Algal Tissue Nutrients as Indicators of Nutrient Enrichment in the Florida Keys

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Draft Final Report submitted to:

EPA's Florida Keys National Marine Sanctuary
Water Quality Protection Program

and

South Florida Water Management District

July 1999

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1.0 Executive Summary

This study used the tremendous biochemical and ecological diversity of macroalgae to assess nitrogen and phosphorus availability at a broad, ecosystem-level scale in the Florida Keys and nearby waters. Tissue nutrients were used as integrative measures of nutrient availability because concentrations and trends in nutrient pollution are often too low or ephemeral to be detected by conventional water sampling protocols. This study recognized and addressed the variable physiographic regimes in the Keys and temporal variability (both seasonal and interannual).

Spatial variation in tissue nutrients (carbon = C, nitrogen = N, phosphorus = P) of dominant macroalgae were assessed, both as ratios and absolute values, along 12 inshore-offshore transects in the Florida Keys (three transects for each of the Biscayne Bay, Upper Keys, Middle Keys, and Lower Keys "segments"), and at 10 stations in nearby Florida Bay. Stations were sampled twice a year (summer and winter) to incorporate seasonal variability. Following the initial sampling of the entire macroalgal community, sampling focused on ten widespread and abundant species. The resulting detailed analysis demonstrated spatial and temporal patterns in macroalgal tissue nutrients. These patterns depended upon location, season, and species.

The transect data revealed no universal inshore-offshore patterns in tissue nutrients and no obvious "hotspots" of nutrient enrichment. Similarly, when data were compared among segments, there was no universal geographical pattern in tissue nutrients for all species. The most striking result was that the N and P status of macroalgae in Florida Bay was significantly different than other locations. Macroalgae collected from Florida Bay generally had higher N and lower P levels than algae collected elsewhere.

Comparisons among the four other segments revealed a much more uniform tissue nutrient level. The relatively few differences among these segments were rather species-specific. P composition was generally more variable for a species than was N. When there were significant differences among segments, the Biscayne Bay and Upper Keys segments tended to have lower N levels than the Middle and Lower Keys, and the Middle Keys segment tended to have higher P levels than the other segments. There were no consistent patterns among segments in N:P and C:P ratios for the ten species. C:N ratio tended to be lower in the Lower Keys. Based on the comparison of these segments with Florida Bay stations, there was little similarity of macroalgal nutrient status in Florida Bay to stations more proximal to the Bay, and presumably more exposed to Florida Bay influences (i.e., the Middle Keys transect).

The most common, but by no means universal, inshore-offshore pattern was higher %N and lower %P availability inshore. However, limited inshore-offshore differences in N:P ratio suggests that both nutrients were generally readily available in proportional amounts required by the various species.

Seasonality in macroalgal tissue nutrients was evident, although there was less seasonality than what has been found in more temperate systems. Most species in this study had higher %N, and to a lesser extent, higher %P and %C in March than in July. These patterns were probably a reflection of higher metabolic demands in the summer when macroalgae were growing more rapidly than in the winter. Excess nutrients stored internally during the winter may, in part, support macroalgal growth later in the year.

There were considerable differences in N and P status among species; the primary cause of these differences was calcification and, to a lesser extent, habit (lithophytic vs. psammophytic). Calcified algae (e.g., *Halimeda, Penicillus, Udotea*) had higher %N and lower %P than non-calcified species (e.g., *Dictyota, Laurencia*) . The only psammophytic, non-calcified species (*Avrainvillea* sp.) had higher levels of N than lithophytic, non-calcified species.

An important question addressed by this study was: "Is nitrogen or phosphorus limiting macroalgal growth in the Florida Keys?" Critical N or P levels for macroalgae in the Florida Keys are unknown. Based on the published literature on other species of macroalgae, it appears that N and P are generally available in sufficient quantities that macroalgal growth is not limiting by either nutrient, with the exception that the growth of lithophytic non-calcified species may be moderately limited by N.

Application of the results in this study include providing a strong baseline for the nutrient status of the macroalgal community against which future, long-term changes can be determined and recommending that macroalgal tissue nutrients be included in resource-oriented water quality standards (biocriteria), as part of the Sanctuary's longer term monitoring plans.

A better understanding of macroalgal growth as a function of nutrients and other environmental factors is needed for major species in the Florida Keys. What is particularly required is careful, methodical studies that examine the relationship of the growth of dominant algal species as a function of internal tissue nutrient status. Such studies should be conducted under carefully controlled laboratory studies and verified by *in situ* manipulative experiments. More research is also required to determine the impacts of nutrient enrichments on macroalgal community structure.

2.0 Introduction

When nearshore environments become nutrient enriched, severe ecological disturbances can result. During the past decade, serious water quality and ecological problems have become apparent in the Florida Keys and nearby Florida Bay. Of critical concern to the Florida Keys National Marine Sanctuary is whether poorer quality water from Florida Bay, and/or wastewater pollutants directly, threaten the Sanctuary's diverse biotic resources. Sewage outfalls exist near the north (Miami) and south (Key West) ends of the Keys, and septic tanks that leach nutrients into the nearshore waters are pervasive throughout the Keys. It is widely believed that Florida Bay waters restrict the distribution of coral reefs opposite the major tidal passes in the Middle Keys. But the extent to which anthropogenic nutrients are impacting Sanctuary resources is unknown. This project utilized algal tissue nutrients as an indicator of nitrogen and phosphorus enrichment in the Florida Keys.

2.1 Background

Maintaining the long-term health of the Florida Reef Tract and Florida Bay ecosystems is an issue of national concern, as recognized by scientific workshops (J. Miller 1988, S. Miller 1992, Boesch et al. 1996) and by Congress through creation of the Florida Keys National Marine Sanctuary. Part of the reason for this designation was the perception of rapidly declining ecosystem health, particularly related to coral demise and macroalgal blooms (Lapointe 1989a, Ward 1990, Keating 1991, Caputo 1991). However, historical perspective for the region is largely absent and long-term studies have only recently been initiated (Ogden 1990). Indeed, several Caribbean-wide phenomenon in the last 10-15 years (e.g., sea urchin die-off, hurricane damage, coral bleaching, coral disease, and over-utilization of coastal resources) have fundamentally changed our view of natural system variability in coral reefs. Thus, it is extremely difficult to ascribe causes to any of the short-term changes in ecosystem structure that have recently been reported in the Keys: changes such as the algal bloom off Key Largo near Grecian Rocks (J. Halas, pers. comm.), deep water algal blooms off Key West (B. Lapointe, pers. comm.) and Palm Beach (Lapointe and Hanisak 1998), coral demise at several reefs (J. Porter, pers. comm.), coral diseases (L. Richardson, pers. comm.), and sponge die-offs (H. Hudson, pers. comm.). Although the decline of nearshore ecosystems in the Keys (and throughout the Caribbean) is probably caused by a combination of factors, nutrient enrichment is recognized as a research need of high priority (D'Elia et al. 1991, NOAA/U. Miami Workshop 1991, S. Miller 1992, Boesch et al. 1996).

The most likely reef organisms to be first affected by additional nutrient inputs are macroalgae because of their rapid rates of nutrient assimilation and utilization (Hanisak 1983). Macroalgae respond rapidly to increases in nutrient availability, initially by uptake and storage, then by increased growth. Macroalgal growth is more related to internal tissue nutrients than to nutrients in the external medium.

A growing number of studies have related macroalgal blooms to anthropogenic increases in nutrient availability and declining ecological health of tropical ecosystems throughout the world (e.g., Australia: Gordon et al. 1981, Schramm and Booth 1981, Birch et al. 1983, Bell 1991; Gulf of Aqaba: Fishelson 1973; and Bermuda: Bach and Josselyn 1979, Lapointe and O'Connell 1989). Perhaps the best known case of nutrient impacts on coral reefs is Kaneohe Bay in Hawaii, where a green alga, *Dicytosphaeria cavernosa*, bloomed and overgrew coral reefs in response to sewage discharge. When the sewage was subsequently diverted, the bloom subsided and the reefs began to recover (Maragos et al. 1985).

Coral reefs presumably assimilate excess nutrients prior to showing symptoms of nutrient pollution, but the amount of nutrient loading needed to cause detectable shifts in community structure and function is unknown. Reefs with elevated nutrient concentrations generally have higher standing crops of benthic macroalgae than reefs in nutrient-poor waters (Hatcher 1984, Pastorok and Bilyard 1985, Birkland 1988, Hatcher 1990), but there is a serious question of whether chronic low-level nutrient enrichment can be detected in reef environments (as described below).

In Florida, sewage outfalls exist at both the north and south ends of the Reef Tract, respectively off Miami (discharging over 160 million gallons of sewage per day) and Key West. Additionally, septic systems that leach nutrients into nearshore waters are found throughout the Keys (Lapointe et al. 1990). While it appears likely that the Key West outfall, only 2 kilometers offshore in 20 feet of water, affects the ecological health of reefs in its immediate vicinity (unpublished observations), and while studies are underway to determine the reach of the Miami outfall (J. Proni, pers. comm.), there are few data that indicate nutrient pollution from shore reaches the Reef Tract itself. Lapointe et al. (1992b) documented elevated ammonium concentrations during the wet season in water that entered the lower Keys east of Big Pine Key from the Gulf of Mexico/Florida Bay and was transported into Hawk Channel westward to Looe Key. Waters from Florida Bay have long been thought to be inimical to reef growth (Ginsberg and Shinn 1964), and elevated ammonium is probably one factor among many (temperature and turbidity being two others) that affect the reefs. An additional complication is that high-latitude coral reefs may be naturally nutrient enriched, with larger algal standing crops a result (Johannes et al. 1983).

Algal-nutrient relationships are complex and responses to nutrient pollution may be reef specific, dependent upon factors such as algal and herbivore abundance, depth, temperature, and other environmental factors (Littler and Littler 1984). For example, grazing by herbivores is an important factor regulating algal biomass and species composition (Littler et al. 1989, Morrison 1988, Hughes et al. 1987, Scott and Russ 1987, Carpenter 1986, Lewis 1986, Hay 1981, 1984), but herbivores also generate a source of nutrients (ammonium) for benthic macroalgae (Williams and Carpenter 1988).

In the Florida Keys, anecdotal evidence that algal blooms are killing the reefs is mounting (Ward 1990, Keating 1991, Torrance 1991, Lapointe pers. comm.), but no data exist to support the contention that nutrient pollution is the cause of the blooms. Water circulation in the Florida Keys is complex; the system is both open (bathed by the Florida Current) and subjected to water from Florida Bay which is a more semi-enclosed system. However, as stated during the Florida Keys Nutrient Workshop (S. Miller 1992), the potential exists for the outward spread of nutrient enriched water from nearshore to the Reef Tract: what remains unknown is the extent of the nearshore problem and the rate at which the problem may spread offshore. Surprisingly few nutrient data sets are available in the Keys (EPA 1991), a problem currently being addressed by the EPA Water Quality Monitoring Program (R. Jones, pers. comm.).

Seawater nutrient concentrations are too ephemeral or too low to routinely be used as parameters to detect natural or anthropogenic sources in nearshore reef environments (Hanisak and Miller, unpublished). On the other hand, tissue analysis is an excellent integrator of nutrient availability to macroalgae (Hanisak 1983). Determination of carbon:nitrogen:phosphorus (C:N:P) ratios and critical analyses of N:P ratios are a sensitive index to determine whether N or P limits macroalgal productivity (Atkinson and Smith 1983), to determine how coral reefs respond to nutrients (Atkinson 1988), and to identify spatial/temporal trends in nutrient limitation or abundance (see references below). Measuring these parameters along a spatial gradient should detect any significant enrichment from either natural (e.g., upwelling, bird colonies) or anthropogenic (e.g., sewage outfalls, Florida Bay) sources.

Benthic macroalgae are effective integrators of nutrient availability (e.g., Chapman and Craigie 1977, Hanisak 1979, Gagne et al. 1982, Rosenberg and Ramus 1982, Asare and Harlin 1983, Hardwick-Whitman and Mathieson 1986, Hanisak 1990). A large collection of macroalgal species from variable environments (Atkinson and Smith 1983) led to a modified Redfield ratio (Redfield 1958) for macroalgae of 550 mol C: 30 mol N: 1 mol P. These generally high N:P ratios, compared to phytoplankton, suggest a greater probability of P limitation.

In a study of five macroalgal species common to the Pacific northeast, all species were N-limited at least part of the year, and P limitation occurred in four of the species (Wheeler and Björnsater 1992). Frondose epilithic macroalgae from several carbonate tropical waters (including the Florida Keys) were significantly depleted in P relative to C and N when compared to seaweeds from temperate siliciclastic waters (Lapointe et al. 1992a); N limitation in the temperate algae was suggested by decreased ratios in C:P and N:P. Seasonal trends in N and P macroalgal dynamics are common (Hanisak 1979; McComb et al. 1981; Birch et al. 1981; D'Elia et al. 1986; Lapointe 1987; Lapointe et al. 1987b). While the determination of C:N:P ratios for coral reef algae should help understand how reefs respond to nutrients (Atkinson 1988), few studies have applied this technique to discern ecosystem-scale processes.

Elemental analysis of the seagrass, *Thalassia testudinum*, was used effectively in Florida Bay as an indicator of the relative availability of N and P (Fourqurean et al. 1992). C:P and C:N ratios varied on a local scale that correlated with a point source of nutrient additions (a bird colony) and on a regional scale across the bay, with greatest P availability in the northwest and least P availability in eastern Florida Bay. This pattern suggests that the source of P in the bay lies to the west and was hypothesized to be water from the Gulf of Mexico. Further, the C:N ratio did not vary across the bay, which indicates that the plants were saturated with respect to N. This study demonstrated the utility of elemental analysis of seagrass as a tool to integrate long-term nutrient availability and to help infer ecosystem-scale processes. Continued measurements of elemental composition of *Thalassia* are now being conducted over a much broader area in the Keys (Zieman and Fourqurean, pers. comm.).

However, there are limitations to using seagrasses for nutrient assessments. Responses to water column enrichments are dampened because of the dependence of seagrass on sediment, not water column, nutrients (Short 1987; Zieman, pers. comm.). Seagrasses are restricted to soft-bottom habitats; hard-bottom habitats (e.g., coral reefs) cannot be sampled by seagrass analyses. Moreover, it is likely that macroalgae and seagrass provide different integrating scales for nutrient availability. Most coral reef macroalgae acquire nutrients directly from the surrounding waters (not sediments) and are probably integrating nutrient availability at shorter temporal scales (days to weeks, Hanisak 1990) relative to seagrass; thus, algae may be more responsive to nutrient variations associated with seasonal changes, interannual variability, and stochastic events (e.g., major storms).

