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E. Andrew Hart

James R. Lovvorn
Southern Illinois University Carbondale

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ALGAL VS. MACROPHYTE INPUTS TO FOOD WEBS OF INLAND SALINE WETLANDS

E. Andrew Hart and James R. Lovvorn[1]

Department of Zoology, University of Wyoming, Laramie, Wyoming 82071 USA

Abstract. Invertebrate food webs in wetlands were traditionally thought to be fueled mainly by decaying macrophytes, but recently it has been recognized that microalgae may be more important. In particular, the paradigm that shredders of vascular plant litter dominate food web processes may not apply to many wetlands where shredders are rare and microalgae more abundant. This issue is complicated by potential consumption of flocs of dissolved organic matter (DOM) released from living plants, and of exopolymer secretions (EPS) from both autotrophic and heterotrophic microbes. In Wyoming, we used gut contents and stable isotopes to investigate organic matter sources for the dominant invertebrates in oligosaline (0.5–5 g/L total dissolved solids) and mesosaline (5–18 g/L) wetlands. We examined the trophic importance of microalgae vs. macrophytes in wetlands with and without emergent vegetation (*Scirpus acutus*), with different growth forms and species of submersed plants (*Chara* spp. vs. *Potamogeton pectinatus*), with dominance by different microalgal types (phytoplankton, epiphyton, epipelon), and with different primary consumers (mainly amphipods vs. chironomid larvae). In all wetlands studied, guts of the major primary consumers contained little or no macrophyte tissue, but rather mostly amorphous detritus (organic particles with no recognizable cellular structure). Values of $\delta^{13}C$ indicated that organic matter entering foodwebs was not from submersed macrophytes, but that emergent plants might be a source of DOM or EPS in amorphous detritus. However, in some wetlands, amphipods eating mainly amorphous detritus had the same $\delta^{13}C$ values as chironomids eating a much higher fraction of diatoms, indicating that amorphous detritus was derived mainly from diatoms. Patterns of temporal change of $\delta^{13}C$ in consumers, seston, and emergent plants supported this interpretation. We conclude that microalgae rather than macrophytes provided most organic matter for these food webs via amorphous detritus. Amorphous detritus is often thought to have poor nutrient quality and low assimilation efficiency, but this idea may not be true if amorphous detritus is largely flocs of labile DOM/EPS. Our results suggest that characterizing the origin and nature of amorphous detritus is key to understanding variations in macroinvertebrate production among saline wetlands and a broad range of wetland types.

Key words: algal forms; amorphous detritus; dissolved organic matter; exopolymer secretions; invertebrate food webs; invertebrate gut contents; macrophytes; organic matter sources; saline wetlands; stable isotopes; wetland food webs.

Introduction

In nontidal wetlands, invertebrate food webs were traditionally thought to be fueled mainly by decomposing macrophyte tissue, especially of emergent plants (Murkin 1989, Batzer and Wissinger 1996, Mitsch and Gosselink 2000). Accordingly, basic texts, as well as wetland creation and restoration manuals, generally treat food webs in nontidal wetlands as detritus-based (e.g., Marble 1992, Horne and Goldman 1994, Hammer 1997, Mitsch and Gosselink 2000). More recently attention has shifted to algae—despite lower standing stocks, the higher production and digestibility of microalgae might make them more important to invertebrate production (Campeau et al. 1994, de Szalay and Resh 1996, Goldsborough and Robinson 1996, Euliss et al. 1999). For inland saline wetlands, microalgae might be especially critical because emergent plants are restricted by unstable water levels and high salinities; however, such wetlands usually contain submersed macrophytes (Hart and Lovvorn 2000). Identifying organic sources is complicated by potential consumption of flocs of dissolved organic matter (DOM) released by plants or algae while alive or in early decomposition (Mann 1988), and of exopolymer secretions (EPS) from algae and from microbes consuming different plant species (Decho 1990). These materials can form highly digestible amorphous detritus (organic particles with no recognizable cellular structures) that might increase the availability of macrophyte production. Both production and consumer use of macrophytes and microalgae can vary with community composition (Boschker et al. 1995, Currin et al. 1995, Kwak and Zedler 1997, Page 1997), and different types of saline wetlands differ in

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[1] Corresponding author. E-mail: lovvorn@uwyo.edu

dominant macrophytes, microalgal forms, and invertebrates (Lovvorn et al. 1999, Hart and Lovvorn 2000). Thus, pathways and flows of macrophyte and microalgal carbon to different invertebrates are key to food web functions of different wetland types, and their ability to support diverse consumers at a range of trophic levels (Wollheim and Lovvorn 1995).

