

Dual-Carbon Sources Fuel the OCS Deep-Reef Community, a Stable Isotope Investigation

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Abstract. The hypothesis that phytoplankton is the sole carbon source for the OCS deep-reef community (>60 m) was tested. Trophic structure for NE Gulf of Mexico deep reefs was analyzed via carbon and nitrogen stable isotopes. Carbon signatures for 114 entities (carbon sources, sediment, fishes, and invertebrates) supported surface phytoplankton as the primary fuel for the deep reef. However, a second carbon source, the macroalga *Sargassum*, with its epiphytic macroalgal associate, *Cladophora liniformis*, was also identified. Macroalgal carbon signatures were detected among 23 consumer entities. Most notably, macroalgae contributed 45 % of total carbon to the ¹³C isotopic spectrum of the particulate-feeding reef-crest gorgonian *Nicella*. The discontinuous spatial distribution of some sessile deep-reef invertebrates utilizing pelagic macroalgal carbon may be trophically tied to the contagious distribution of *Sargassum* biomass along major ocean surface features.

Key words: trophic structure, Gulf of Mexico, OCS reefs, macroalgal carbon

Introduction

Trophic relationships for deep-water communities of the outer continental shelf (OCS) remain poorly studied, particularly in warm temperate and tropical oceans. The present study investigated tissue ¹³C and ¹⁵N stable isotope signatures for the fauna of deep-reef biotopes at 65-120 m on the northeastern Gulf of Mexico (NEGOM) OCS. The objective for this phase of a broader surface-to-substrate ecosystem trophic investigation was to identify carbon sources fueling the NEGOM deep-reef fauna.

Coastal and offshore ecosystems are fueled by organic carbon in the form of dissolved organic carbon (DOC) and/or particulate organic matter (POM) from photosynthesis, sometimes supplemented by chemosynthesis. Terrestrial C3 plants, emergent saltmarsh C4 plants (Thayer et al. 1978), submerged aquatic seagrasses, and benthic macroalgae may also supply carbon to nearshore ecosystems (Thayer et al. 1983). For OCS ecosystems, the only carbon source ubiquitously and continuously available is phytoplankton, classically considered the sole oceanic carbon source (Thayer et al. 1983; Fry and Sherr 1984; Dauby 1989), excluding local primary production from seafloor chemosynthesis (Kennicutt et al. 1985; Paull et al. 1985; Brooks et al. 1987). At high latitudes, sea ice algae may be an important supplementary carbon source (Hobson et al. 1995, 2002). Similarly, benthic macroalgae may contribute carbon to some coastal ecosystems (Dunton and Schell 1982; Stephenson et al. 1984; Simenstad and Wissmar 1985; Dunton and

Schell 1987). However, the potential role of pelagic macroalgae as a distinct and important oceanic carbon source has generally been little investigated.

Material and Methods

Study area and sample collection. Sampling was conducted hard-bottom reef areas [ESM: Fig. 1] on the Mississippi-Alabama OCS west of DeSoto Canyon, and the West Florida OCS to the east, during three U.S. Geological Survey (USGS) cruises (2001-2003). Potential carbon sources sampled included near-surface and near-bottom plankton, pelagic macroalgae, and bottom sediment. Holoplankton and POM were sampled simultaneously using horizontal 5-min tows of nested 0.5 m diameter plankton nets, an inner 335 µm mesh net to retain holoplankton, within a 125 µm mesh net to retain POM. Near-surface nets were towed at 3-5 m depth, near-bottom nets at 5-10 m altitude. Bottom sediment was sampled in a 0.0484 m² box grab. Consumers sampled included benthic, benthopelagic, and epipelagic fishes and invertebrates. Samples were obtained by angling, fish traps, otter and sled trawls, tangle device, and ROV suction sampler. Macroalgae, attached epibiota, and associated fauna, were obtained in dip nets and 1.0 m diameter plankton nets.

A target of N ≥ 20 samples per trophic entity was set, attempting to obtain sample sizes sufficient to determine statistically robust isotopic means and standard deviations (Monteiro et al. 1981; Fry and Sherr 1984). Carbon source spectrum analysis

(Jennings et al. 1997) was undertaken when sample N ≥ 20 for a given consumer entity.