2.2 Objectives

This project measured internal tissue nutrients (C, N, and P) of macroalgae throughout the Florida Keys and in adjacent waters to determine their nutrient status across space and time. Specific objectives of the proposed project were:

(1) to determine spatial variations in tissue C, N, and P of dominant macroalgae;

(2) to determine temporal variations in tissue C, N, and P of dominant macroalgae;

(3) to identify nutrient hot spots using tissue analyses of macroalgae; and

(4) to select indicator species and sampling protocol for future long-term monitoring.

The primary null hypotheses tested was:

H_o: Spatial and temporal variations in tissue C, N, and P concentrations of benthic macroalgae are not detectable along or among transects from inshore to the offshore reefs.

3.0 Methods

3.1 Stations

A total of 80 stations (Fig. 1, Table 1) were established to assess the spatial variation in tissue nutrients (C, N, P), both as ratios and absolute values, of the dominant macroalgae. Most of these stations were located along a series of 12 inshore-offshore transects, three each off of Biscayne Bay and the Upper, Middle, and Lower Florida Keys; ten additional stations were located in Florida Bay. The sampling design incorporates the variation that exists among the Upper, Middle, and Lower Keys, the three distinct physiographic regimes described for the Keys and based on geology, degree of reef development, and magnitude of exchange with Florida Bay and the Gulf of Mexico, perhaps first recognized by Ginsberg and Shinn (1964).

The number of stations and their locations were considerably different than what had been initially proposed (i.e., 24 stations had been proposed, 80 were sampled).

While the principal result of additional stations was a substantial increase in spatial coverage of the study, several other benefits of this enhanced strategy were:

(1) Sampling three transects (not two, as initially proposed) in each of the Biscayne Bay, Upper Keys, Middle Keys, and Lower Keys segments permitted better replication of inshore-offshore and between-transect differences; if there were not significant differences among transects within a segment, then, in the future, sampling one or two transects would be sufficient to characterize nutrient conditions within the region.

(2) Instead of the proposed three sites per transect on the ocean-side of the Keys, five or six stations were selected along each transect to encompass both hard and soft-bottom communities as they appear to provide different, but complementary, information (see "Results"). Accordingly, two stations per transect were located between Hawk Channel and the Keys and were considered "inshore" stations; the remaining stations were located offshore of Hawk Channel: two between Hawk Channel and the Reef Tract, and usually two at the reef (one back-reef station and one fore-reef station).

(3) The ten Florida Bay sites were selected in pairs to complement five of the transects that were located in the vicinity of tidal channels between various Keys (see Fig. 1). The intent of these stations was to determine the tissue composition of algae in Florida Bay and whether stations located near Florida Bay influences have significantly different algal tissue nutrients than stations less influenced by the Bay (i.e., stations further removed from the tidal passages).

Additional considerations in selecting the location of these stations were:

(1) Previous work experience by the author in the Keys was helpful, particularly in regard to the Key Largo area and to reefs sampled during a series of three Keys-wide cruises conducted in August-October 1995.

(2) Coordination of sampling of Biscayne Bay, Upper Keys, Middle Keys, and Florida Bay stations was initiated with Principal Investigators on other projects associated with water quality issues in Biscayne Bay and the Florida Keys, in particular Drs. Larry Brand and Alina Szmant of RSMAS. The author was a Co-Principal Investigator on the RSMAS-COP (Coastal Ocean Program) project, in which he was responsible for sampling algal tissue nutrients.

(3) Consideration for station selection was also given to locating sites near existing stations used in the EPA Water Quality Monitoring and Seagrass Monitoring projects.

Sampling was conducted in 1996 and 1997 during winter (February-March) and summer (July-August). These two periods of the year were selected because they represent approximate minima (winter) and maxima (summer) for macroalgal abundance. Thus, these periods would be reasonably assumed to provide the widest range of internal nutrient levels during the course of the year.

There were differences in sampling approaches between years. During 1996, all species that could be reasonably collected at a station in ca. 20 minutes were sampled, with the idea that the species sampled would represent the whole algal community at that station. During 1997, emphasis was placed on collecting a smaller list of species that had been found to be most widespread (i.e., present at as many sites as possible) to maximize comparisons of the chemical composition of individual species and to recommend a list of candidate species for future monitoring efforts.

For the purposes of this report, the 1996 collection was considered preliminary and the 1997 collection provided the data presented in this report for comparisons among species, seasons, and locations. The reasons for relying on the 1997 data set were: (1) the 1996 winter collection was impacted by bad weather, thus reducing the ability to make seasonal comparisons, and, more importantly (2) the emphasis in 1997 on a more thorough sampling of the most widespread species provided a much great capability for comparisons among locations (i.e., transects, segments, and distance from shore). A brief overview of the results of the 1996 collection is provided below.

3.2 Year 1 Sampling (1996)

During 1996, winter field work was scheduled for late February and early March. The three Biscayne Bay and three Upper Keys transects and the Alligator Reef transect were successfully completed, but poor weather conditions prevented sampling of the other two transects in the Middle Keys, as well as the Lower Keys and the Florida Bay stations. All stations, except the Florida Bay stations, were sampled during the summer period of July 24-28, 1996. Bad weather delayed the sampling of Florida Bay sites, and their sampling was re-scheduled to the first date available for boat support and personnel. The Florida Bay sites were all sampled on August 13, 1996.

The results of the initial analyses were presented at the November 1996 project review meeting. In summary, key points of the 1996 results were:

- N and P status varied considerably among species. Thus, spatial and temporal comparisons of macroalgal tissue nutrients require a species-specific approach (Note: this conclusion lead to the 1997 sampling design).

- Tissue P was much more variable than tissue N. Thus, N:P ratios were more influenced by P than by N.

- A major cause of interspecific difference appeared to be habit (lithophytic, or growing on rocks, vs. psammophytic, or growing in sediments). Tissue N:P ratios were higher for psammophytic species than for lithophytic ones. (Note: the effect of calcification, see below, had not yet been addressed).

- Thus, psammophytic species were more likely to be limited by P; lithophytic algae were more likely to be limited by N.

- There was an inshore-offshore gradient of N and P, with higher N:P ratios inshore and lower N:P ratios offshore. Thus, macroalgae inshore would more likely be P-limited; macroalgae offshore would more likely be N-limited.

3.3 Year 2 Sampling (1997)

Following preliminary analysis of the Year 1 collections, which were presented at the November 1996 review meeting, and discussions at that meeting, it was decided that Year 2 collections should focus on spatial and temporal (seasonal) variations in tissue nutrients for a shorter list of target species, rather than following the Year 1 approach of sampling all abundant species located at each station. The major limitation with the Year 1 approach was that (a) differences in tissue nutrients among species at a given site were significant, due to differences in habit, morphology, and taxonomic group, and (b) not all species were found at each station. Comparisons among stations were limited by the number of species found in common among the stations. Thus, the following guidelines were developed for Year 2 sampling:

(1) The most widespread taxa, that provided a range of tissue nutrients, based primarily on habit (lithophytic vs. psammophytic), calcification (calcified vs. non-calcified), and taxonomic group (= class: red, green, or brown algae), were selected from the Year 1 collections. These taxa were:

(a) *Avrainvillea* - an uncalcified chlorophyte (= green alga), which grows in the sediment (i.e., this species may derive significant nutrients from the sediments as well as from the water column);

(b) *Dictyota* - an uncalcified phaeophyte (= brown alga), which grows on hard substrate (i.e., this species must derive all of its nutrients from the water column);

(c) *Halimeda incrassata* - a larger, segmented, calcified chlorophyte, which grows in the sediment;

(d) *Laurencia* (*intricata* and *poiteaui*) - an uncalcified rhodophyte (= red alga), which grows on hard substrate;

(e) *Penicillus capitatus* - a smaller, partly filamentous, calcified chlorophyte, which grows in the sediment; and

(f) *Udotea flabellum* - a larger, fan-shaped, calcified chlorophyte, which grows in the sediment.

In addition, other *Halimeda* species (*H. discoidea*, *H. goreauii*, *H. opuntia*, and *H. tuna*; all of these species are lithophytic, with the exception of *H. opuntia* which can also grow in sediments) were collected when present.

(2) Stations along transects were characterized as "inshore" (between the Keys and Hawk Channel) or "offshore" (between Hawk Channel and the Reef Tract).

(3) For each transect, one or more stations were sampled within each of the "inshore" and "offshore" areas, until all six target taxa were collected. Usually, a more exhaustive SCUBA survey was required than in Year 1. Back reefs and fore reefs for each transect and the 10 Florida Bay stations, were also sampled. All six taxa were normally encountered at the back reef sites. Fore reef collections were usually limited to *Dictyota* and *Halimeda*.

(4) To provide more appropriate and complete comparisons of tissue nutrients among species, analyses of carbonate and organic composition were also performed (these analyses were not included in the proposed work plan).

This sampling strategy permitted a much stronger data set for comparisons of inshore vs. offshore stations and among segments and facilitated the recommendations of specific taxa for longer term monitoring in the Florida Keys and other reef systems.

Using this modified sampling design, the winter collection of all transects was successfully completed during the period February 26 to March 7, 1997, and the summer collection of all transects was successfully completed during the period July 23 to July 28, 1997.

3.4 Sampling Protocol

A DGPS (Northstar 941XD) was used to navigate and locate each sampling station in the field. Algal samples were collected by SCUBA and consisted of common or abundant benthic macroalgae (usually 3-5 replicate individuals per species sampled per station). Samples were stored by species in plastic bags, labeled with the station number and collection date. The plastic bags were stored in a cooler with ice for transport to the field laboratory.

Each evening, upon return to the field lab, the algal samples were picked clean of animals and other contaminants prior to being dried at 80°C. Following drying, each individual algal sample was placed in a whirl-pak bag, labeled (station, date, and sample code), and secured for the trip back to HBOI.

3.5 Laboratory Analyses

A total of 4,422 macroalgal samples were analyzed over the two years. Prior to tissue analyses, the dried algal samples were re-dried at 80°C. In cases where carbonate-free determinations were made, the algae were soaked in 5% HCl to remove any calcium carbonate and re-dried at 80°C.

The dried algal samples were homogenized and milled to fine powder with a mortar and pestle or a Wiley Mill. Samples were stored in capped glass vials at room temperature. Prior to analyses, samples were re-dried at 80°C overnight to remove any small amounts of moisture that may have been absorbed by the powder during grinding or storage.

Tissue Carbon and Nitrogen

Sub-samples of the dried algal powders were sent to MSI Analytical Lab (Marine Science Institute, University of California, Santa Barbara). Tissue carbon and nitrogen were analyzed with either of two automated CHN analyzers, a Control Equipment Corporation Model 240ZA and a Leeman Labs Model CE440. These functionally similar instruments use a modified Pregl-Dumas technique to combust appropriately weighed microgram to milligram size samples in an oxygen-enriched helium atmosphere at 1000°C, and analyze the combustion products [CO_2, NOx (reduced to N_2), and H_2O] with three pairs of thermal conductivity detectors.

Samples of ground material were accurately weighed on a Cahn micro-balance before being loaded into the analyzer. A two-point calibration was used (blank and one weight of standard), as recommended by the manufacturers. The standard material was acetanilide. NBS reference material #1572 (ground citrus leaves) was used as a reference material. NBS analysis of carbon and nitrogen for this material was 44.0% and 2.85% respectively. An acceptable range for these elements was 44.0±1.0% and 2.85±0.3%.

Tissue Phosphorus

Tissue phosphorus was determined by a modification of Solórzano and Sharp (1980), as described by Fourqurean et al. (1992). Total phosphorus was determined by oxidizing and hydrolyzing all of the phosphorus-containing compounds in a sub-sample to soluble reactive phosphorus concentration by the absorbic acid/molybdate method. The sample preparation method involved the addition of 200 μl of 0.17 N $MgSO_4$ to 50 mg of dried, powdered algal sample in a 20-ml glass scintillation vial and evaporated to dryness in an 80°C oven. Once dry, the sample was ashed at 550°C in a muffle furnace for 3.5 hours and allowed to cool overnight. The sample was hydrolyzed with the addition of 10 ml of 0.025 N HCl. The samples were put into an 80°C oven for 3 hours, shaken every 30 minutes, and cooled overnight. The samples were analyzed for soluble reactive phosphate according to standard oceanographic methods (Strickland and Parsons 1972).

In addition to the standard blanks and standards used in the inorganic P analysis, each sample was run in duplicate. NBS reference material #1572, ground citrus leaves, was also analyzed with each season's samples following the same protocol. NBS analysis of phosphorus for this material was 0.13%, with an acceptable range of 0.13±0.02%.

Carbonate-Free Dry Weight and Organic Weights

The carbonate content of calcified species was determined by de-calcifying dried sub-samples with 5% HCl. The amounts of carbonate and percent carbonate-free dry weight (CFDW) were determined by weighing the samples, on an analytical balance, before and after de-calcification and re-drying at 80°C.

The organic content was determined by ashing dried (or for calcified species, decalcified) sub-samples at 550°C in a muffle furnace for four hours. The percent ash-free dry weight (= % organic weight; AFDW) was determined by weighing the samples, on an analytical balance, before and after ashing and re-drying.

Tissue nutrients derived on a dry weight basis were converted to a carbonate-free dry weight (CFDW) basis and an ash-free dry weight (AFDW) using the appropriate conversions determined for each sample.

3.6 Statistical Analyses

In this report, data are presented as means ± standard errors (SE). Statistical analyses were performed with SAS statistical software (SAS Institute 1988). Statistical significance among means was tested with analysis of variance (ANOVA). When ANOVA indicated the existence of significant differences, the Tukey-Kramer test determined which means were significantly different. The minimal level of significance for any analysis was $P \leq 0.05$.

4.0 Results

Results are presented in sequence for ten dominant macroalgae species, at increasing higher levels of spatial synthesis (Section 4.1). Data are presented for: (1) all inshore-offshore transects, with inshore and offshore delineations, and the combined Florida Bay stations for each collection; (2) all segments, with inshore and offshore delineations, and the combined Florida Bay stations for each collection; and (3) an overall inshore-offshore comparison for the two collections. Seasonality (comparison of the March and July 1997 collections) is presented for all species (Section 4.2). Lastly, overall comparisons among species are presented (Section 4.3).

For each species, data are presented in the following order:

(1) % N and % P, with N:P ratios, on a dry weight basis;

(2) % C, with C:N and C:P ratios, on a dry weight basis;

(3) % N and % P, with N:P ratios, on a carbonate-free dry weight basis (CFDW);

(4) % C, with C:N and C:P ratios, on a carbonate-free dry weight basis (CFDW);

(5) % N and % P, with N:P ratios, on an organic or ash-free dry weight basis (AFDW);

(6) % C, with C:N and C:P ratios, on an organic or ash-free dry weight basis (AFDW).