In wetlands of prairies and plains, the traditional focus on emergent macrophytes as the base of food webs stemmed largely from their obviously high biomass and production (Murkin 1989). With little direct herbivory, most macrophyte production accumulates through the growing season and enters the water as dead stems and leaves. Such wetlands were perceived as detritus-based systems in which secondary production depends mainly on organic input from senescent macrophytes. In such a situation, shredding macroinvertebrates are thought to play a vital role in invertebrate communities and organic matter cycling, by consuming coarse particulate organic matter (CPOM) such as leaf fragments and egesting fine particulate organic matter (FPOM) (Webster and Benfield 1986, Cummins et al. 1989, Cuffney et al. 1990). However, for many nonforested wetlands with few shredding invertebrates, the shredder paradigm has been questioned (Wissinger 1999). Much senescent emergent tissue is decomposed by fungi while the plants are still standing, before they enter the water and become available to aquatic invertebrates (Newell et al. 1995, Barlocher and Biddiscombe 1996). Thus, in prairie and plains wetlands, physical and microbial action may be far more important than shredders in processing macrophyte CPOM and generating FPOM.

Standing stocks of microalgae are usually much smaller than for macrophytes, but can turn over rapidly. In prairie and plains wetlands, total microalgal production can be comparable to that of macrophytes (Robinson et al. 1997, Hart and Lovvorn 2000) and algae are much more digestible (Mann 1988). In a model that parallels cyclic succession of macrophytes, Goldsborough and Robinson (1996) envisioned four wetland states, each dominated by a different form of microalgae: epipelon on and in sediments, epiphyton on macrophyte surfaces, phytoplankton in the water column, or metaphyton growing in mats. Secondary production was presumed to be linked to the dominant microalgal form, but the importance of each algal type to macroinvertebrates has not been widely examined.

In prairie and plains wetlands, attempts to discern the trophic role of microalgae for macroinvertebrates have included both stable isotope surveys and fertilization experiments. In prairie wetlands of Manitoba, $\delta^{13}C$ and $\delta^{15}N$ indicated that macroinvertebrates did not consume metaphyton or submersed aquatic plants, but the significance of epiphyton, emergent macrophytes, and floating macrophytes (*Lemna minor*) could not be distinguished (Neill and Cornwell 1992). In North Dakota, $\delta^{13}C$ suggested that most invertebrates depended on carbon derived from microalgae, with little contribution of emergent, submersed, or floating macrophytes (Euliss et al. 1999). Also in Manitoba, available foods were manipulated by reducing macrophyte litter, replacing fallen dead stems with polyurethane foam, and increasing algae by adding nutrients (Campeau et al. 1994). Results varied for different invertebrates, but the biomass of abundant chironomid larvae did not differ between treatments with foam vs. macrophyte stems. However, over the whole season, more chironomids emerged from treatments with real stems than from those with foam. Chironomids responded to nutrient-induced algal increases with earlier peak emergences. These studies raise several questions about the role of microalgae in secondary production. Is the relative importance of algae related to standing stocks of emergent or submersed plants of different species? Is the form of microalgae with dominant biomass the most important form (sensu Goldsborough and Robinson 1996)? Does the role of microalgae depend on the taxa of macroinvertebrates present?

In the Laramie Basin, Wyoming, we used stable isotopes and gut contents to examine the importance of macrophyte vs. algal inputs to food webs for two types of saline wetlands dominated by different macrophyte, microalgal, and invertebrate communities. The oligosaline wetlands (0.5–5 mg/L total dissolved solids, TDS) have peripheral stands of hardstem bulrush (*Scirpus acutus*) surrounding open water dominated by the low-growing macroalga *Chara* spp. Microalgal biomass and production are dominated by epiphyton growing on the surfaces of *Chara* (Hart and Lovvorn 2000), and primary consumer biomass is dominated mainly by amphipods (Wollheim and Lovvorn 1995, 1996). The mesosaline wetlands (5–18 g/L TDS) lack emergent plants and have a fringe of unvegetated mudflat often with a crust of salt; submersed macrophytes are mostly angiosperms with erect growth forms, mainly sago pondweed (*Potamogeton pectinatus*). Microalgal biomass and production are more evenly distributed between phytoplankton, epiphyton, and epipelon. Amphipods are uncommon in mesosaline wetlands, and chironomid larvae and zooplankton (copepods and cladocerans) dominate primary consumer biomass. Thus, we compared the trophic importance of microalgae vs. macrophytes between wetlands with and without emergent vegetation, with different growth forms and species of submersed macrophytes, with dominance by different microalgal types, and with different invertebrate communities.

Methods

Use of stable isotopes to identify carbon sources and food web pathways is typically based on the assumptions that $\delta^{13}C$ changes by $<1‰$ and $\delta^{15}N$ by a mean of $\sim 3.4‰$ per trophic level (Fry 1991, Neill and Cornwell 1992). However, fractionation of ^{15}N can vary appreciably from this mean value in different situations

and for different trophic levels (Vander Zanden and Rasmussen 2001, Hart and Lovvorn 2002). Moreover, the mean of more than one food with different isotope values can erroneously indicate consumption of yet another item that is not eaten. Consequently, we used both gut contents and stable isotopes at different times in different wetlands to examine trophic relationships (Mihuc and Toetz 1994).