Sampling at sea and laboratory preparation. For most fishes a 1-5 g sample of dorsal white muscle was excised, excluding scales, skin and bone. This tissue displays the least variance in ^{13}C and ^{15}N among all fish tissues, and is low in problematic inorganic carbonates and lipids (Pinnegar and Polunin 1999). Slow white muscle turnover rates integrate carbon source signatures over months to years (Hesslein et al. 1993; Post 2002). For invertebrates, a 1-5 g sample of soft tissue was obtained. A 2.0 ml subsample of undisturbed surface sediment was taken from each box grab sample. Outer leaf blades of *Sargassum* spp. (least enriched in ^{13}C : Stephenson et al. 1984, Ishihi et al. 2001) were scraped with a scalpel to remove encrustations, rinsed with de-ionized water (DI), and frozen. *Cladophora liniformis* samples were harvested from *Sargassum*. Plankton samples (excluding fish larvae, chaetognaths, and gelatinous macroplankton) were concentrated into a plug by vacuum filtering through a micropore filter.

Invertebrate tissue and sediment samples were each divided into two portions. One portion was treated with 3N HCl for 48 h to dissolve inorganic carbonates, DI rinsed, centrifuged, dried and plated for assay. Only $\delta^{13}\text{C}$ was determined from acidified samples since acid treatment has a significant effect on $\delta^{15}\text{N}$ values (Pinnegar and Polunin 1999). All samples were oven-dried at 60°C for 12 h. For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses, a 100 \pm 10 μg portion of each ground sample was placed in a foil capsule in a numbered cell in a 96-cell plastic well-plate.

Stable isotope assays. Samples analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (N = 1,265) at the University of California-Davis Stable Isotope Facility represented seven potential carbon sources (N = 104 samples) and 107 consumer taxa (N = 1,161 samples) [ESM: Table 1]. The $\delta^{13}\text{C}$ reference standard was Pee Dee Belemnite (mean value: -23.83 ± 0.07 ‰, N = 262). The standard for $\delta^{15}\text{N}$ was atmospheric nitrogen (mean: 1.33 ± 0.11 ‰, N = 262). Sulfur isotope ($\delta^{34}\text{S}$) assays were accomplished at the USGS Menlo Park, California, Stable Isotope and Tritium Laboratory using Canyon Diablo meteoric triolite as the reference standard (analytical precision to < 0.2 ‰).

Trophic guilds. Seven potential carbon source guilds included: near-surface POM (> 125 μm , < 335 μm), near-surface holoplankton (> 335 μm), near-bottom POM, near-bottom holoplankton, bottom sediment, and two pelagic macroalgae (*Sargassum* spp. and *C. liniformis*). Reef consumers were classified into

11 empirically-defined guilds [ESM: Table 1] based on food habits (Weaver et al. 2002): *Sargassum* associates (SA), epipelagic microvores (EMI), epipelagic intermediate macrovores (EIM), benthic particulate feeders (BPF), benthic miniparticulate feeders (BMF), benthic planktivores (BPV), benthic deposit feeders (BDF), benthic microvores (BMI), benthic omnivores (BOM), benthic intermediate macrovores (BIM), and benthic macrovores (BMV).

Two-way ANOVA was used to test the hypothesis that four POM and holoplankton carbon sources did not differ from one another by size fraction or surface versus bottom. One-way ANOVA was performed to test significant $\delta^{13}\text{C}$ differences between consumer guilds. If necessary to satisfy ANOVA assumptions of normality and homogeneity of variances, data were log transformed. If ANOVA results indicated significant treatment effects, a Tukey's multiple comparison test for differences among individual treatments (Sokal and Rolfe 1995). The criterion of statistical difference for all tests was $p < 0.05$. Trophic spectra (Monteiro et al. 1981) were plotted for selected entities (if N ≥ 20) as $\delta^{13}\text{C}$ frequency histograms.

Results

Among 114 producers and consumers (N = 1,265 specimens) analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, sample size of N ≥ 20 was achieved for 21 entities. Only four sediment samples had sufficient mass of organic matter for $\delta^{13}\text{C}$ analysis. Ten tissue samples of the benthic planktivorous fish, *Pronotogrammus martinicensis* were analyzed, returning a mean $\delta^{34}\text{S}$ value of 19.93 ± 0.55 .