Comparisons of species means using the three different basis (dry weight, CFDW, AFDW) are presented for both collections (Section 4.3). For most algae, the most common means of reporting this type of data is on a dry weight basis, but for calcified algae, a carbonate-free dry weight basis is more appropriate, particularly in regards to reporting %C and ratios involving C, to distinguish metabolically active organic carbon from carbonate. Similarly, the use of organic or ash-free dry weights eliminates the complications of inorganic salts (ash) in species comparisons. In the following sections, while all data are presented, the AFDW basis is generally used to eliminate the complications of carbonate and salt composition and for simplicity of presentation.

4.1 Spatial Patterns of Algal Tissue Nutrients

Examination of transect data (Figs. 2-93) revealed no universal inshore-offshore patterns in tissue nutrients and no obvious "hotspots" of nutrient enrichment, where most or all species sampled would have substantially elevated N or P levels. In most cases, adjacent transects differed little in the parameters measured.

Spatial patterns in tissue nutrients were examined among segments and for inshore-offshore patterns within segments (Figs. 94-185) and for overall inshore-offshore differences (Figs. 186-197). Because of differences among species, these spatial patterns were examined for each algal species.

Avrainvillea sp.

In March 1997, significant differences among segments were found for all parameters, except C:N ratio (AFDW basis; Figs. 96-97): %N was significantly higher in the Upper Keys than in Florida Bay; %P was significantly higher and %C was significantly lower in Florida Bay than in all other segments; N:P ratio was significantly higher in the Lower and Middle Keys than in Florida Bay; and C:P ratio was significantly higher in the Lower Keys than in Florida Bay.

In July 1997, significant differences among segments were found for only two parameters (AFDW basis; Figs. 100-101): %N and %C were both significantly higher in the Middle Keys than in Florida Bay.

Overall, there were no significant inshore-offshore differences in March 1997 (AFDW basis; Figs. 190-191). Florida Bay stations had significantly lower %N and N:P ratio than offshore stations and significantly higher %P and significantly lower %C than both inshore and offshore stations (AFDW basis; Figs. 96-97). In July 1997, the only significant inshore-offshore difference (AFDW basis; Figs. 196-197) was for %N, which was significantly higher offshore. Florida Bay stations had significantly lower %N and %C than offshore stations (AFDW basis; Figs. 100-101).

Dictyota cervicornis

In March 1997, the only significant difference among segments was for C:N ratio (AFDW basis: Figs. 104-105), which was significantly higher in the Upper Keys than in Florida Bay.

In July 1997, there were five significant differences among segments (AFDW basis: Figs. 108-109): %N was significantly higher and C:N ratio was significantly lower in Florida Bay and in the Lower Keys than in the Biscayne Bay segment; %P was significantly higher in the Middle and Lower Keys than in Florida Bay; and N:P and C:P ratios were significantly higher in Florida Bay than in all other segments.

Overall, in both March and July 1997, there were no significant inshore-offshore differences (AFDW basis; Figs. 190-191, 196-197). In March, there were no significant differences between Florida Bay stations and inshore or offshore stations (AFDW basis; Figs. 104-105). In July, Florida Bay stations had significantly lower %P than offshore stations, significantly higher N:P and C:P ratios than both inshore and offshore stations, and significantly lower C:N ratio than inshore stations (AFDW basis; Figs. 108-109).

Halimeda incrassata

In March 1997, significant differences among segments were found for four parameters (AFDW basis; Figs. 113-114): %N was significantly higher in Florida Bay than in the Biscayne Bay segment and in the Lower Keys; N:P ratio was significantly higher in Florida Bay than in the Middle Keys; %C was significantly higher in the Biscayne Bay segment and in the Middle Keys than in the Lower Keys; and C:N ratio was significantly higher in the Biscayne Bay segment and in the Lower Keys than in Florida Bay.

In July 1997, significant differences among segments were found for all parameters (AFDW basis; Figs. 118-119): %N was significantly higher in Florida Bay, followed by Biscayne Bay and the Middle and Lower Keys, and then by the Upper Keys; %P was significantly higher in the Biscayne Bay segment and in the Middle Keys than in Florida Bay; N:P and C:P ratios were significantly higher in Florida Bay than in all other segments; %C was significantly higher in the Middle Keys than in the Biscayne Bay segment; and C:N ratio was higher in the Lower Keys than in Florida Bay.

Overall, there were no significant inshore-offshore differences in March 1997 (AFDW basis; Figs. 190-191). Florida Bay stations had significantly higher %N and significantly lower C:N ratio than both inshore and offshore stations and significantly lower %P and significantly higher N:P ratios than offshore stations (AFDW basis; Figs. 113-114). In July 1997, there were three significant inshore-offshore differences (AFDW basis; Figs. 196-197): inshore stations had significantly higher %N and N:P ratio and significantly lower C:N ratio. Florida Bay stations had significantly higher %N, N:P ratio, and C:P ratio and significantly lower %P than both inshore and offshore stations (AFDW basis; Figs. 118-119).

Halimeda opuntia

In March 1997, there were no significant differences among segments for any parameter (AFDW basis; Figs. 123-124).

In July 1997, significant differences among segments were found for all parameters, except %P (AFDW basis; Figs. 128-129): %N was significantly higher in Florida Bay and in the Upper Keys than in the Biscayne Bay segment; N:P and C:P ratios were significantly higher in Florida Bay than in all other segments; %C was significantly higher in the Middle and Upper Keys than in the Lower Keys and Florida Bay; and C:N ratio was higher in the Middle Keys and the Biscayne Bay segment than in the Lower Keys and Florida Bay.

Overall, the only significant inshore-offshore difference in March 1997 (AFDW basis; Figs. 190-191) was for %P, which was significantly higher offshore than inshore. Florida Bay stations had significantly higher %N than inshore stations (AFDW basis; Figs. 123-124). In July 1997, there were two significant inshore-offshore differences (AFDW basis; Figs. 196-197): %P was significantly higher offshore and C:P ratio was significantly higher inshore. Florida Bay stations had significantly lower %P and C:N ratio and significantly higher C:P ratio than offshore stations and significantly higher N:P ratio and significantly lower %C than both inshore and offshore stations.

Halimeda tuna

In March 1997, significant differences among segments were found for all parameters, except %N and %C (AFDW basis; Figs. 133-134): %P was significantly higher in the Middle Keys than in the Biscayne Bay segment; N:P and C:P ratios were significantly higher in the Biscayne Bay segment than in all other segments; and C:N ratio was significantly higher in the Lower Keys and Biscayne Bay than in Florida Bay.

In July 1997, the only significant difference among segments was for C:N ratio (AFDW basis; Figs. 138-139), which was significantly higher in the Middle Keys than in the Upper Keys.

There were no significant inshore-offshore differences for either March or July 1997 (AFDW basis; Figs. 190-191, 196-197). The only significant differences with Florida Bay stations occurred in March 1997 for two parameters (AFDW basis; Figs. 133-134): Florida Bay stations had significantly lower %C than offshore stations and significantly lower C:N ratio than inshore stations.

Laurencia intricata

In March 1997, significant differences among segments were found for all parameters, except %C (AFDW basis; Figs. 142-142): %N was significantly higher in the Lower and Upper Keys than in the Middle Keys and Florida Bay; %P was significantly higher and C:N ratio was significantly lower in the Upper and Lower Keys than in Florida Bay; N:P was significantly higher in Florida Bay than in the Upper Keys; and C:P was significantly higher in Florida Bay than in all other segments.

In July 1997, significant differences among segments were found for all parameters, except C:P ratio (AFDW basis; Figs. 146-147): %N and N:P ratio were significantly higher and %C was significantly lower in Florida Bay than in the Upper Keys and in the Biscayne Bay segment; %P was significantly higher in the Upper Keys than in Florida Bay; and C:N ratio was significantly higher in the Biscayne Bay segment and in the Upper Keys than in the Lower Keys and in Florida Bay.

Overall, there were three significant inshore-offshore differences in March 1997 (AFDW basis; Figs. 190-191): offshore stations had significantly higher %N and %P and significantly lower C:N ratio. Florida Bay stations had significantly lower %N and %P and significantly higher N:P, C:N and C:P ratios than both inshore and offshore stations (AFDW basis; Figs. 142-143). In July 1997, *Laurencia intricata* had an unusual distribution, being found only offshore in the Biscayne Bay segment and in Upper Keys, but inshore in the Middle and Lower Keys, as well as in Florida Bay (Figs. 146-147). There were two significant inshore-offshore differences (AFDW basis; Figs. 196-197): inshore stations had significantly higher %N and significantly lower C:N ratio. Florida Bay stations had significantly higher %N and significantly lower %P than offshore stations, significantly higher N:P and C:P ratios than inshore stations, and significantly lower %C and C:N ratio than both inshore and offshore stations (AFDW basis; Figs. 146-147).

Laurencia poiteaui

In March 1997, significant differences among segments were found for three parameters (AFDW basis; Figs. 150-151); %P was significantly higher in the Middle Keys than in Florida Bay; and N:P and C:P ratios were both significantly higher in Florida Bay than in all other segments.

In July 1997, significant differences among segments were found for all parameters (AFDW basis; Figs. 154-155): %N was significantly higher and C:N ratio was significantly lower in Florida Bay than in the Middle and Lower Keys and in the Biscayne Bay segment; %P was significantly higher in the Middle Keys and in the Biscayne Bay segment than in Florida Bay; N:P ratio was significantly higher in Florida Bay than in all other segments; %C was significantly higher in the Biscayne Bay segment and the Upper Keys than in Florida Bay; and C:P ratio was significantly higher in Florida Bay than in the Biscayne Bay segment and in the Middle Keys.

In March 1997, there were three significant inshore-offshore differences (AFDW basis; Figs. 190-191): inshore stations had significantly higher %N and significantly lower %P and C:N ratio. Florida Bay stations had significantly higher %N and lower C:N ratio than offshore stations and significantly lower %P and higher N:P and C:P ratios than both inshore and offshore stations (AFDW basis; Figs. 150-151). In July 1997, there were four significant inshore-offshore differences (AFDW basis; Figs. 196-197): inshore stations had significantly lower %P and C:N ratio and significantly higher

N:P and C:P ratios. Florida Bay stations had significantly higher %N and N:P ratio and lower C:N than both inshore and offshore stations and significantly lower %P and %C and significantly higher C:P ratio than offshore stations (AFDW basis; Figs. 154-155).

Penicillus capitatus

In March 1997, significant differences among segments were found for all parameters (AFDW basis; Figs. 159-160): %N and %C were significantly higher and C:N ratio significantly lower in Florida Bay than in all other segments; %P was significantly higher in the Middle Keys than in the Biscayne Bay segment and in Florida Bay; N:P ratio was significantly higher in Florida Bay than in the Middle Keys; and C:P ratio was significantly higher in Florida Bay than in the Upper Keys and in the Biscayne Bay segment.

In July 1997, significant differences among segments were found for all parameters, except %P (AFDW basis; Figs. 164-165): %N and N:P ratio were significantly higher and C:N ratio was significantly lower in Florida Bay than in all other segments; %C was significantly higher in Florida Bay than in the Biscayne Bay segment; and C:P ratio was significantly higher in Florida Bay than in the Lower Keys and the Biscayne Bay segment.

Overall, there were five significant inshore-offshore differences in March 1997 (AFDW basis; Figs. 190-191): inshore stations had significantly higher %N, %C, N:P ratio, and C:P ratio and significantly lower %P. Florida Bay stations had significantly lower %P and C:N ratio than offshore stations, and significantly higher %N, %C, N:P ratio, and C:P ratio than both inshore and offshore stations (AFDW basis; Figs. 159-160). In July 1997, significant inshore-offshore differences were found for all parameters (AFDW basis; Figs. 196-197): inshore stations had significantly higher %N, %C, N:P ratio, and C:P ratio and significantly lower %P and C:N ratio. Florida Bay stations had significantly higher %N, %C, and N:P ratio than both inshore and offshore stations, and significantly lower %P and C:N ratio and significantly higher C:P ratio than offshore stations (AFDW basis; Figs. 164-165).

Penicillus dumetosus

In March 1997, significant differences among segments were found for all parameters, except %C (AFDW basis; Figs. 169-170): %N was significantly higher in Florida Bay than in the Middle Keys and the Biscayne Bay segment; %P was significantly higher in the Lower Keys than in the Biscayne Bay segment, the Upper Keys, and Florida Bay; N:P ratio was significantly higher in the Upper Keys than in

Florida Bay and the Middle and Lower Keys; C:N ratio was significantly higher in the Middle Keys than in Florida Bay; and C:P ratio was significantly higher in the Upper Keys than in Florida Bay and in the Lower Keys.

In July 1997, significant differences among segments were found for three parameters (AFDW basis; Figs. 174-175): %N was significantly higher in Florida Bay and in the Middle Keys than in the Biscayne Bay segment; %C was significantly higher in the Middle Keys and in Florida Bay than in the Biscayne Bay segment; and C:N ratio was significantly higher in the Lower Keys and in the Biscayne Bay segment than in Florida Bay.

Overall, there were three significant inshore-offshore differences stations in March 1997 (AFDW basis; Figs. 190-191): inshore stations had significantly higher %P and significantly lower N:P and C:P ratios. Florida Bay stations had significantly higher %N than both inshore and offshore stations, significantly higher %C than offshore stations, and significantly lower C:N ratio than inshore stations (AFDW basis; Figs. 169-170). In July 1997, there were four significant inshore-offshore differences (AFDW basis; Figs. 196-197): inshore stations had significantly higher %N and %P and significantly lower C:N and C:P ratios. Florida Bay stations had significantly higher %N and %P and significantly lower C:N ratio than offshore stations (AFDW basis; Figs. 174-175).

Udotea flabellum

In March 1997, significant differences among segments were found for all parameters, except C:P ratio (AFDW basis; Figs. 179-180): %N was significantly higher and C:N ratio was significantly lower in Florida Bay than in the Middle Keys; %P was significantly higher in Florida Bay than in the Upper Keys; N:P ratio was significantly higher in the Upper Keys than in the Middle Keys; and %C was significantly higher in Florida Bay and the Lower and Upper Keys than in the Middle Keys.

In July 1997, significant differences among segments were found for four parameters (AFDW basis; Figs. 184-185): %N was significantly higher in Florida Bay, the Upper Keys, and the Biscayne Bay segment than in the Middle and Lower Keys; %P was significantly higher in the Lower Keys than in the Biscayne Bay segment and Florida Bay; N:P ratio was significantly higher in Florida Bay and the Biscayne Bay segment than in the Lower Keys; and C:N ratio was significantly higher in the Lower and Middle Keys than in the other three segments.