Macroinvertebrates, seston, epiphyton, plants, and sediments were collected in early June and mid-August 2000 in two oligosaline (George and Nelson) and two mesosaline wetlands (Creighton and Gibbs) in the Laramie Basin, Wyoming (Peck and Lovvorn 2001) (see see Plate 1). Samples were collected at three different sites per wetland and analyzed separately. Water depth at each site was ~0.5 m, and sites were in submersed macrophyte stands with representative density and height for each wetland. In the field, invertebrates for stable isotope analysis were quick frozen in vials of distilled water placed in an ice–isopropanol bath. Reference samples for gut-content analysis were preserved in 10% formalin.

Seston was collected on precombusted glass-fiber filters (Whatman GF/F or Gelman AE). To prevent contamination of seston, zooplankton were removed from samples by prefiltering through a 243-μm mesh and by carefully inspecting the residue retained by the glass-fiber filters. Epiphyton was separated from macrophytes by a shaking method (Hart and Lovvorn 2000). Macrophyte samples were shaken vigorously in a water-filled jar for 1 min, the solution decanted through a 500-μm screen, water added again, and the shaking repeated a total of three times. The water in the jar was clear after the third shaking. The three decanted solutions were pooled and three 10-mL subsamples of the pooled solution were filtered onto precombusted glass-fiber filters. The cleaned macrophytes were kept for analysis.

Sediments were collected with a plastic corer 5 cm in diameter and dried immediately upon return to the laboratory. We use the term ''small sediments'' for particles <100 μm sieved from the top 1–2 cm of sediments after oven drying. This fraction had very high organic content, and microscopic inspection revealed few if any vascular plant fragments. Subsequently, we used the small sediment fraction to represent the organic matter in epipelon.

Samples for $\delta^{13}C$ analysis were rinsed with 10% HCl to remove $CaCO_3$ precipitates; samples for $\delta^{15}N$ analysis were not acid rinsed. All samples were rinsed with distilled water before being homogenized. For amphipods (*Hyalella azteca*) and chironomid larvae (*Chironomus* spp. and Orthocladinae), gut contents were removed before isotope analysis. Most isotope measurements were made at the University of Wyoming Stable Isotope Facility using a MicroMass Isoprime continuous-flow isotope-ratio mass spectrometer (MicroMass, Manchester, UK). Precision was ±0.1‰ for $\delta^{13}C$ and ±0.3‰ for $\delta^{15}N$. Some samples with particularly low nitrogen content were measured with a dual-inlet isotope-ratio mass spectrometer at The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts. When measurements were compared for the same samples between laboratories, all results were consistent.

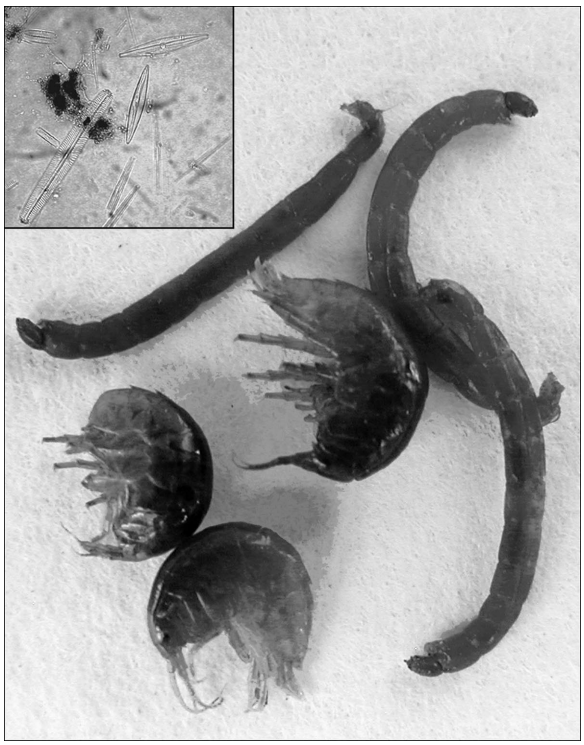

PLATE 1. Amphipods (*Hyalella azteca*), chironomid larvae, diatoms, and amorphous detritus (dark, formless material in inset) from a wetland in the Laramie Basin, Wyoming (USA). Photo by E. A. Hart.

For amphipods and chironomid larvae, the entire foregut was removed and transferred to a depression microscope slide where gut contents were separated from stomach walls. Gut contents were suspended in deionized water, filtered onto 0.45-μm membrane filters, mounted on a slide, and cleared with immersion oil. Each slide included the pooled gut contents of two to five chironomids or five to 10 amphipods. For each treatment of wetland and sampling period, three slides were analyzed for each invertebrate taxon. Slides were examined at 400× magnification, and the first 50 particles found along a transect across the slide were classified and measured with an ocular micrometer. Percent mass of a food ingested was assumed equivalent to the area occupied by a given particle type as a percentage of the total area occupied by all 50 particles (Hall et al. 2000).

