighting the existence of individual variations in fish movement behavior that can mediate the direction and scale of food web subsidies (e.g., Lesser et al., 2020; Rezek et al., 2020).

The trophic position of the two studied fish species was not different according to the marsh-plain type. This result is not surprising as we found a very weak contribution of terrestrial primary producers to fish diet in the MSMB. In the Seine Estuary, despite the higher contribution of terrestrial primary producers to fish diet, the trophic position of fish did not vary with vegetation type.

We indeed found a strong, unexpected site effect on all characteristics of the food web. All best diet partitioning models included site and in a lesser extent vegetation type as a predictive variable. Nevertheless, the large uncertainty on the contribution of the two variables renders any comparison hard. A long-term study combining stable isotopes and stomach content identification approaches could probably confirm our findings. Nevertheless, diet and food availability have been largely studied over the last two decades notably in MSMB (Laffaille et al., 2001, 2005; Carpentier unpublished data from 2015 to 2017), limiting potential errors in preys identification through isotopes. The contribution of terrestrial sources to predatory fish diet was much higher in the Seine Estuary. At a larger spatial scale, a

recent review by Ziegler et al. (2019) emphasized the key role of tidal amplitude in structuring food webs. We believe that a similar process (i.e., tides regulate the access to salt marshes for transient estuarine fishes) can be observed within the same biogeographic area. We finally hypothesize that the importance of nursery function of macrotidal salt marshes in Western Europe would be more diverse than expected given the large inter-site variability and overall low terrestrial contribution to fish diet we found in this study.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://gitlab.com/DenisLafage/marsh_veget_foodweb.

AUTHOR CONTRIBUTIONS

AC and JP conceived and designed the experiment. AC, SD, and SL conducted the field and lab work. DL performed the statistical analyses. AC, DL, and JP wrote the manuscript draft. All authors contributed critically to the drafts and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.669759/full#supplementary-material

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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