Overall, there were three significant inshore-offshore differences in March 1997 (AFDW basis; Figs. 190-191): inshore stations had significantly higher %N and significantly lower C:N and C:P ratios. Florida Bay stations had significantly higher %N than both inshore and offshore stations, and significantly higher %P and significantly lower C:N and C:P ratios than offshore stations (AFDW basis; Figs. 169-170). In July 1997, there were no significant inshore-offshore differences (AFDW basis; Figs. 196-197). Florida Bay stations had significantly higher %N and N:P ratio and significantly lower C:N ratio than both inshore and offshore stations and significantly lower %P and %C than offshore stations (AFDW basis; Figs. 174-175).

4.2 Temporal Patterns (Seasonality) of Algal Tissue Nutrients

For any species, there were usually significant differences in tissue nutrients between the March and July 1997 collections, and similar patters were found irrespective of dry weight, CFDW, or AFDW basis (Figs. 198-203).

Eight out of the 10 species had significantly higher %N in March than in July (AFDW basis; Figs. 202-203). *Avrainvillea* sp. was the only species with significantly higher %N in July.

Five species (*Dictyota cervicornis*, *Halimeda opuntia*, *Laurencia intricata*, *Laurencia poiteaui*, and *Penicillus capitatus*) had significantly higher %P in March than in July (AFDW basis; Figs. 202-203). *Avrainvillea* sp. was the only species with significantly higher %P in July.

Three species (*Avrainvillea* sp., *Halimeda incrassata*, and *Udotea flabellum*) had significantly higher N:P ratios in March than in July (AFDW basis; Figs. 202-203). *Dictyota cervicornis* was the only species with a significantly higher N:P ratio in July.

Six species (*Avrainvillea* sp., *Dictyota cervicornis*, *Halimeda incrassata*, *Halimeda opuntia*, *Halimeda tuna*, and *Laurencia intricata*) had significantly higher %C in March than in July (AFDW basis; Figs. 202-203). *Penicillus capitatus* and *Penicillus dumetosus* had significantly higher %C in July.

Three species (*Avrainvillea* sp., *Dictyota cervicornis*, and *Halimeda incrassata*) had significantly higher C:N ratios in March than in July (AFDW basis; Figs. 202-203). Six species (*Halimeda opuntia*, *Halimeda tuna*, *Laurencia intricata*, *Penicillus capitatus*, *Penicillus dumetosus*, and *Udotea flabellum*) had significantly higher C:N ratios in July.

Overall, there were three significant inshore-offshore differences in March 1997 (AFDW basis; Figs. 190-191): inshore stations had significantly higher %N and significantly lower C:N and C:P ratios. Florida Bay stations had significantly higher %N than both inshore and offshore stations, and significantly higher %P and significantly lower C:N and C:P ratios than offshore stations (AFDW basis; Figs. 169-170). In July 1997, there were no significant inshore-offshore differences (AFDW basis; Figs. 196-197). Florida Bay stations had significantly higher %N and N:P ratio and significantly lower C:N ratio than both inshore and offshore stations and significantly lower %P and %C than offshore stations (AFDW basis; Figs. 174-175).

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Five species (*Dictyota cervicornis*, *Halimeda opuntia*, *Laurencia intricata*, *Laurencia poiteaui*, and *Penicillus capitatus*) had significantly higher %P in March than in July (AFDW basis; Figs. 202-203). *Avrainvillea* sp. was the only species with significantly higher %P in July.

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Six species (*Avrainvillea* sp., *Dictyota cervicornis*, *Halimeda incrassata*, *Halimeda opuntia*, *Halimeda tuna*, and *Laurencia intricata*) had significantly higher %C in March than in July (AFDW basis; Figs. 202-203). *Penicillus capitatus* and *Penicillus dumetosus* had significantly higher %C in July.

Three species (*Avrainvillea* sp., *Dictyota cervicornis*, and *Halimeda incrassata*) had significantly higher C:N ratios in March than in July (AFDW basis; Figs. 202-203). Six species (*Halimeda opuntia*, *Halimeda tuna*, *Laurencia intricata*, *Penicillus capitatus*, *Penicillus dumetosus*, and *Udotea flabellum*) had significantly higher C:N ratios in July.

Two species (*Avrainvillea* sp. and *Halimeda incrassata*) had significantly higher C:P ratios in March than in July (AFDW basis; Figs. 202-203). Three species *(Dictyota cervicornis, Halimeda opuntia*, and *Penicillus dumetosus*) had significantly higher C:P ratios in July.

4.3 Comparisons of Species

While absolute values of tissue nutrients are influenced by whether tissue nutrient parameters are indexed to dry weight, CFDW, or AFDW (Figs. 204-207), N:P ratios are not affected at all, and C:N and C:P ratios are only influenced by the carbonate correction. Algal species monitored in this study fall into several groupings based on tissue nutrient patterns.

%N was higher for calcified species than for non-calcified species (AFDW basis; Figs. 202-203). Highest %N was found for *Halimeda tuna* and *Halimeda incrassata*. Lowest %N was found for the three non-calcified, lithophytic species, *Laurencia intricata*, *Dictyota cervicornis*, and *Laurencia poiteaui*. The non-calcified, but psammophytic species, *Avrainvillea* sp. had intermediate levels of %N, along with the calcified species *Halimeda opuntia*, *Udotea flabellum*, *Penicillus capitatus*, and *Penicillus dumetosus*.

%P was higher for non-calcified species than for calcified species (AFDW basis; Figs. 202-203). There were relatively few differences in %C among species; *Halimeda tuna* and *Halimeda incrassata*, the species with the highest %C, had significantly higher %C than *Penicillus dumetosus*, the species with the lowest %C.

The contrasting patterns of %N and %P resulted in two groupings of species based on N:P ratio, with calcified species having significantly higher N:P and C:P ratios than non-calcified species (AFDW basis; Figs. 202-203). Non-calcified, lithophytic species (*Laurencia intricata*, *Dictyota cervicornis*, and *Laurencia poiteaui*) had significantly higher C:N ratios than the non-calcified, but psammophytic species, (*Avrainvillea* sp.) and the six calcified species, but similar N:P and C:P ratios.

5.0 Discussion

This study used the tremendous biochemical and ecological diversity of macroalgae to assess nutrient availability at a broad, ecosystem-level scale in the Florida Keys and nearby waters. The resulting detailed analysis demonstrated significant spatial and temporal patterns in macroalgal tissue nutrients. Differences in tissue nutrients depended upon location, season, and species.

Spatial Patterns

The transect data revealed no universal inshore-offshore patterns in tissue nutrients and no obvious "hotspots" of nutrient enrichment. In most cases, for any particular species, adjacent transects differed little in the parameters measured. Similarly, when data were compared among segments, there was not a universal geographical pattern in tissue nutrients for all species. The most striking result was that the N and P status of macroalgae in Florida Bay was significantly different than other locations.

Macroalgae collected from Florida Bay generally had higher N and lower P levels than algae collected elsewhere. For example, in the July 1997 collection:

- Nine out of ten species (*Avrainvillea* sp. was the exception) had significantly higher %N in Florida Bay than in one or more of the other segments.

- Six species had significantly lower %P in Florida Bay than in one or more of the other segments.

- Five species (*Dictyota cervicornis*, *Halimeda incrassata, Halimeda opuntia, Laurencia poiteaui*, and *Penicillus capitatus*) had significantly higher N:P ratios in Florida Bay than in all other segments; two other species (*Laurencia intricata* and *Udotea flabellum*) had significantly higher N:P ratios in Florida Bay than in one or two other segments.

- Eight species (*D. cervicornis* and *L. intricata* were exceptions) had significantly higher C:N ratios in Florida Bay than in one or more of the other segments.

- Three species (*D. cervicornis, H. incrassata, H. opuntia*) had significantly higher C:P ratios in Florida Bay than in all other segments; two other species (*L. poiteaui, P. capitatus*) had significantly higher C:P ratios in Florida Bay than in two other segments.

Thus, an important contribution of this study was substantiating that the nitrogen and phosphorus status of macroalgae in Florida Bay were significantly different than on the ocean side of the Florida Keys.

Comparisons among the four other segments, all on the ocean-side of the Florida Keys, revealed a much more uniform tissue nutrient level. The relatively few differences among these segments were rather species-specific. P composition was generally more variable for a species than was N. When there were differences among these segments, the Biscayne Bay and Upper Keys segments tended to have lower N levels than the Middle and Lower Keys, and the Middle Keys segment tended to have higher P levels than the other segments. There were no consistent patterns among segments in N:P and C:P ratios for the ten species. C:N ratio tended to be lower in the Lower Keys. Based on the comparison of these segments with Florida Bay stations, there was little similarity of macroalgal nutrient status in Florida Bay to stations more proximal to the Bay, and presumably more exposed to Florida Bay influences (i.e., the Middle Keys transect).

As with segments, there was no universal inshore-offshore pattern in internal tissue nutrients. Rather, there was evidence that inshore-offshore patterns were species-specific:

- Four species (*Avrainvillea* sp., *Dictyota cervicornis*, *Halimeda incrassata*, and *Halimeda tuna*) in March and three species (*D. cervicornis*, *H. tuna*, and *Udotea flabellum)* in July did not have any significant inshore-offshore differences.

- Four species (*Halimeda opuntia*, *Laurencia intricata*, *Laurencia poiteaui*, and *Penicillus capitatus*) in March and three of these same species (*H. opuntia*, *L. poiteaui*, and *P. capitatus*) in July had significantly lower P and/or significantly higher C:P ratio inshore. Two species (*Penicillus dumetosus* and *U. flabellum*) in March and one species (*P. dumetosus*) in July had the opposite pattern (i.e., significantly higher P and/or significantly lower C:P ratio inshore).

- Four species (*L. intricata*, *L. poiteaui*, *P. capitatus,* and *U. flabellum*) in March and five species (*H. incrassata*, *L. intricata*, *L. poiteaui*, *P. capitatus,* and *P. dumetosus*) in July had significantly higher N and/or significantly lower C:N ratio inshore. No species in March and only one species (*Avrainvillea* sp.) in July had the opposite pattern (i.e., significantly lower N and/or significantly higher C:N ratio inshore).

- Only one species (*P. capitatus*) in March and two species (*L. poiteaui and P. capitatus*) in July had significantly higher N:P ratios inshore. Only one species (*P. dumetosus*) in March and none in July had the opposite pattern (i.e., significantly lower N:P inshore).

- The only inshore-offshore difference for %C was for *P. capitatus*, which, in both March and July, was significantly higher inshore.

Thus, the most common, but by no means universal, inshore-offshore pattern was higher N and lower P availability inshore. However, limited inshore-offshore differences in N:P ratio suggested that both nutrients were generally readily available in proportional amounts required by the various species.

Temporal Patterns (Seasonality)

Seasonality in macroalgal tissue nutrients was evident in this study, although there was less seasonality than what has been found in more temperate systems (Chapman and Craigie 1977, Hanisak 1979, Gagne et al. 1982, Rosenberg and Ramus 1982, Asare and Harlin 1983, Hardwick-Whitman and Mathieson 1986, Wheeler and Björnsater 1992). Most species in this study had higher %N, and to a lesser extent, higher %P and %C in March than in July, with only one species (*Avrainvillea* sp.) having higher %N or %P in July. These patterns could be due to seasonal changes either in the environment or in algal metabolism. Most likely, these patterns were more a reflection of higher metabolic demands in the summer when macroalgae are growing more rapidly than in the winter. Excess nutrients stored internally during the winter may, in part, support macroalgal growth later in the year.

While there were significant differences in both %N and %P, as well as in some of the elemental ratios, none of the changes would alter the interpretation of whether N or P was limiting macroalgal growth (see below). As mentioned in the previous section, while there were some seasonal changes in inshore-offshore patterns, overall there was relatively little change in overall macroalgal N and P status.

Comparisons of Species

As previously detailed, patterns in N and P composition were species-specific. There were considerable differences in N and P status among species; the primary cause of these differences was calcification and, to a lesser extent, habit (lithophytic vs. psammophytic). Calcified algae had higher levels of N and lower levels of P than non-calcified species (see Table 3 for calcification and habit status of each species).

The only psammophytic, non-calcified species (*Avrainvillea* sp.) had higher levels of N than the lithophytic, non-calcified species.

Overall Nutrient Status of Macroalgae

An important question addressed by this study was: "Is nitrogen or phosphorus limiting macroalgal growth in the Florida Keys?" This question is better answered when the relationship of algal growth as a function of tissue N and P is known (Hanisak 1983). However, there are no data available that relate the growth of any of these species to tissue nutrients, with one exception (McGlathery et al.1992). In that study, N enrichment, but not P enrichment, increased the *in situ* growth of *Penicillus capitatus* in Bermuda;%N values found in the current study for *P. capitatus* (overall mean = 1.29%, dry weight basis) were similar to those in the unenriched controls in the Bermuda study (1.20%, dry weight basis). %P values found for this species in the Florida Keys (overall mean = 0.048%, dry weight basis) were 41% higher than those in the unenriched Bermuda controls (0.034%, dry weight basis), but N:P ratio in the Florida Keys (overall mean = 64) was only 15% lower than in Bermuda (75). However, the Bermuda study did not determine the relationship of growth as a function of internal N or P concentration.

Comparisons with tissue nutrient data from Jamaica (Lapointe 1997) can also be made, although the relationship with tissue nutrients and growth was not quantified in that study either. The only species in common between the Jamaica study and the Florida Keys study was *Halimeda opuntia* which had very similar %N (means = 0.48% and 0.54%, dry weight basis, respectively for the Florida Keys and Jamaica), %P (means = 0.030% and 0.03%, dry weight basis, respectively, for the Florida Keys and Jamaica), and N:P ratios (means = 38.48 and 39.8, respectively, for the Florida Keys and Jamaica) in the two studies. Comparisons of two species of *Dictyota* (*D. cervicornis* in the Florida Keys study, *D. dichotoma* in the Jamaica study) can also be made. *Dictyota* in the Florida Keys had higher %N (means = 1.24% and 0.89%, dry weight basis, respectively, for the Florida Keys and Jamaica), much higher %P (means = 0.40% and 0.05%, dry weight basis, respectively, for the Florida Keys and Jamaica), and lower N:P ratios (means = 9.44 and 39.4, respectively, for the Florida Keys and Jamaica), which indicates much higher P availability in the Florida Keys than in Jamaica.