Gut contents were classified as vascular plant tissue, green algae, diatoms, or amorphous detritus. Both vascular plant tissue and algae have recognizable cellular

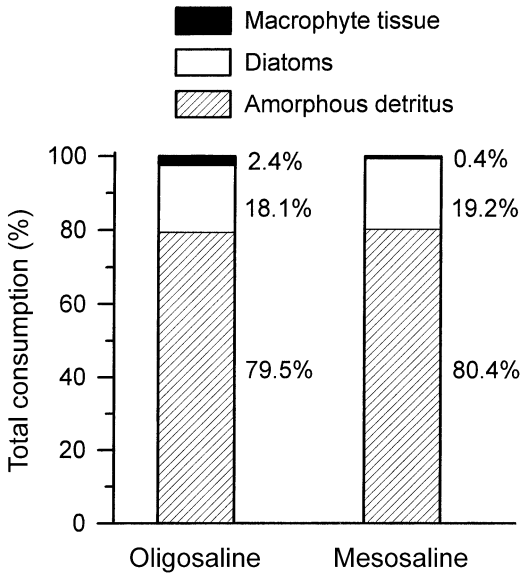

FIG. 1. Total percent mass of foods eaten by the major primary consumers (amphipods and chironomid larvae) in two oligosaline and two mesosaline wetlands in the Laramie Basin, Wyoming. Total percent mass of foods was computed as the percent mass of each food for each invertebrate taxon, weighted by that taxon's mean percentage of total invertebrate dry mass in these wetlands (Table 1). Amorphous detritus was organic particles that contained no recognizable cellular structures.

structures (e.g., rigid cell walls). We defined amorphous detritus according to Hall et al. (2000): particles with no recognizable cellular structure, which appear as discrete aggregations of subcellular-sized particles using phase-contrast microscopy. Examination of many samples indicated that diatoms comprised most of the algal community in the phytoplankton, epiphyton, and epipelon.

RESULTS

Gut contents

For the major primary consumers in oligosaline or mesosaline wetlands, vascular macrophyte tissue comprised 0% of the gut contents of chironomid larvae and only 0–6% for amphipods (Table 1). The highest fraction of macrophyte detritus ingested was 11% by amphipods in early June in Nelson Pond. Instead, chironomid and amphipod guts contained mainly diatoms and amorphous detritus, in terms of both frequency of occurrence and percent mass. When percent mass of each food was weighted by the percentage of total invertebrate biomass comprised by these two taxa (Table 1), ingestion patterns were very similar between wetland types (Fig. 1).

Stable isotopes

Differences between sampling periods.—For $\delta^{13}C$ and $\delta^{15}N$, the most apparent pattern was change between early June and mid-August samples (Figs. 2 and 3). Values changed in all wetlands, and there was no obvious difference in the pattern of change between oligosaline and mesosaline wetlands. Values of $\delta^{13}C$ tended to be heavier in August, while there was no clear trend for $\delta^{15}N$. On average, $\delta^{13}C$ values changed more than $\delta^{15}N$ values. Between early June and mid-August in all wetlands, $\delta^{13}C$ values changed on average by 3.5‰ for macroinvertebrate consumers; 2.1‰ for seston, epiphyton, and small sediments (epipelon); and 0.7‰ for submersed macrophytes. For $\delta^{15}N$, values changed on average by 1.1‰ for macroinvertebrate consumers; 1.4‰ for seston, epiphyton, and small sediments; and 0.4‰ for submersed macrophytes. For a particular sample type, the magnitude of seasonal change ranged from nearly 0 for $\delta^{13}C$ and $\delta^{15}N$ of emergent plants to 8.5‰ $\delta^{13}C$ for zooplankton in Creighton Lake and 3.7‰ $\delta^{15}N$ for seston in Lake George.

Differences between wetland types.—Values of $\delta^{13}C$ in mesosaline wetlands were generally less negative (heavier or less fractionated) than in oligosaline wetlands. This pattern likely corresponded to the higher alkalinity in mesosaline than oligosaline wetlands (three to four times higher, Hart and Lovvorn 2000), and the dominance of HCO_3^- in DIC pools (Fry 1996). Although plants in saline wetlands can use HCO_3^- as

TABLE 1. Percent mass of foods in the guts of amphipods (*Hyalella azteca*) and chironomid larvae (*Chironomus* spp. or Orthocladinae) for early June and mid-August combined, dry mass of these invertebrate taxa as a percentage of the total dry mass of macroinvertebrates averaged for oligosaline vs. mesosaline lakes (Wollheim and Lovvorn 1995), and total percent mass of each food consumed by amphipods and chironomids combined.

	Oligosaline						Mesosaline					
	George			Nelson			Creighton			Gibbs		
Measure	Amphipods	Chironomids	Total	Amphipods	Chironomids	Total	Amphipods	Chironomids	Total	Amphipods	Chironomids	Total
Gut contents												
Macrophyte tissue	0	0	0	6	0	5	3	0	1	0	0	0
Diatoms	17	68	26	4	44	11	3	5	4	13	41	34
Green algae	0	3	1	0	0	0	0	0	0	0	0	0
Amorphous detritus	83	29	74	90	56	84	94	95	95	85	59	66
Invertebrate dry mass	83	17		83	17		26	74		26	74	

Notes: Total percent mass was calculated by weighting the percent mass of each food in each taxon by that taxon's percentage of total invertebrate dry mass. Amorphous detritus was organic particles with no recognizable cellular structures.