Two-way ANOVA contrasts of data for organic carbon source guilds revealed no statistical differences in mean $\delta^{13}\text{C}$ between four plankton guilds (near-surface versus near-bottom, and POM versus net holoplankton). Therefore, all four plankton guilds were combined into one overall 'holoplankton' group representing the primary carbon source available to OCS consumers in this study. A t-test revealed no significant difference ($p < 0.05$) in mean $\delta^{13}\text{C}$ between the combined holoplankton group and bottom sediment. However, bottom sediment was not grouped with holoplankton as a common carbon source, since it remains unknown if sedimentary carbon becomes resuspended and available to consumers at depth on the OCS. No significant difference was found between $\delta^{13}\text{C}$ means for *Sargassum* spp. and *C. liniformis*, which were accordingly grouped into a single macroalgae producer guild. However, there was a significant difference ($p < 0.001$) in $\delta^{13}\text{C}$ data between holoplankton (mean $\delta^{13}\text{C} = -19.35 \pm 1.16$ ‰) and macroalgae (mean $\delta^{13}\text{C} = -16.41 \pm 2.13$ ‰), readily

distinguishing these two different OCS carbon sources (Fig. 1).

Across all consumer samples, $\delta^{13}\text{C}$ values ranged from -9.29 to -22.00 ‰, corresponding with the range determined for holoplankton and macroalgae combined (-12.62 to -24.18 ‰), allowing for trophic enrichment. No ^{13}C consumer or sediment signatures indicative of terrestrially-derived POM ($\delta^{13}\text{C} \leq -26$ ‰) (Shultz and Calder 1976) were obtained.

One-way ANOVA contrast in $\delta^{13}\text{C}$ data for six benthic invertebrate consumers revealed that the particulate-feeding gorgonian *Nicella* sp. was statistically distinct (mean $\delta^{13}\text{C} = -15.01 \pm 2.17$ ‰) from the other five invertebrate consumers analyzed (overall mean $\delta^{13}\text{C} = -17.29 \pm 0.90$ ‰) (Table 1). One-way ANOVA contrast of the 11 empirically-defined consumer guilds resolved them into three statistically distinct ($p < 0.05$) consumer groups via $\delta^{13}\text{C}$ data, with the BMV and BMF guilds forming two single-guild groups, distinct from a large group comprised of nine guilds of intermediate predators-

Benthic invertebrate consumer	N	$\delta^{13}\text{C} \pm \text{S.D.}$ (‰)	$\delta^{15}\text{N} \pm \text{S.D.}$ (‰)
<i>Nicella</i> sp.	30	-15.01 ± 2.17*	9.45 ± 0.55
<i>Argopecten</i> sp.	30	-17.59 ± 0.51	7.17 ± 0.32
<i>Cidaris rugosa</i>	8	-18.93 ± 0.83	8.93 ± 0.53
<i>Plesionika longicauda</i>	17	-16.79 ± 0.48	9.40 ± 1.06
Portunid crab	30	-17.02 ± 0.54	11.10 ± 0.46
<i>Crangon</i> sp.	10	-16.75 ± 1.41	10.22 ± 0.87

Table 1. Comparative $\delta^{13}\text{C}$ signatures for six benthic invertebrate consumer entities. * Statistically distinct, $p < .05$.

omnivores (hereafter termed the IPO group) (Fig. 1). Within the IPO group, two guilds, the SA guild and the BPV guild, formed statistically distinct subgroups.

Two of the three major consumer groups form a 1-2-step carbon chain based on holoplankton (Fig. 1). This chain includes all consumer guilds except for the distinctive BMF guild/group, which appears linked to a distinct macroalgal carbon source via a 1-step trophic chain along a parallel $\delta^{13}\text{C}:\delta^{15}\text{N}$ trophic enrichment regression line (Fig. 1).