Again, without the appropriate experimental manipulation to determine critical internal N and P levels for growth of these species, it is unknown what the "critical" N:P, C:N, or C:P ratios are for any of these species, or to what extent those values might vary among species. Additional problems in interpreting elemental ratios are that ratios can vary as a function of the denominator, numerator, or both and that ratios are more sensitive to absolute changes in the denominator than in the numerator

Given those caveats, a reasonable starting point for approximating a critical N:P ratio would be the Redfield Ratio of 16:1, as well as the mean (35:1) and median (30:1) values given by Atkinson and Smith (1983). N:P ratios below 16 would be considered N-limited and N:P ratios above 35 would be considered P-limited. These criteria suggested that calcified species would be more likely to be P-limited than N-limited, as their overall means ranged from 38.48 for *Halimeda opuntia* to 77.98 for *Udotea flabellum.* In contrast, with one exception (*Dictyota cervicornis*, N:P = 9.44) the means of non-calcified species tightly ranged between 13.34 (*Laurencia poiteaui*) and 16.45 (*Laurencia intricata*), suggesting that these species were only slightly N-limited, or not limited by either N or P (i.e., "balanced growth"). The low N:P ratio of *Dictyota cervicornis* would suggest that it was N-limited.

The mean and median values of Atkinson and Smith (1983) for C:N were 20 and 18, respectively. The mean values for the calcified species in the current study all tightly ranged between 9.22 (*Halimeda tuna*) and 11.42 (*Udotea flabellum*), indicative of excess N being stored by these species (i.e., N was not limiting). With one exception (*Avrainvillea*, C:N = 11.97), the mean values for the non-calcified species ranged between 21.20 (*Laurencia intricata*) and 29.10 (*Dictyota cervicornis*), suggesting mild N-limitation of these species. The relatively low N:P ratio of *Avrainvillea* sp., the only psammophytic, non-calcified species in the study, would suggest that it was not N-limited, perhaps because it was either directly or indirectly utilizing N from the sediments, which would be less accessible to the lithophytic species.

The mean and median values of Atkinson and Smith (1983) for C:P are 700 and 550, respectively. The mean values for the non-calcified species are all considerably below those values, ranging from 168 (*Avrainvillea* sp.) to 349 (both for *Laurencia intricata* and *Laurencia poiteaui*), indicative that excess P was being stored (i.e., P is not limiting to growth). With one exception (*Udotea flabellum*; C:P = 864), the mean values for the calcified species ranged between 405 (*Halimeda opuntia*) and 626 (*Penicillus capitatus*), which would suggest that P availability was adequate for these species. The relatively high C:P ratio of *Udotea flabellum* would suggest that it was P-limited.

Thus, in general, N and P were generally available in sufficient quantities that macroalgal growth was not limiting by either nutrient. Exceptions to this general conclusion were: *Udotea flabellum* was probably P-limited and the growth of lithophytic non-calcified species may have been moderately limited by N. While there is no appropriate information available for these species, if one assumes a critical N level of 2% (dry weight for non-calcified species; CFDW or AFDW for calcified species), which has generally been shown to be the critical internal nitrogen level, including *Gracilaria tikvahiae* from the Indian River Lagoon in Florida (Hanisak 1990), the conclusions concerning N status are supported (*Dictyota cervicornis, Laurencia intricata*, and *Laurencia poiteaui* were the only species with %N lower than 2%). Extrapolation from other studies for P is even more problematical, due to limited previous research; if one uses the 0.07% value found by Lewis and Hanisak (1996) for *Gracilaria* sp., again from the Indian River Lagoon, then all species in this study had excess P in their tissues (i.e., P was not limiting growth).

Future Research and Monitoring

This study demonstrated that tissue analyses of benthic macroalgae can be used to assess N and P status in the Florida Keys. The data collected can be used in nutrient budgets and models of nutrient flux. These data comprise a strong baseline for measurements of long-term change in macroalgal tissue nutrients in the Florida Keys, as part of assessments of future changes in this important ecosystem.

It might be desirable to incorporate macroalgal tissue nutrients into resource-oriented water quality standards (biocriteria), as part of the Sanctuary's longer term monitoring plans. Based on the current study, it would probably be best to do a single extensive sampling during the late summer (August-September), when macroalgal standing crop is usually maximal, and nutrient status is likely to be most critical. Given the complexities of nutrient sources, algal nutrition, and distribution, multi-species assessments of nutrient status are recommended.

Provisionally recommended for this purpose is *Halimeda incrassata*, which is widespread through the Florida Keys, readily identifiable, and indicative of calcareous green algae which are probably the most widespread and abundant macroalgae in the Florida Keys. It would also be desirable to monitor one or two lithophytic species. Their utility is limited to hard-bottom habitats, but those habitats are the ones generally considered to be most critical in need of study and protection. Two lithophytic species are recommended: *Dictyota cervicornis* and *Laurencia poiteaui*, which are generally fairly recognizable and are usually the most readily collectable species of their respective genera. Monitoring of these three indicator species, either as natural populations or transplants, would be helpful to sanctuary managers interested in long-term changes and/or in determining the impacts of specific nutrient loadings.

Further research is required to determine if these conclusions based on the current state of knowledge can be substantiated. Better understanding of macroalgal growth as a function of nutrients and other environmental factors is needed for major species in the Florida Keys. What is particularly required is careful, methodical studies that examine the relationship of algal growth for the dominant species as a function of internal tissue nutrient status. Such studies should be conducted under carefully controlled laboratory studies and verified by *in situ* manipulative experiments. More research is also required to determine the impacts of nutrient enrichments on macroalgal community structure.

6.0 Acknowledgments

Primary funding for the support of this project was provided by the South Florida Water Management District, in support of EPA's Florida Keys National Marine Sanctuary Water Quality Protection Program. Additional support was provided by NOAA's Coastal Ocean Program via the project "Human-Environment Linkages in the South Florida Coastal Ecosystem: Effects of Natural and Anthropogenic Stressors" (University of Miami, RSMAS, primary contractor).

Valuable contributions to this project were made by: Laura Overdorf, Bida Chen, Patrick Monaghan, Marty Ripa, and Stephanie Hanisak who assisted in the field sampling, sampling processing, phosphorus analyses, data entry, and/or report graphics; Captain Dave Ward, who, as Captain of the *RV Magic*, provided tremendous boat and logistic support; Steve Miller, who generously provided both dorm and lab space at NURC-UNCW's Florida Keys Laboratory in Key Largo and advice on various aspects of this study; MSI Analytical, who performed the CHN analyses; and project managers, Bill Kruczynski (EPA) and Susan Olson (South Florida Water Management District), who provided support and patience.

Without the collective help of all of these people, this project could not have been completed, or probably even attempted.

7.0 References Cited

Asare, S.O. and M.M. Harlin. 1983. Seasonal fluctuations in tissue nitrogen for five species of perennial macroalgae in Rhode Island Sound. J. Phycol. 19:254-257.

Atkinson, M.J. 1988. Are coral reefs nutrient-limited? Proc. 6th Int. Coral Reef Symposium 1:157-166.

Atkinson, M.J. and S.V. Smith. 1983. C:N:P ratios of benthic marine plants. Limnol. Oceanogr. 28:568-574.

Bach, S.D. and M.N. Josselyn. 1979. Production and biomass of *Cladophora prolifera* (Chlorophyta, Cladophorales) in Bermuda. Bot. Mar. 22:163-168.

Bell, P.R.F. 1991. Status of eutrophication in the Great Barrier Reef Lagoon. Mar. Poll. Bull. 23:89-93.

Birch, P.B., D.M. Gordon, and A.J. McComb. 1981. Nitrogen and phosphorus nutrition of *Cladophora* in the Peel-Harvey estuarine system, Western Australia. Bot. Mar. 24:381-387.

Birkland, C. 1988. Geographic comparisons of coral-reef community processes. Proc. 6th Int. Coral Reef Symp. 1:211-220.

Boesch, D.F., J.M. Caffrey, J.E. Cloern, C.F. D'Elia, D.M. DiToro, and W.W. Walker, Jr. 1996. Florida Bay Nutrients: Perspectives on the July 1-2, 1996 Workshop. Report of the Florida Bay Science Oversight Panel *Ad Hoc* Committee on Nutrients. Submitted to the Program Management Committee, Florida Bay Research Program. 18 pp.

Caputo, P. 1992. New York Times Magazine. December 6th issue.

Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecol. Monogr. 56:345-363.

Chapman, A.R.O. and J.S. Craigie. 1977. Seasonal growth in *Laminaria longicruris:* Relations with dissolved inorganic nutrients and internal reserves of nitrogen. Mar. Biol. 40:197-205.

D'Elia, C.F., R.W. Buddemeier, and S.V. Smith. 1991. Workshop on coral bleaching, coral reef ecosystems and global change: Report of Proceedings. Maryland Seagrant Publication UM-SG-TS-91-03.

D'Elia, C.F., J.G. Sanders, and W.R. Boynton. 1986. Nutrient enrichment studies in a coastal plain estuary: Phytoplankton growth in large-scale, continuous cultures. Can. J. Fish. Aquat. Sci. 43:397-406.

Environmental Protection Agency. 1991. Water quality protection program for the Florida Keys National Marine Sanctuary Program, Phase 1 Report. Prepared by Continental Shelf Associates, Inc. for Battelle Ocean Services.

Fishelson, L. 1973. Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. Oecologia 12:55-67.

Fourqurean, J.W., J.C. Zieman, and G.V.N. Powell 1991. Phosphorus limitation of primary production in Florida Bay: evidence from the C:N:P ratios of the dominant seagrass *Thalassia testudinum.* Limnol. and Oceanogr. 37:162-171.

Gagne, J.A., K.H. Mann, and A.R.O. Chapman. 1982. Seasonal patterns of growth and storage in *Laminaria longicruris* in relation to differing patterns of availability of nitrogen in the water. Mar. Biol. 69:91-101.

Ginsberg, R.N. and E.A. Shinn. 1964. Distribution of the reef-building community in Florida and the Bahamas. Am. Assoc. Petrol. Geol. Bull. 48:527.

Gordon, D.M., P.B. Birch, and A.J. McComb. 1981. Effects of inorganic phosphorus and nitrogen on the growth of an estuarine *Cladophora* in culture. Bot. Mar. 24:93-106.

Hanisak, M.D. 1979. Nitrogen limitation of *Codium fragile* ssp. *tomentosoides* as determined by tissue analysis. Mar. Biol. 50:333-337.

Hanisak, M.D. 1983. The nitrogen relationships of marine algae. Pp. 699-728 in E.J. Carpenter and D.G. Capone (eds.), Nitrogen in the Marine Environment. Academic Press, New York.

Hanisak, M.D. 1990. The use of *Gracilaria tikvahiae* as a model system to understand the nitrogen nutrition of cultured seaweeds. Hydrobiologia 204/205:79-87.

Hardwick-Witman, M.N. and A.C. Mathieson. 1986. Tissue nitrogen and carbon variations in New England estuarine *Ascophyllum nodosum* (L.) Le Jolis populations (Fucales, Phaeophyta). Estuaries 9:43-48.

Hatcher, B.G. 1984. A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. Coral Reefs 3:199-204.

Hatcher, B.G. 1990. Coral reef primary productivity: A hierarchy of pattern and process. Trends Ecol. Evol. 5:149-155.

Hay, M.E. 1981. Herbivory, algal distribution and the maintenance of between-habitat diversity on a tropical fringing reef. Am. Nat. 118:520-540.

Hay, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: Are previous results typical? Ecol. 65:446-454.

Hughes, T.P., D.C. Reed, and M. Boyle. 1987. Herbivory on coral reefs: Community structure following mass mortalities of sea urchin. J. Exp. Mar. Biol. Ecol. 113:39-59.

Johannes, R.E., W.J. Wiebe, C.J. Crossland, D.W. Rimmer, and S.V. Smith. 1983. Latitudinal limits of coral reef growth. Mar. Ecol. Prog. Ser. 11:105-111.

Keating, D. 1991. Pollution killing coral reef, biologist says. Miami Herald. 13 March.

Kinsey, D.W. 1991. The Coral Reef: an owner-built, high-density, fully-serviced, self-sufficient housing estate in the desert -- or is it? Symbiosis 10:1-22.

Lapointe, B.E. 1987. Phosphorus- and nitrogen-limited photosynthesis and growth of *Gracilaria tikvahiae* (Rhodophyceae) in the Florida Keys: An experimental field study. Mar. Biol. 93:561-568.

Lapointe, B.E. 1989a. Caribbean coral reefs: Are they becoming algal reefs? Sea Frontiers (March-April) 83:83-91.

Lapointe, B.E. 1989b. Macroalgal production and nutrient relations in oligotrophic areas of Florida Bay. Bull. Mar. Sci. 44:312-323.

Lapointe, B.E. and M. D. Hanisak. 1997. Algal Blooms in Coastal Waters: Eutrophication on Coral Reefs of Southeast Florida. Final Report submitted to Florida Sea Grant. Project R/C-E-34. 23 pp., plus tables and figures.

Lapointe, B.E., M.M. Littler, and D.S. Littler. 1987. A comparison of nutrient-limited productivity in macroalgae from a Caribbean barrier reef and from a mangrove ecosystem. Aquat. Bot. 28:243-255.

Lapointe, B.E. and J.D. O'Connell. 1989. Nutrient-enhanced growth of *Cladophora prolifera* in Harrington Sound, Bermuda: Eutrophication of a confined, phosphorus-limited marine ecosystem. Est. Coast. Shelf Sci. 28:347-360.

Lapointe, B.E., J.D. O'Connell, and G.S. Garrett. 1990. Effects of on-site sewage disposal systems on nutrient relations of groundwaters and nearshore surface waters of the Florida Keys. Biogeochemistry 10:289-307.

Lapointe, B.E., M.M. Littler, and D.S. Littler. 1992a. N:P availability in siliciclastic versus carbonate-rich waters. Estuaries 15:76-83.

Lapointe, B.E., N.P. Smith, P.A. Pitts, and M.W. Clark. 1992b. Baseline characterization of chemical and hydrogeographic processes in the water column of Looe Key National Marine Sanctuary. Final Report to NOAA's Office of Ocean and Coastal Resource Management, NA86AA-H-CZ071. 65 pp.

Lewis, R.J. and M.D. Hanisak. 1996. Effects of phosphate and nitrate supply on productivity, agar content and physical properties of agar of *Gracilaria* strain G-16S. J. Appl. Phycol. 8:41-49.

Lewis, S.M. 1986. The role of herbivorous fish in the organization of a Caribbean reef community. Ecol. Monogr. 56:183-200.

Littler, M.M. and D.S. Littler. 1984. Models of tropical reef biogenesis: The contribution of algae. Progress in Phycological Research 3:323-364.

Littler, M.M., P.R. Taylor, and D.S. Littler. 1989. Complex interactions in the control of coral zonation on a Caribbean reef flat. Oecologia 80:33-340.

Maragos, J.E., C. Evans, and P. Holthus, 1985. Reef corals in Kaneohe Bay six years before and after termination of sewage discharges (Oahu, Hawaii). Proc. Fifth Coral Reef Congress 4:189-194.