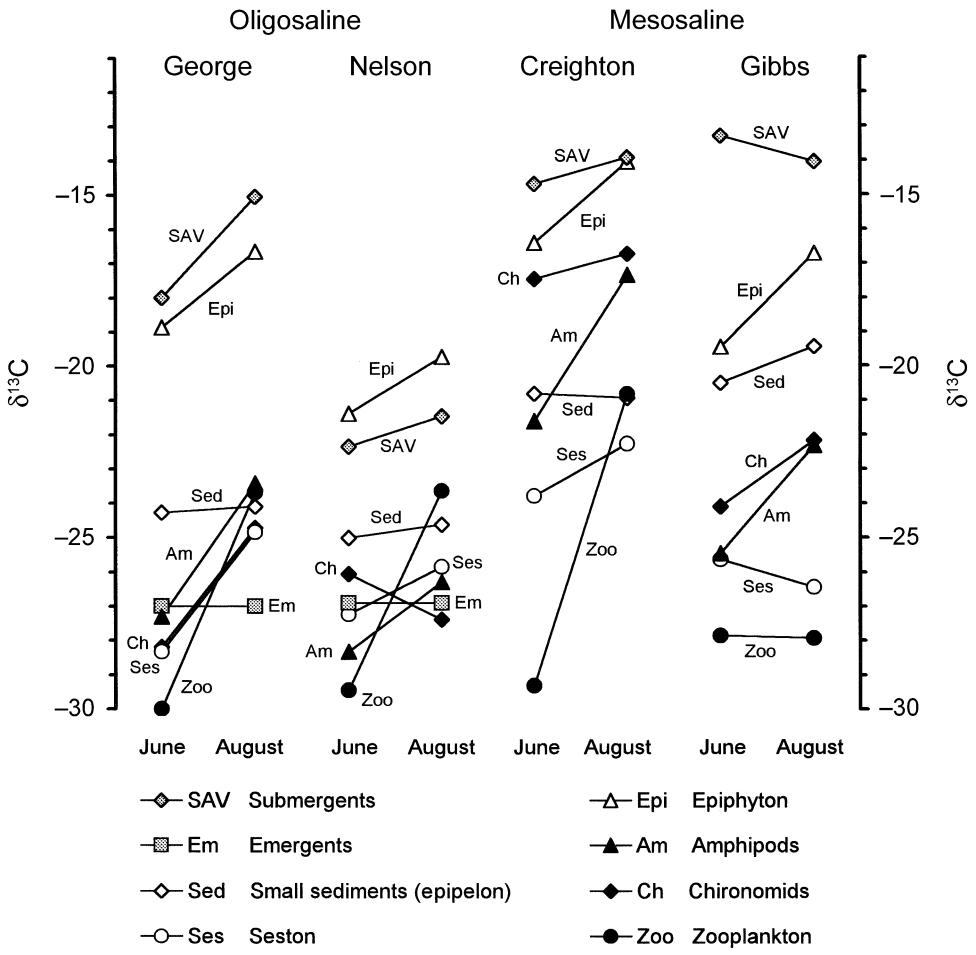

FIG. 2. Mean $\delta^{13}C$ values ($n = 3$ samples per wetland) in early June and mid-August in oligosaline wetlands George and Nelson and mesosaline wetlands Creighton and Gibbs in the Laramie Basin, Wyoming. Submersed aquatic vegetation (SAV) was *Chara* spp. in oligosaline wetlands and *Potamogeton pectinatus* in mesosaline wetlands; emergents were *Scirpus acutus*. Amphipods were *Hyalella azteca*, chironomid larvae were *Chironomus* spp. and Orthocladinae, and zooplankton were copepods (mainly *Diaptomus* spp.) and cladocerans (mainly *Daphnia* spp.). Shaded symbols are for macrophytes, open symbols for algae, and solid symbols for primary consumers. For standard deviations, see Hart (2001) or the Appendix.

a source of inorganic carbon, they prefer CO_2 (Maberly and Madsen 1998); with more CO_2 in oligosaline wetlands, plants will be more selective of the preferred light isotope. Within wetlands, $\delta^{13}C$ values were always lowest (most selection against heavy isotope) for seston and always highest (least selection against heavy isotope) for submersed macrophytes and associated epiphyton. In oligosaline wetlands, $\delta^{13}C$ of submersed macrophytes and epiphyton tended to group apart from values for emergent plants, seston, small sediments (epipelon), and consumers. In mesosaline wetlands, $\delta^{13}C$ values were more evenly distributed.

For $\delta^{15}N$, samples from mesosaline wetlands tended to have greater and more varied values than those from oligosaline wetlands. In all wetlands, $\delta^{15}N$ for organic matter in seston was greater in mid-August than in early June. Beyond this trend, few patterns in $\delta^{15}N$ were evident and we chose not to interpret results further. Effects of varying food quality (C:N ratios, Adams and Sterner 2000), relative turnover rates at different trophic levels, and the seasonal change of $\delta^{15}N$ at the base of foodwebs rendered assumptions about trophic-level ^{15}N enrichment unreliable (Hart and Lovvorn 2002). That is, $\delta^{15}N$ could have been enriched by anywhere from 0 to 3.4‰ (or an even wider range) with each trophic level, and we had no basis for assuming a particular value.