Statistical contrasts revealed a very small (0.4 ‰), but significant difference between $\delta^{13}\text{C}$ means for all pelagic consumers versus all benthic consumers, and between means ($\Delta = 0.2$ ‰) for all epipelagic microvores (EMI) versus all benthic microvores (BMI). However, these differences are negligible compared to the >3.0 ‰ difference in $\delta^{13}\text{C}$ up the $\delta^{15}\text{N}$ progression, between the holoplankton and

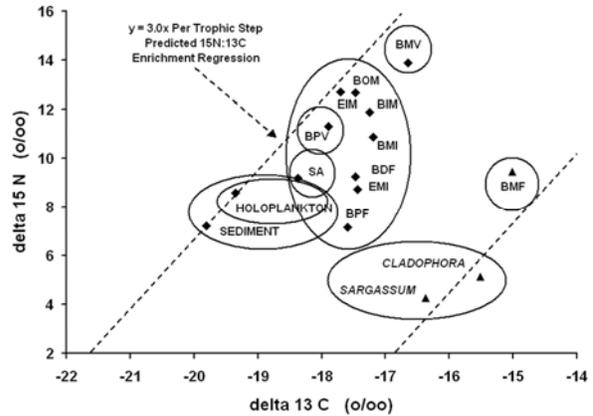


Figure 1: Producer and consumer groups and subgroups (ellipses) defined by mean $\delta^{13}\text{C}$ signatures. Abbreviations identify empirically-defined consumer guilds (points are mean $\delta^{13}\text{C}$ signatures per guild).

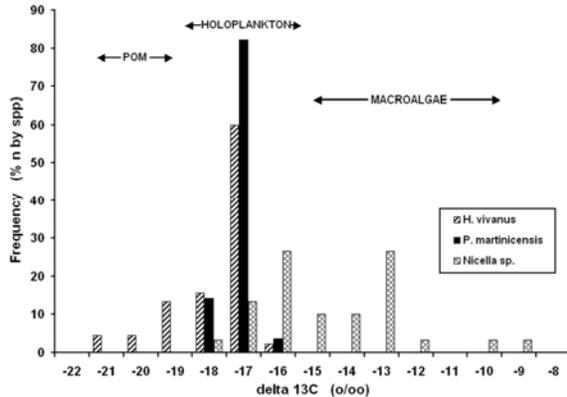
macroalgal trophic chains (Fig. 1). Thus, benthic versus pelagic consumer ^{13}C enrichment (McConnaughey and McRoy 1979; Fry and Sherr 1984; France 1995; Jennings et al. 1997; Pinnegar and Polunin 2000; Hobson et al. 2002) alone cannot account for the enriched $\delta^{13}\text{C}$ signatures of *Nicella* or individuals in other benthic taxa (Table 2).

Trophic spectra for most NEGOM deep-reef consumers displayed a sharp unimodal $\delta^{13}\text{C}$ peak corresponding with phytoplankton-derived carbon, as in the planktivorous fish *P. martinicensis* (-17.71 ± 0.37 ‰) (Fig. 2). A few consumers such as the planktivorous fish, *Hemanthias vivanus*, displayed a broad $\delta^{13}\text{C}$ spectrum (-16 to -22 ‰), but a similar mean (-18.25 ± 1.15 ‰) (Fig. 2). The miniparticulate feeding gorgonian, *Nicella*, displayed a distinctive strongly bimodal $\delta^{13}\text{C}$ spectrum (Fig. 2), one mode centered at -16 ‰ (phytoplankton carbon), another at -13 ‰ (macroalgal carbon). Trophic selectivity is

Trophic guild	N	Mean $\delta^{13}\text{C}$ range
Miniparticulate feeders (<i>Nicella</i> sp.)	17	-9.19 to 15.87
<i>Sargassum</i> associates	1	-15.92
Epipelagic intermediate macrovores	4	-14.43 to -15.69
Benthic microvores	5	-12.90 to -15.00
Benthic deposit feeders	1	-15.68
Benthic intermediate macrovores	17	-14.12 to -15.95
Benthic macrovores	11	-15.00 to -15.97

Table 2. Consumer guilds containing taxa with individuals (n) yielding notably enriched (≥ -16 ‰) $\delta^{13}\text{C}$ signatures.

evident in the comparative spectra of these three syntopic reef-crest particulate feeders, which all feed within a meter of the reef surface. The broad $\delta^{13}\text{C}$ spectrum of *H. vivanus* indicates consumption of both POM and larger holoplankton. In contrast, *P. martinicensis* appears to be a zooplankton specialist, while *Nicella* appears to shift between holoplankton versus macroalgae-derived particles, utilizing a



carbon source not selected by its competitors.