McComb, A.J., R.P. Atkins, P.B. Birsh, D.M. Gordon, and R.J. Lukatelich. 1981. Eutrophication in the Peel Harvey estuarine system, Western Australia. Pp. 323-342 in B.J. Nielson and L.E. Cronin (eds.), Estuaries and Nutrients. Jumana Press, Clifton, NJ.

McGlathery, K.J., R.W. Howarth, and R. Marino. 1992. Nutrient limitation of the macroalga, *Penicillus capitatus*, associated with subtropical seagrass meadows in Bermuda. Estuaries 15:18-25.

Miller, J.W. 1988. Results of a workshop on coral reef research and management in the Florida Keys. A blueprint for action. National Undersea Research Program Research Report 88-5. 49p.

Miller, S.L. 1992. Florida Keys Nutrient Workshop: June 1991. Sponsored by NOAA's National Undersea Research Center at the University of North Carolina, Wilmington.

Morrison, D. 1988. Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 68:1367-1382.

Ogden, J.C. 1990. Sustained ecological research related to management of the Florida Keys seascape (SEAKEYS). First year report, submitted to The John D. and Catherine T. MacArthur Foundation, World Environment and Resources Program.

Pastorok, R.A. and G.R. Bilyard. 1985. Effects of sewage pollution on coral reef communities. Mar. Ecol. Prog. Ser. 21:175-189.

Redfield, A.C. 1958. The biological control of chemical factors in the environment. Am. Sci. 46:561-600.

Rosenberg, G. and J. Ramus. 1982. Ecological growth strategies in the seaweeds *Gracilaria tikvahiae* (Rhodophyta) and *Ulva* sp. (Chlorophyceae): Soluble nitrogen and reserve carbohydrates. Mar. Biol. 66:251-259.

SAS Institute. 1988. SAS/STAT User's Guide, Release 6.03 Edition. SAS Institute, Inc., Cary, NC. 1028 pp.

Schramm, W. and W. Booth. 1981. Mass bloom of the algal *Cladophora prolifera* in Bermuda: Productivity and phosphorus accumulation. Bot. Mar. 24:419-426.

Scott, F.J. and G.R. Russ. 1987. Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. Mar. Ecol. Prog. Ser. 39:293-304.

Smith, S.V. 1984. Phosphorus versus nitrogen limitation in the marine environment. Limnol. Oceanogr. 29:1149-1160.

Short, F.T. 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. Aquat. Bot. 27:41-57.

Solórzano, L. and J.H. Sharp. 1980. Determination of total dissolved phosphorus and particulate phosphorus in nature waters. Limnol. Oceanogr. 25:754-758.

Strickland, J.D.H. and T.R. Parsons. 1972. A Practical Handbook of Seawater Analysis. Fisheries Research Board of Canada, Ottawa. 310 pp.

Torrance, D.C. 1991. Deep ecology: Rescuing Florida's reefs. Nature Conservancy, Jul-Aug:9-17.

Ward, F. 1990. Florida coral reefs are imperiled. Natl. Geograph. (July):115-132.

Wheeler, P.A. and B.R. Björnsäter. 1992. Seasonal fluctuations in tissue nitrogen, phosphorus, and N:P for five macroalgal species common to the Pacific Northwest Coast. J. Phycol. 28:1-6.

Williams, S.L. and R.C. Carpenter. 1988. Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum*. Mar. Ecol. Prog. Ser. 47:145-152.

8.0 Tables

Table 1 List of segments, transects, and station locations (DGPS) for algal tissue nutrients sampling. Segment codes and transect codes are in parentheses.

Segment	Transect	Station	Latitude	Longitude
Biscayne Bay (BB)	Fowey Rocks (FR)	FR1	25 35.256	80 09.184
		FR2	25 35.371	80 08.602
		FR3	25 35.273	80 06.772
		FR4	25 35.076	80 06.658
		FR5	25 35.456	80 05.906
		FR6	25 35.395	80 05.693
Biscayne Bay (BB)	Triumph Reef (TR)	TR1	25 28.816	80 10.293
		TR2	25 28.691	80 09.207
		TR3	25 28.994	80 08.478
		TR4	25 28.530	80 07.498
		TR5	25 28.718	80 06.835
		TR6	25 28.344	80 06.699
Biscayne Bay (BB)	Pacific Reef (PA)	PA1	25 23.728	80 12.928
		PA2	25 23.259	80 11.757
		PA3	25 22.899	80 10.698
		PA4	25 22.516	80 09.211
		PA5	25 22.300	80 08.626
		PA6	25 22.179	80 08.368
Upper Keys (UK)	Carysfort Reef (CF)	CF1	25 14.747	80 17.844
		CF2	25 14.289	80 17.004
		CF3	25 14.398	80 15.381
		CF4	25 14.162	80 14.706
		CF5	25 13.468	80 12.860
		CF6	25 13.284	80 12.607

Table 1 (Continued)

Segment	Transect	Station	Latitude	Longitude
Upper Keys (UK)	Elbow Reef (EL)	EL1	25 08.858	80 21.198
		EL2	25 08.271	80 20.139
		EL3	25 08.841	80 17.574
		EL4	25 08.905	80 16.503
		EL5	25 08.882	80 15.644
		EL6	25 08.626	80 15.435
Upper Keys (UK)	Pickles Reef (PI)	PI1	25 00.246	80 28.938
		PI2	25 00.096	80 28.493
		PI3	25 00.587	80 27.502
		PI4	25 00.000	80 26.213
		PI5	24 59.466	80 25.056
		PI6	24 59.152	80 24.916
Middle Keys (MK)	Crocker Reef (CR)	CR1	24 55.679	80 35.457
		CR2	24 55.809	80 33.979
		CR3	24 56.086	80 32.974
		CR4	24 55.412	80 32.426
		CR5	24 54.756	80 31.897
		CR6	24 54.555	80 31.495
Middle Keys (MK)	Long Key (LK)	LK1	24 49.393	80 45.608
		LK2	24 48.676	80 44.555
		LK3	24 48.186	80 43.916
		LK4	24 47.708	80 43.091
		LK5	24 47.310	80 42.530

Table 1 (Continued)

Segment	Transect	Station	Latitude	Longitude
Middle Keys (MK)	Tennessee Reef (TN)	TN1	24 47.348	80 51.811
		TN2	24 46.457	80 51.638
		TN3	24 45.498	80 51.548
		TN4	24 45.119	80 49.369
		TN5	24 44.784	80 47.139
Lower Keys (LK)	Sombrero Reef (SR)	SR1	24 41.611	81 09.253
		SR2	24 41.058	81 08.948
		SR3	24 39.136	81 07.754
		SR4	24 38.162	81 07.464
		SR5	24 37.744	81 06.790
		SR6	24 37.523	81 06.714
Lower Keys (LK)	Looe Key (LO)	LO1	24 37.558	81 25.068
		LO2	24 36.700	81 24.850
		LO3	24 35.150	81 24.700
		LO4	24 33.821	81 24.582
		LO5	24 33.200	81 24.450
		LO6	24 32.703	81 24.608
Lower Keys (LK)	Sand Key (SK)	SK1	24 31.180	81 53.300
		SK2	24 30.560	81 53.300
		SK3	24 28.926	81 52.879
		SK4	24 27.642	81 52.841
		SK5	24 27.518	81 52.764
		SK6	24 27.102	81 52.818

Table 1 (Continued)

Segment	Transect	Station	Latitude	Longitude
Florida Bay	Florida Bay (FB)	FB1	25 01.357	80 32.090
		FB2	25 01.011	80 32.800
		FB3	24 58.179	80 37.242
		FB4	24 57.387	80 38.415
		FB5	24 51.045	80 47.740
		FB6	24 53.103	80 45.870
		FB7	24 49.088	80 52.240
		FB8	24 48.599	80 55.222
		FB9	24 49.008	81 08.828
		FB10	24 45.196	81 10.228

Table 2 Analytical Measurements

Parameter	Instrument	Method	Precision (% RSD) (a)	Accuracy (%)
Tissue Carbon	Control Equipment Corp. Model 240ZA	(b)	5	95-105
	Leeman Labs Model CE440			
Tissue Nitrogen	Control Equipment Corp. Model 240ZA	(b)	5	95-105
	Leeman Labs Model CE440			
Tissue Phosphorus	Beckman DU-64 Spectrophotometer	(c)	5	95-105

(a) QA targets for precision and accuracy determined from in-house, historical data

(b) Modified Pregl-Dumas technique, high temperature combustion

(c) Modified Solórzano and Sharp (1980) technique, as described by Fourqurean et al. (1992)

Table 3 List of species, with taxonomic, habit (L = lithophytic, P = psammophytic), and calcification information (C = calcified, NC = not calcified), and species codes, used in Figures 199-207.

Species	Algal Division	Habit	Calcification	Species CodeL
Avrainvillea sp.	Chlorophyta	P	NC	Avr
Dictyota cervicornis	Phaeophyta	L	NC	Diccer
Halimeda incrassata	Chlorophyta	P	C	Halinc
Halimeda opuntia	Chlorophyta	P, L	C	Halopu
Halimeda tuna	Chlorophyta	L	C	Haltun
Laurencia intricata	Rhodophyta	L	NC	Lauint
Laurencia poiteaui	Rhodophyta	L	NC	Laupoi
Penicillus capitatus	Chlorophyta	P	C	Pencap
Penicillus dumetosus	Chlorophyta	P	C	Pendum
Udotea flabellum	Chlorophyta	P	C	Udofla

9.0 Figures

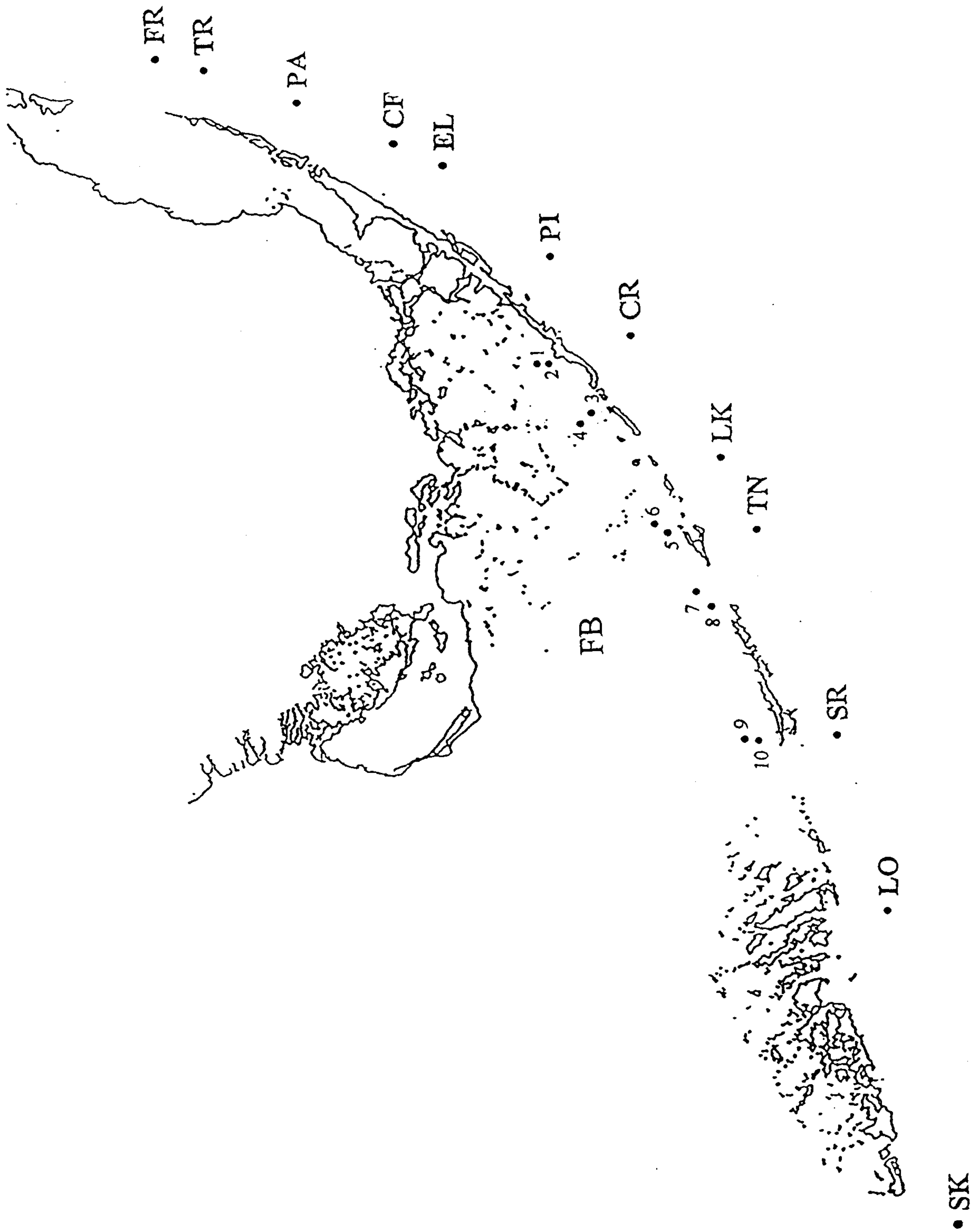

Fig. 1 Chart of the Florida Keys, with sampling stations for 12 inshore-offshore transects and 10 Florida Bay stations. Each transect is labeled with the transect code, at the reef station. Each Florida Bay (FB) station is labeled with a number. See Table 1 for complete listing of stations and DGPS coordinates.