Organic matter sources.—In oligosaline wetlands, $\delta^{13}C$ values for amphipods and chironomid larvae differed strongly from those for submersed macrophytes (*Chara*), epiphyton, and small sediments (epipelon) (Fig. 2). While gut contents of these consumers contained little or no identifiable macrophyte tissues (Table 1, Fig. 1), their $\delta^{13}C$ values overlapped those of emergent plants (*Scirpus acutus*)—emergent carbon might be incorporated into flocs or microbial biofilms and comprise a portion of amorphous detritus. However, in Lake George, chironomids ate 68% diatoms while am-

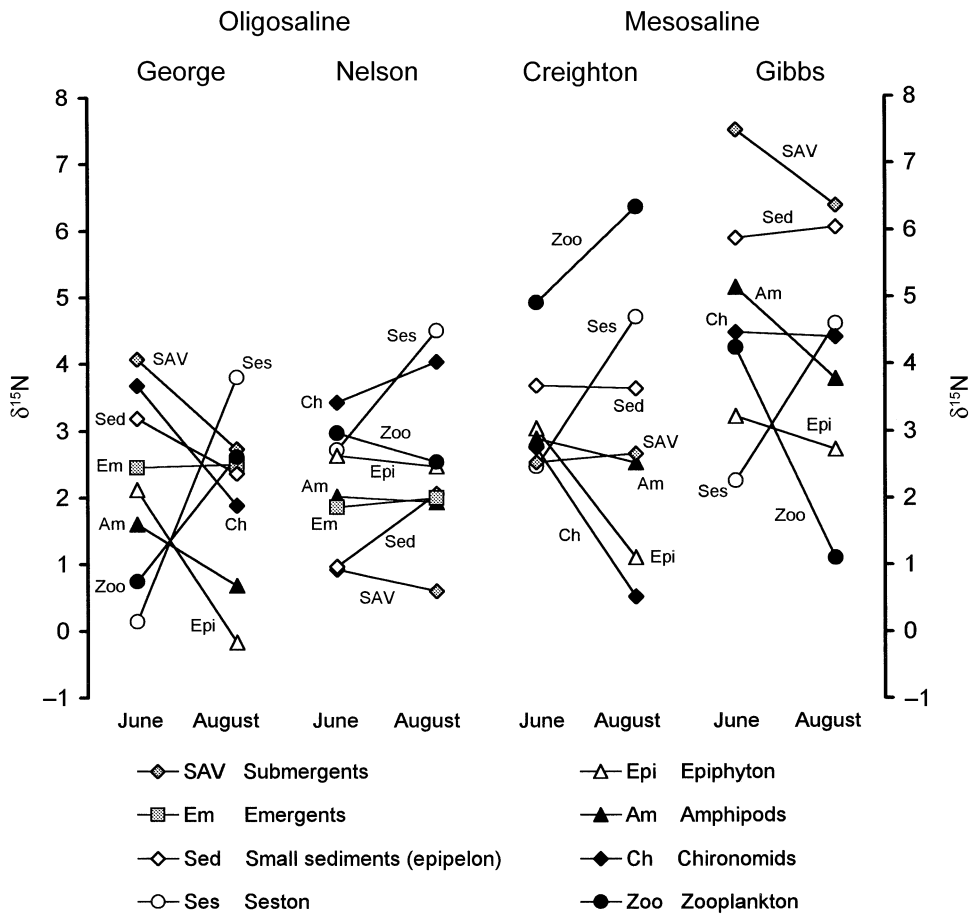

FIG. 3. Mean $\delta^{15}N$ values in early June and mid-August in oligosaline wetlands George and Nelson and mesosaline wetlands Creighton and Gibbs. Conventions are as in Fig. 2.

phipods ate only 17% diatoms (Table 1), yet their $\delta^{13}C$ values showed very similar magnitudes and seasonal trends (Fig. 2). Moreover, these values and trends differed from those for emergent plants and closely resembled those for seston. Patterns were similar in Lake Nelson for amphipods, but data for chironomids were inconclusive.

In mesosaline wetlands, $\delta^{13}C$ of amphipods and chironomid larvae varied in their similarity to organic matter sources. However, values for these consumers were much different from those for submersed macrophytes (*Potamogeton pectinatus*) and epiphyton (there were no emergents in these wetlands). Thus, as in oligosaline wetlands, strong differences in $\delta^{13}C$ between consumers and submersed macrophytes were consistent with lack of macrophyte tissue in gut contents, and suggest that microalgae were the main source of organic matter for invertebrate food webs.