Figure 2. Comparative ^{13}C isotopic spectra (versus probable carbon sources) for three deep-reef particulate feeders: *Hemanthias vivanus* (hatched bars) and *Pronotoqrammus martinicensis* (black bars), and the gorgonian *Nicella* sp. (cross-hatched bars).

NEGOM OCS carbon sources. No highly depleted $\delta^{13}\text{C}$ signatures typical of terrestrial plant carbon (e.g., $\delta^{13}\text{C} \leq -26$ ‰) were observed among the analyzed consumer entities. Additionally, $\delta^{34}\text{S}$ values determined for 10 specimens of the benthic planktivorous fish, *P. martinicensis* ranged from +19.20 to +20.89 ‰, (mean +19.93 ‰). These values lie within the range of $\delta^{34}\text{S}$ values (+16.6 to +20.3 ‰) previously reported for seawater sulfate, marine plankton, oceanic fish, and offshore consumers (Rees et al. 1978; Peterson et al. 1985, 1986; Fry 1988; Hesslein et al. 1993), providing no evidence of terrestrial sulfur from either C3 plant detritus ($\delta^{34}\text{S} +4.7$ ‰, Peterson and Howarth 1987) or deposited freshwater sediment ($\delta^{34}\text{S} -14$ ‰, France 1995). These ^{13}C and ^{34}S results confirm earlier findings from larval fishes (Thayer et al. 1983), bottom sediments (Shultz and Calder 1976; Eadie et al. 1978), indicating that terrestrial organic input is limited to NEGOM estuarine and nearshore waters (Gearing et al. 1977; Fry and Sherr 1989).

However, findings herein challenge the fundamental assumption that phytoplankton is the sole source of fixed carbon for offshore food webs (Fry and Sherr 1984). Enriched $\delta^{13}\text{C}$ signatures (≥ -16 ‰) for individuals in 23 consumer taxa in six guilds (Table 2) provide evidence of a second OCS carbon source. Given a ^{13}C turnover time in fish

tissue of months to years (Hesslein et al. 1993), sustained selective feeding on an enriched food source would be required to be reflected in signatures from tissues analyzed (Post 2002). The bimodal spectrum of *Nicella* (Fig. 2) is particularly instructive. The ^{13}C depleted mode at -16 ‰ corresponds with intake of phytoplankton-chain derived particles (holoplankton mean $\delta^{13}\text{C} = -19.35$ ‰), allowing for 1-step trophic enrichment. The enriched mode centered upon -13 ‰ (Fig. 2) suggests intake of particles from a macroalgal source, e.g. *Sargassum* (mean $\delta^{13}\text{C} = -16.37$ ‰) and *C. liniformis*. (mean $\delta^{13}\text{C} = -15.51$ ‰), after one step enrichment.

While oceanic phytoplankton is ubiquitous in time and space, *Sargassum* is discontinuously distributed in both regards. Thus, carbon contributed to tropical and temperate oceanic ecosystems by *Sargassum* would typically be swamped (Parr 1939) in the long-term integrated ^{13}C data presented by most consumer species. Only individuals which have fed on items carrying *Sargassum* carbon for an extended period would display correspondingly enriched $\delta^{13}\text{C}$ signatures. A specialist using a trophic switching strategy would display two dominant modes (Monteiro et al. 1981), as seen in *Nicella*. This suspensivore, which inhabits the current-ward crests of deep reefs, appears to selectively switch between particulates derived from macroalgae, or alternatively from plankton-based particulates. Approximately 45% of the *Nicella* $\delta^{13}\text{C}$ frequency distribution (signatures from -9 to -15 ‰) (Fig. 2) appears attributable to macroalgal carbon. A related Mediterranean gorgonian, *Eunicella stricta*, is a specialist deriving most of its carbon from algae and the seagrass *Posidonia*, a refractory carbon source not otherwise utilized by many consumers (Dauby 1989). The $\delta^{13}\text{C}$ value reported for *E. stricta* (-14.2 ‰) is close to the mean herein for *Nicella* sp. (-15.01 ± 2.17). Ribes et al. (2003) reported that the gorgonian *Leptogorgia sarmentosa* feeds on a broad range of suspended particles, from nanoeukaryotes $< 3.6 \mu\text{m}$ to zooplankton $> 100 \mu\text{m}$. This species specializes seasonally, utilizing food sources as a function of availability, with a summer minimum in detrital POM use. However, POM accounted for 30.4% of total assimilated carbon. Another gorgonian, *Paramuricea clavata*, derived 48% of its food spectrum from detrital POM (Ribes et al. 1999). A pattern of seasonal selectivity or switching could result in the bimodal $\delta^{13}\text{C}$ trophic spectrum of *Nicella* sp.