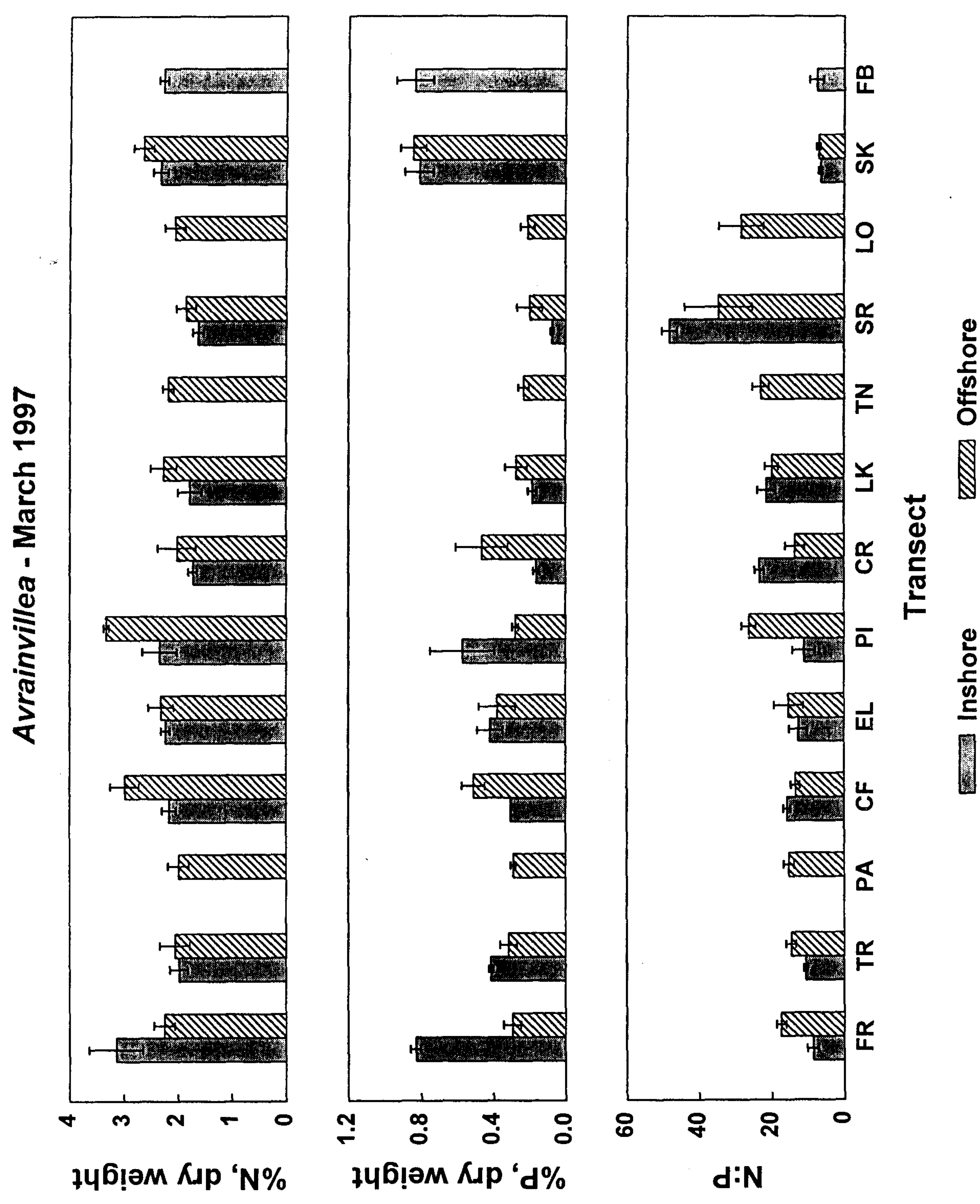

Fig. 2 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Avrainvillea* sp., March 1997.

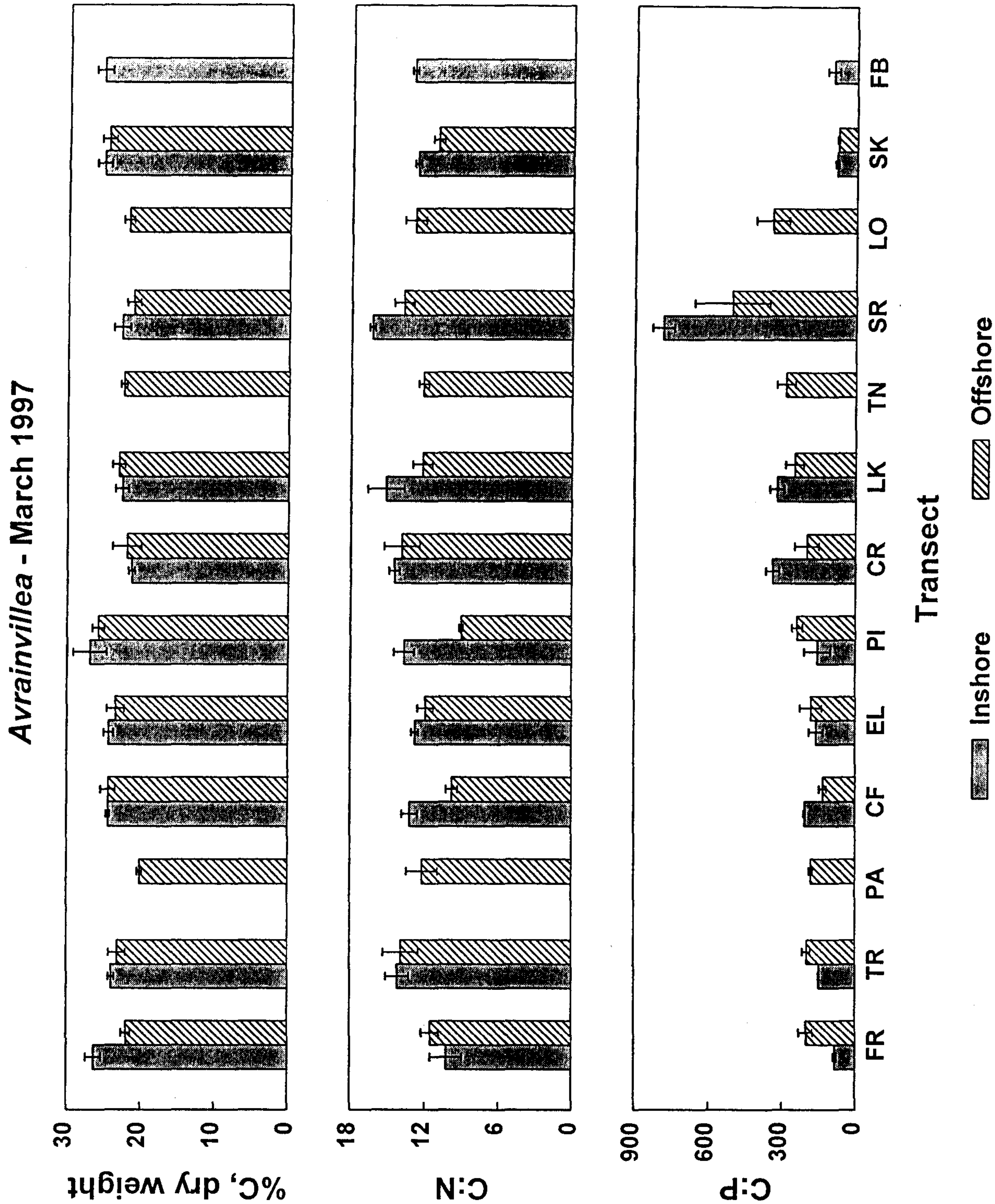

Fig. 3 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Avrainvillea* sp., March 1997.

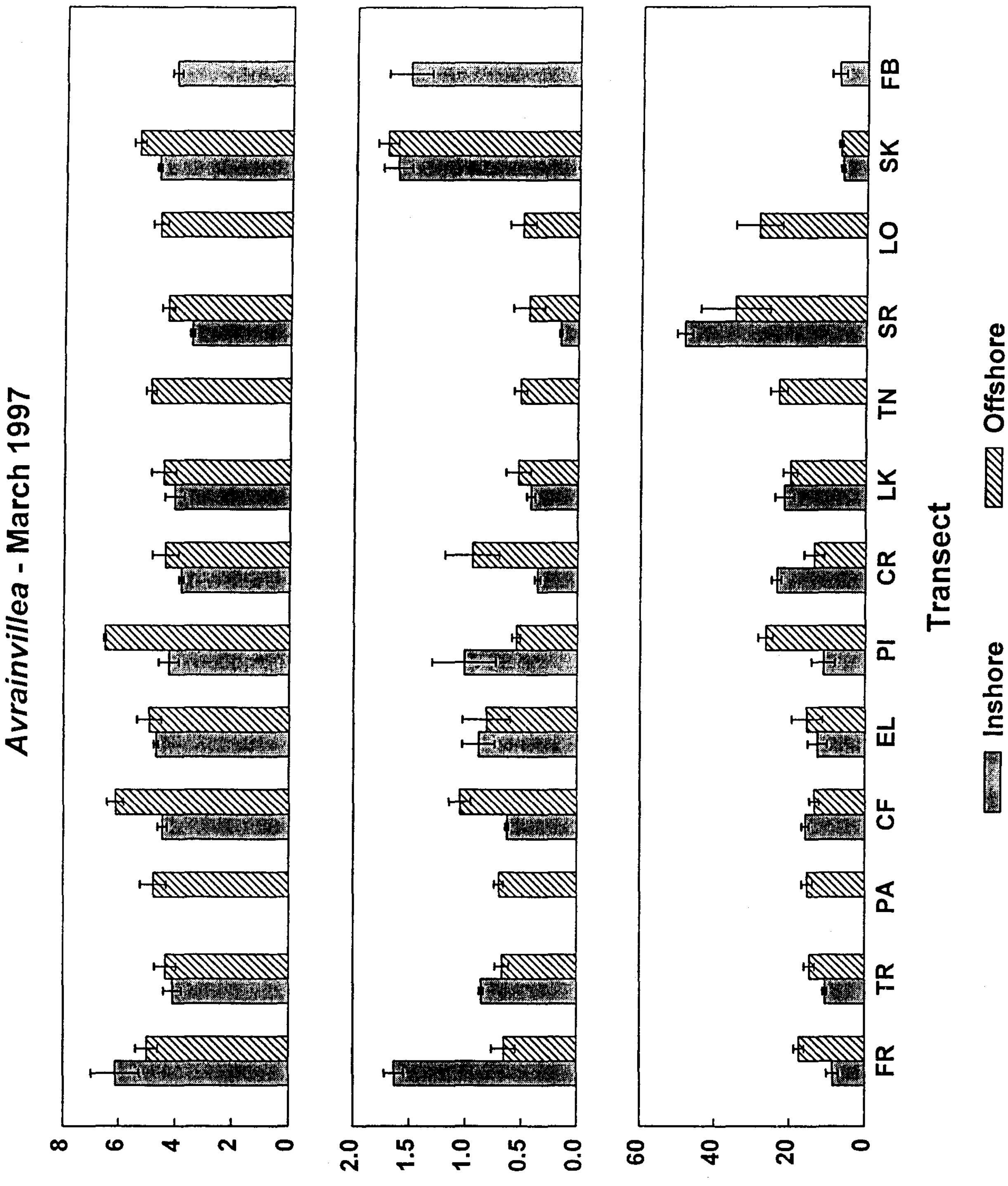

Fig. 4 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Avrainvillea* sp., March 1997.

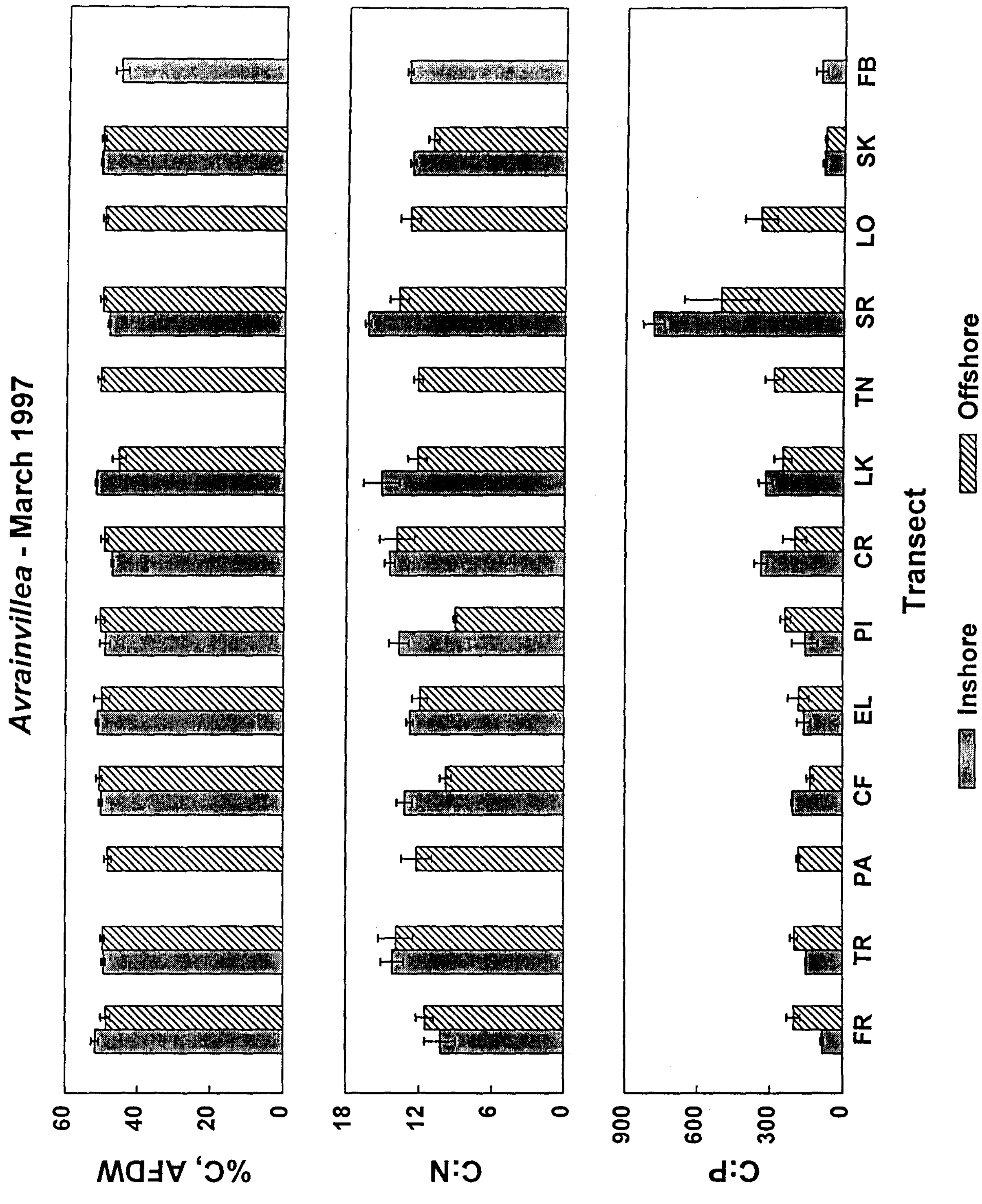

Fig. 5 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Avrainvillea* sp., March 1997.