DISCUSSION

Macrophyte tissue, microalgae, and amorphous detritus as food sources

Despite major differences in macrophytes and macroinvertebrates present, very little macrophyte tissue was directly ingested by the main primary consumers in either oligosaline or mesosaline wetlands. We did not expect consumption of live tissue, but oligosaline wetlands contained abundant dead macrophyte material both from *Scirpus acutus* and *Chara* spp. In mesosaline wetlands that lacked emergent plants, submersed macrophyte stands were dense; however, availability of dead *Potamogeton pectinatus* to macroinvertebrates may be limited because much of it is washed to the shore and accumulates there as wrack. Lack of macrophyte CPOM in consumer guts indicates that the paradigm of FPOM being generated mainly by shredding macroinvertebrates does not apply to all wetland types (Wissinger 1999), and certainly not to wetlands in this study. Note that the dominant amphipod in these wetlands was *Hyalella azteca*, and *Gammarus* spp. were rare. The few *Gammarus lacustris* collected (only in Lake George) had a high fraction of *Chara* tissue in their guts.

The bulk of consumer gut contents was amorphous detritus, but many diatoms were also consumed (Fig. 1). The relative dietary (and isotopic) contribution of these two food types depends on consumer assimilation

efficiencies. Consumer uptake of carbon from diatoms and amorphous detritus would have been equal if diatom assimilation efficiency were four times that of amorphous detritus. Such a difference is possible. Macroinvertebrate assimilation efficiencies for diatoms can be as high as 90%, and those for amorphous detritus as low as 10% (50–90% for diatoms of various taxa, Wotton 1994; 10–27% for amorphous detritus in streams, Benke and Wallace 1980, 1997). However, in some cases in our study, amorphous detritus was consumed in such high fractions that it seems unlikely that most assimilated energy came directly from whole diatoms. Also, consumer assimilation efficiencies for amorphous detritus may vary widely among different systems. Specifically, the fraction of amorphous detritus derived from bacterial production is critical, as the assimilation efficiency of bacterial EPS by macroinvertebrates can exceed 80% (>80% for copepods, Decho and Moriarty 1990; 80–90% for black fly larvae, Couch et al. 1996).

We expected stable isotopes to help resolve which sources of organic matter were most important to consumers, but our experience was not completely satisfying. We originally intended to use multiple stable isotopes: ^{34}S, ^{15}N, and ^{13}C. We found that $\delta^{34}S$ values were too variable to be useful in answering our questions, e.g., with up to 30‰ difference among seston samples collected in the same wetland (cf., Neill and Cornwell 1992, Stribling and Cornwell 1997). A major cause of variation in $\delta^{34}S$ in wetlands is reduction of sulfate during bacterial respiration in anaerobic sediments, which can fractionate ^{34}S by 20–70‰ (Chambers and Trudinger 1979). Given the large vertical and horizontal variation in redox states of wetland soils (Cornwell et al. 1995), high variation of $\delta^{34}S$ in plants and consumers can confound its use in food web analyses. Also because of high variability in our wetlands, we were not comfortable applying a trophic-level enrichment factor of +3.4‰, or any other enrichment factor, to interpret $\delta^{15}N$ data (Hart and Lovvorn 2002). Thus, for inferences about organic matter sources for primary consumers and the origin of amorphous detritus, we limited our analyses to $\delta^{13}C$.

In both oligosaline and mesosaline wetlands, $\delta^{13}C$ values appeared to preclude submersed macrophytes as a carbon source for consumers. In mesosaline wetlands, exclusion of submersed macrophytes indicates that consumers rely on microalgae, the only other group of primary producers. In oligosaline wetlands, $\delta^{13}C$ of consumers changed between June and August by 1.3 to 4.4‰; since gut contents did not indicate a diet switch, this pattern requires a food source with high turnover such as microalgae. However, even with no macrophyte tissue in gut contents, it is still possible that emergent macrophytes contributed to consumer diets if amorphous detritus contained a high fraction of assimilable emergent carbon. This situation could occur if amorphous detritus contained assimilable flocs of DOM produced by emergent macrophytes, or contained EPS from bacteria that had consumed such flocs or had directly consumed emergent macrophyte tissue (Gallagher et al. 1976, Camilleri and Ribi 1986, Alber and Valiela 1995, 1996, Mann and Wetzel 1996). Diatoms dominated the epipelon and epiphyton in our wetlands (Hart 1998), and in some systems diatom-rich biofilms can exude up to 73% of carbon fixed depending on growth phase (Goto et al. 1999). In contrast, exudation of DOM by vascular macrophytes and macroalgae is generally <12% of carbon fixed and usually <5% (Brylinsky 1977, Søndergaard 1981, Pregnall 1983, Moriarty et al. 1986). Based on relative primary production of labile extracellular material, it is more likely that bacterial production during our study was based mainly on algal exudates and algal detritus (Søndergaard et al. 1995). We conclude that in both oligosaline and mesosaline wetlands, food webs were based mainly on microalgae.

Nature of amorphous detritus

In our study, macroinvertebrate gut contents were mostly amorphous detritus. In oligosaline wetlands, amphipods that ate mainly amorphous detritus but some diatoms, and chironomids that ate a much higher fraction of diatoms, had similar $\delta^{13}C$ values. This result suggests either (1) that consumer assimilation efficiency of diatoms was much greater than that of amorphous detritus (see *Discussion: Macrophyte tissue, microalgae, and amorphous detritus as food sources*), or (2) that most carbon in amorphous detritus was originally fixed by diatoms. If amorphous detritus were assimilated with low efficiency, one would expect it to be largely recalcitrant material of macrophyte origin. However, inspection of gut contents revealed no cellular structures, and the substance was sticky and slime-like (cf., Engel 2000). Much of the amorphous detritus in chironomid and amphipod guts retained Alcian blue stain; this staining indicates muco-polysaccharides, the main component of microbial EPS (Passow and Alldredge 1995). These aspects support case (2) that most amorphous detritus was extracellular material derived from algal photosynthesis, including flocculated DOM and surface-bound EPS.