Parr (1939) estimated the biomass of *Sargassum* in the Sargasso Sea as $3.6-10.0 \times 10^9$ kg, three orders of magnitude less than estimated phytoplankton biomass for that region. Despite this fact, and the refractory nature of brown algae (Montgomery and Gerking

1980), it seems unlikely that such a biomass of carbon would go unutilized in the world ocean. Present findings suggest it does not. Evidence of selective use of pelagic macroalgal carbon by one deep-reef gorgonian suggests that other OCS reef consumers may depend in part upon this carbon source. Accordingly, their spatial occurrence and abundance may be tied to the predictable concentration of macroalgae along major ocean surface features.

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References

- Brooks JM, Kennicutt MC II, Fisher CR, Macko SA, Cole K, Childress JJ, Bidigare RR, Vetter RD (1987) Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources. *Science* 238:1138-1142.
- Dauby PA (1989) The stable carbon isotope ratios in benthic food webs of the Gulf of Calvi, Corsica. *Cont Shelf Res* 9:181-195.
- Dunton KH, Schell DM (1982) The use of $^{13}\text{C}/^{12}\text{C}$ ratios to determine the role of macrophyte carbon in an Arctic kelp community. *EOS* 63:54.
- Dunton KH, Schell DM (1987) Dependence of consumers on macroalgal (*Laminaria solidungula*) carbon in an Arctic kelp community: $\delta^{13}\text{C}$ evidence. *Mar Biol* 93:615-625.
- Eadie, B.J, Jeffrey LM, Sackett WM (1978) Some observations on the stable carbon isotope composition of dissolved and particulate organic matter in the marine environment. *Geochem et Cosmochim Acta* 42:1265-1269.
- France R (1995) Differentiation between littoral and pelagic food webs in lakes using stable carbon isotopes. *Limnol Oceanogr* 40:1310-1313.
- Fry B (1988) Food web structure on Georges Bank from stable C, N, and S isotopic compositions. *Limnol Oceanogr* 33:1182-1190.
- Fry B, Sherr E (1984) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contrib Mar Sci* 27:13-47.
- Fry B, Sherr E (1989) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. Pp. 196-229, IN: Stable isotopes in ecological research (Rundel PW, Ehleringer JR, Nagy KA, eds.), Springer-Verlag Publ., NY.
- Gearing P, Plucker FE, Parker PL (1977) Organic carbon stable isotope ratios of continental margin sediments. *Mar Chem* 5:251-266.
- Hesslein RH, Hallard KA, Ramlal P (1993) Replacement of sulphur, carbon, and nitrogen of growing broad whitefish (*Coregonus nausius*) in response to a change in diet traced by $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$. *Can J Fish Aquat Sci* 50:2071-2076.
- Hobson KA, Ambrose WG Jr, Renaud PE (1995) Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis. *Mar Ecol Prog Ser* 128:1-10.
- Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon J-M, Fortier M (2002) A stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. *Deep-Sea Res II* 49:5131-5150.
- Ishihara Y, Yamada Y, Ajisaka T, Yokoyama H (2001) Distribution of stable isotope ratios in *Sargassum* plants. *Fisher Sci* 67:367-369.
- Jennings S, Reñones O, Morales-Nin B, Polunin NVC, Moranta J, Coll J (1997) Spatial variation in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope composition of plants, invertebrates and fishes on Mediterranean reefs: implications for the study of trophic pathways. *Mar Ecol Prog Ser* 146:109-116.