Understanding the nature of amorphous detritus and DOM/EPS is a central issue for future research in wetlands. It will be difficult to understand the trophic dynamics of macroinvertebrates without knowing the assimilation efficiency of amorphous detritus vs. other foods. Also, if amorphous detritus is highly assimilable (e.g., DOM/EPS) then standard measures of microalgae and bacteria will not reflect their trophic importance: extracellular production may be poorly represented by traditional measures such as cell counts, chlorophyll *a*, and tracer incorporation into cells. Because amorphous detritus is probably an important component of macroinvertebrate diets in most wetlands (e.g., Johnson et al. 2000), we suggest that characterizing its nature

among wetland types (e.g., prairie vs. forested wetlands) and under different conditions (e.g., wet and dry cycles) will be key to understanding patterns of secondary production in wetlands.

Importance of different microalgal types

If microalgae are the trophic base of food webs in these wetlands, one might expect production by different invertebrate groups to be linked to production by different forms of microalgae (Goldsborough and Robinson 1996). That is, in oligosaline wetlands where most algal production is in epiphyton, epiphytic grazers (amphipods) would dominate invertebrate biomass. In mesosaline wetlands where phytoplankton and epipelon are more productive, filter-feeding zooplankton and deposit-feeding chironomid larvae would be more abundant. In several cases, the carbon isotope data appeared to contradict a direct link between forms of macroinvertebrate production and forms of microalgal production. For example, in oligosaline wetlands where most algal biomass and production was epiphytic (Hart and Lovvorn 2000), $\delta^{13}C$ values for *Hyalella azteca* and chironomid larvae differed by 5 to 9‰ from that for epiphyton. The $\delta^{13}C$ signal for epiphyton was surprisingly absent in macroinvertebrates, whose values were most similar to seston (Fig. 2).

If production by epiphyton is so high in these wetlands, then why is its $\delta^{13}C$ signal so weak in primary consumers? The $\delta^{13}C$ data may rightly indicate that planktonic processes are much more important to consumers than expected from the biomass and production of different algal types, in which the contribution by phytoplankton was relatively small (Hart and Lovvorn 2000). Epiphytic chironomid larvae might mainly filter feed on seston, but amorphous detritus in the guts of *Hyalella azteca* probably came from feeding on surfaces (epipelon or epiphyton). A possible explanation is that epiphytic carbon assimilated by consumers does not reflect the $\delta^{13}C$ of bulk epiphyton as we measured it. Similarity in $\delta^{13}C$ of epiphyton and macrophyte hosts (Fig. 2) suggests that macrophytes influenced the $\delta^{13}C$ of epiphyton. In these wetlands, particularly on *Chara* spp., epiphyton was very dense. Algae in the inner layers of epiphyton (nearest leaf surfaces) may incorporate CO_2 produced by respiration of organic matter fixed by the macrophyte host: either DOC leaked from the macrophyte and respired by microbes to yield CO_2, or else leaked DIC (CO_2) produced by respiration within the macrophyte. In contrast, algae in the outer layers of epiphyton would be exposed to the different inorganic carbon pool used by algae in the seston. Amphipods and chironomids might graze mainly the outer layers of epiphyton (Steinman 1996), explaining why their $\delta^{13}C$ values resemble that of seston. Also, the outer layers of epiphyton might be a repository for planktonic production: microalgae and DOM/EPS released in the water column may flocculate into ''wetland snow'' (sensu Grossart et al. 1997) that settles on surfaces of submersed macrophytes. Resolving these issues will be key to tracing the relative roles of phytoplankton and periphyton in food web dynamics (Golsborough and Robinson 1996, Goto et al. 1999, 2001), and ensuring that contributions by macrophytes are distinguished from those of epiphytes growing on them (cf., Reitner et al. 1999, Ziegler and Benner 1999).

Conclusions

In saline wetlands of Wyoming, there was almost no direct ingestion of macrophyte tissue by dominant primary consumers. Guts contained some diatoms but mostly amorphous detritus. Patterns of $\delta^{13}C$ at different times yielded strong inference that microalgae were the ultimate source of organic matter for macroinvertebrates. Thus, the traditional paradigm that wetland food webs are based mainly on decomposing macrophyte tissue does not apply to these wetlands and probably many others. Our results suggest that characterizing the nature of amorphous detritus (origins, production patterns, nutritional value) will be important to understanding macroinvertebrate production and food web structure in a broad range of wetland types.

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APPENDIX

Tables of δ^{13}C and δ^{15}N values are available in ESA's Electronic Data Archive: *Ecological Archives* E084-090-A1.