- Kennicutt MC, Brooks JM, Bidigare RR, Fay RR, Wade TL, McDonald TJ (1985) Vent-type taxa in a hydrocarbon seep region on the Louisiana slope. *Nature* 317:351-353
- McConnaughey T, McRoy CP (1979) Food-web structure and fractionation of carbon isotopes in the Bering Sea. *Mar Biol* 53:257-262.
- Montgomery WL, Gerking SD (1980). Marine macroalgae as foods for fishes: an evaluation of potential food quality. *Env Biol Fish* 5:143-153
- Monteiro, MS, James AG, Sholto-Douglas AD, Field JG (1981) The $\delta^{13}\text{C}$ trophic position isotope spectrum as a tool to define and quantify carbon pathways in marine food webs. *Mar Ecol Prog Ser* 78:33-40.
- Parr, AE (1939) Quantitative observations on the pelagic *Sargassum* vegetation of the western Atlantic Ocean. *Bull Bingham Oceanogr Coll* 6:1-93.
- Paull, CK, Jill AJT, Toolin LJ, T. Linick T (1985) Stable isotope evidence for chemosynthesis in the abyssal seep community. *Nature* 317:709-711.
- Peterson BJ, Howarth RW, Garritt RH (1985) Multiple stable isotopes used to trace the flow of organic matter in estuarine food webs. *Science* 227:1361-1363.
- Peterson BJ, Howarth RW, Garritt RH (1986) Sulphur and carbon isotopes as tracers of salt-marsh organic matter flow. *Ecology* 67:865-874.
- Pinnegar JK, Polunin NVC (1999) Differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fish tissues: implications for the study of trophic interactions. *Funct Ecol* 13:225-231.
- Pinnegar JK, Polunin NVC (2000) Contribution of stable-isotope data to elucidating food webs of Mediterranean rocky littoral fishes. *Oecologia* 122:399-409.
- Post DM (2002) Using stable isotopes to estimate trophic position, methods and assumptions. *Ecology* 83:703-718.
- Rees CE, Jenkins WJ, Monster J (1978) The sulphur isotopic composition of ocean water sulfate. *Geochem et Cosmochim Acta* 42:377-381.
- Ribes M, Coma R, Gili J-M (1999) Heterogeneous feeding in benthic suspension feeders: the natural diet and grazing rate of the temperate gorgonian *Paramuricea calvata* (Cnidaria: Octocorallia) over a year cycle. *Mar Ecol Prog Ser* 183:125-137.
- Ribes M, Coma R, Rossi S (2003) Natural feeding of the temperate symbiotic octocoral-gorgonian *Leptogorgia sarmentosa* (Cnidaria: Octocorallia). *Mar Ecol Prog Ser* 254:141-150.
- Shultz DJ, Calder JA (1976) Organic carbon $^{13}\text{C}/^{12}\text{C}$ variations in estuarine sediments. *Geochem et Cosmochim Acta* 40:381-385.
- Simenstad CA, Wissmar RC (1985) $\delta^{13}\text{C}$ evidence of the origins and fates of organic carbon in estuarine and near-shore food webs. *Mar Ecol Prog Ser* 22:141-152.
- Sokal RR, Rolfe FJ (1995) Biometry: the principals and practice of statistics in biological research, 3rd edn., WH Freeman, NY.
- Stephenson RL, Tan FC, Mann KH (1984) Stable carbon isotope variability in marine macrophytes and its implications for food web studies. *Mar Biol* 81:223-203.
- Thayer GW, Parker PL, LaCroix MW, Fry B (1978) The stable carbon isotope ratio of some components of an eelgrass, *Zostera marina*, bed. *Oecologia* 35:1-12.
- Thayer GW, Govoni JJ, Connally DW (1983) Stable carbon isotope ratios of the planktonic food web in the northern Gulf of Mexico. *Bull Mar Sci* 33:247-256.
- Weaver DC, Dennis GD III, Sulak KJ (2002) Community structure and trophic ecology of demersal fishes on the Pinnacles Reef tract. U.S. Geological Survey Biol Sci Rep USGS BSR 2001-0008.