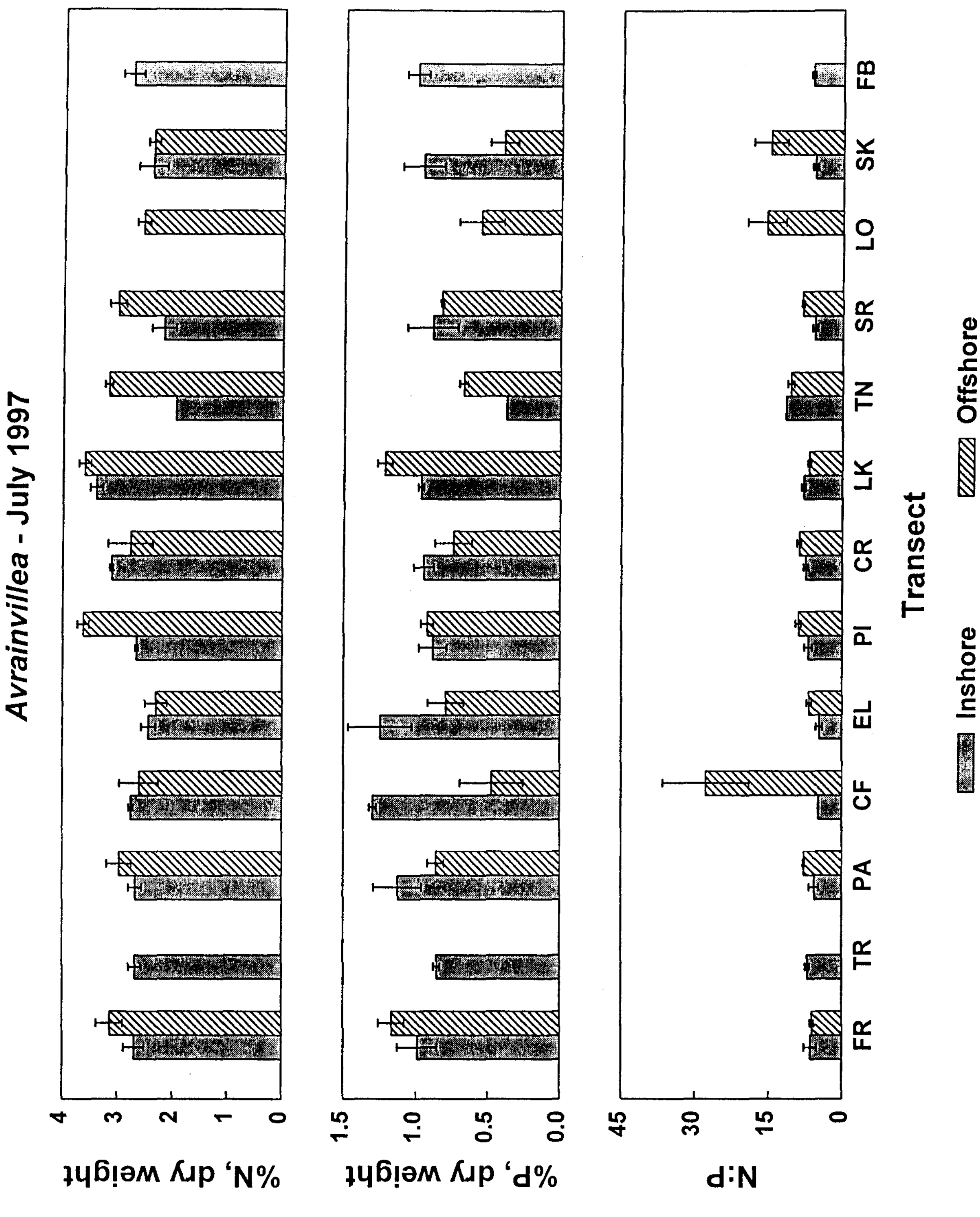

Fig. 6 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Avrainvillea* sp., July 1997.

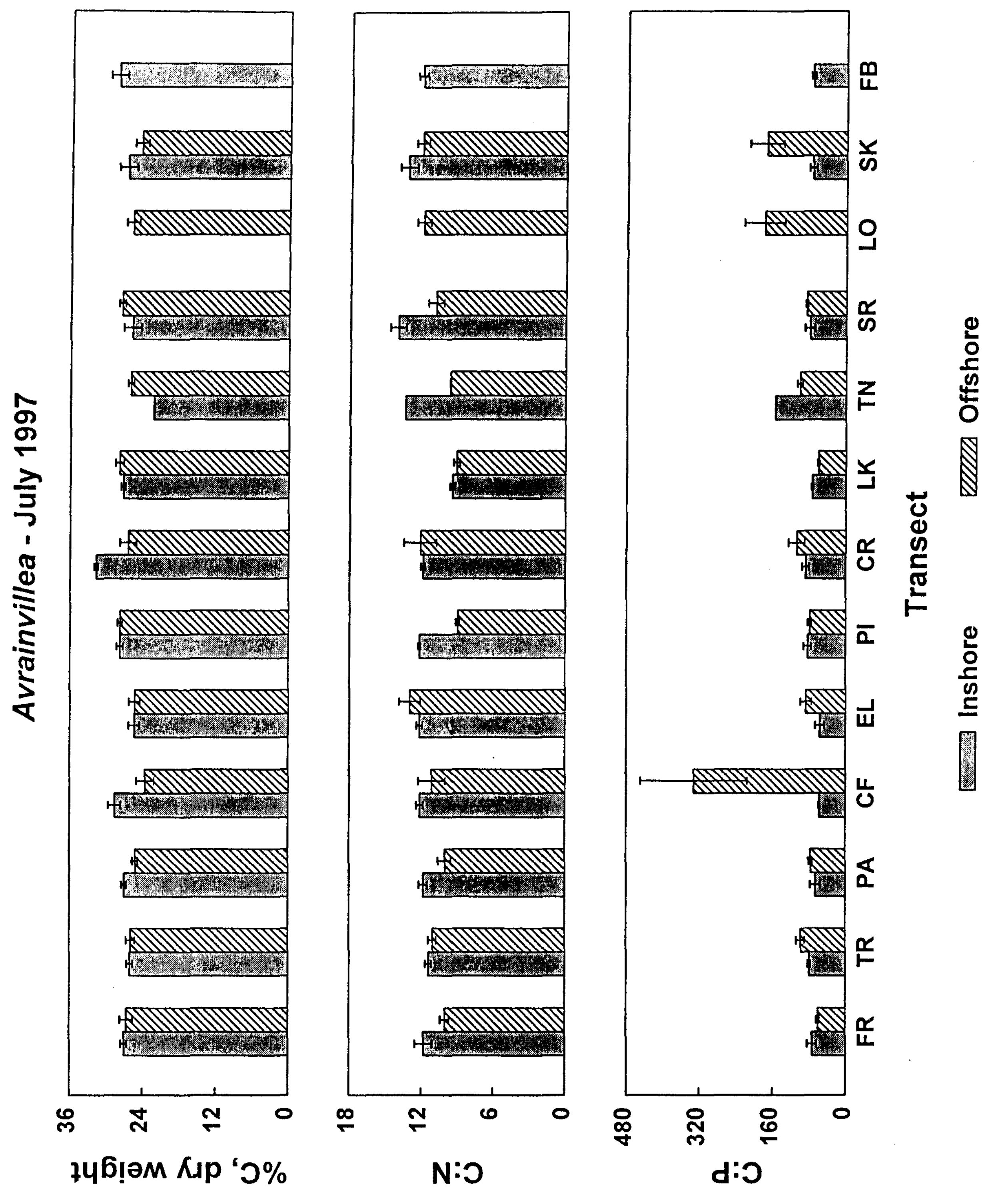

Fig. 7 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Avrainvillea* sp., July 1997.

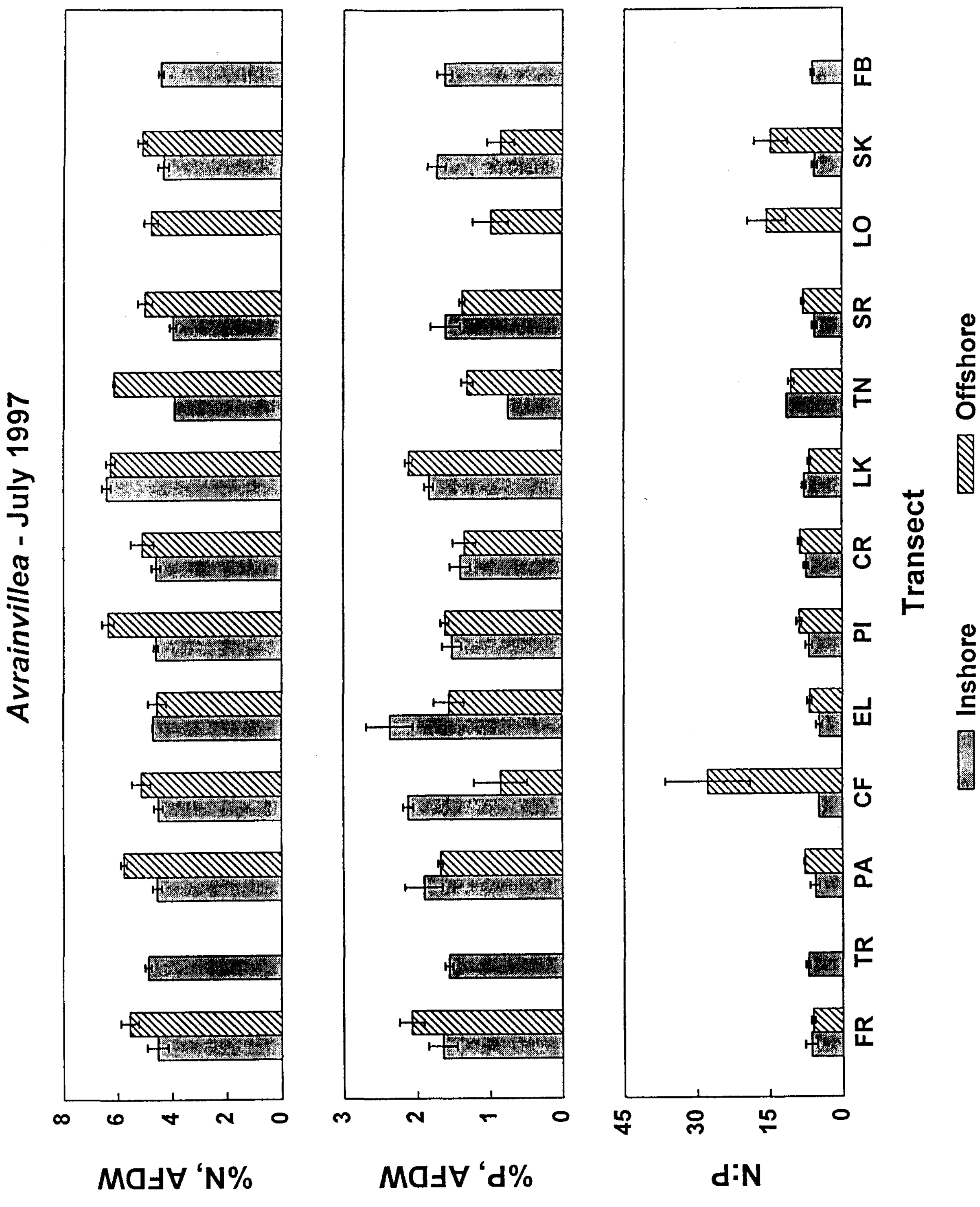

Fig. 8 **Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free, dry weight basis (AFDW), for inshore and offshore samples of *Avrainvillea* sp., July 1997.**

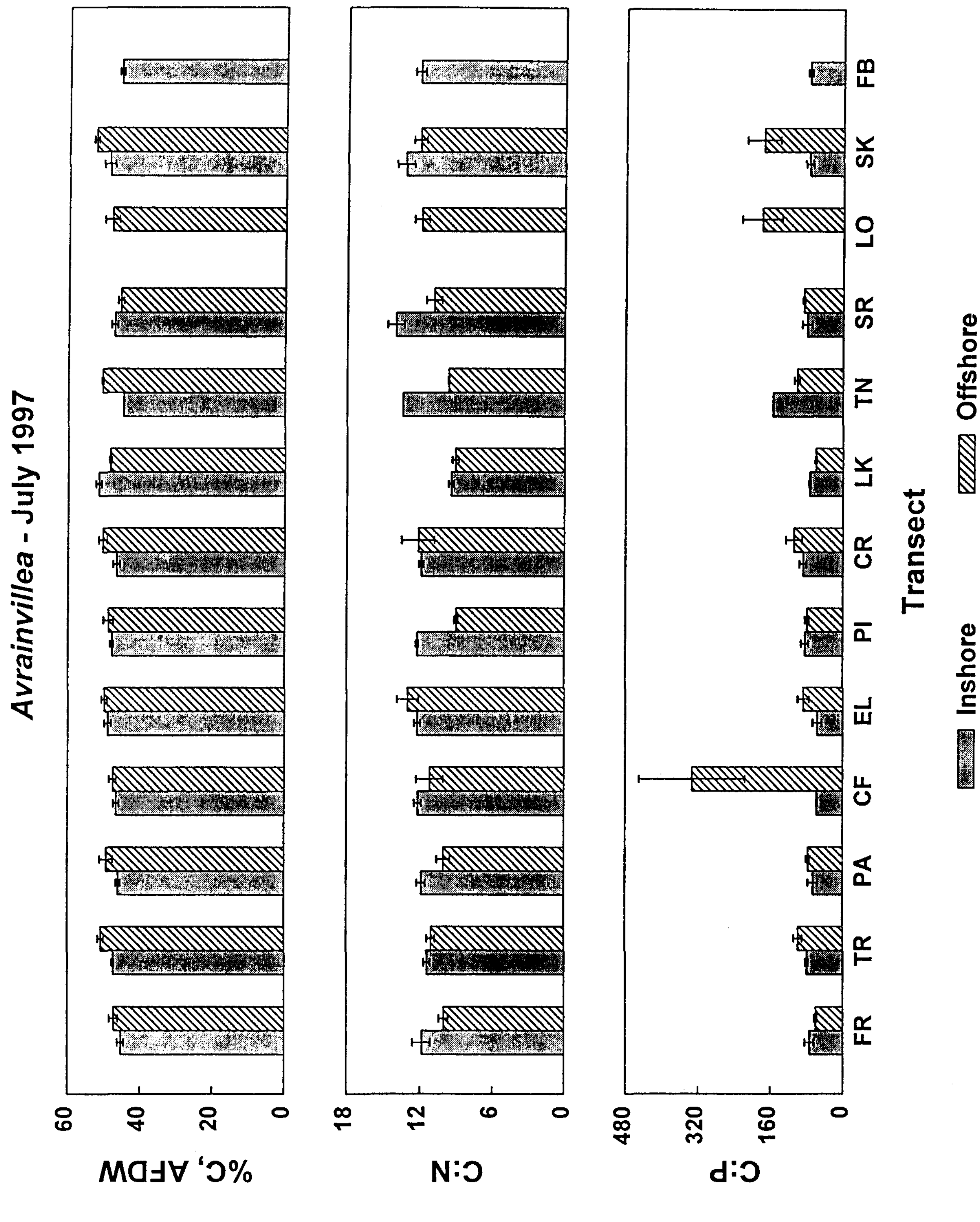

Fig. 9 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Avrainvillea* sp., July 1997.

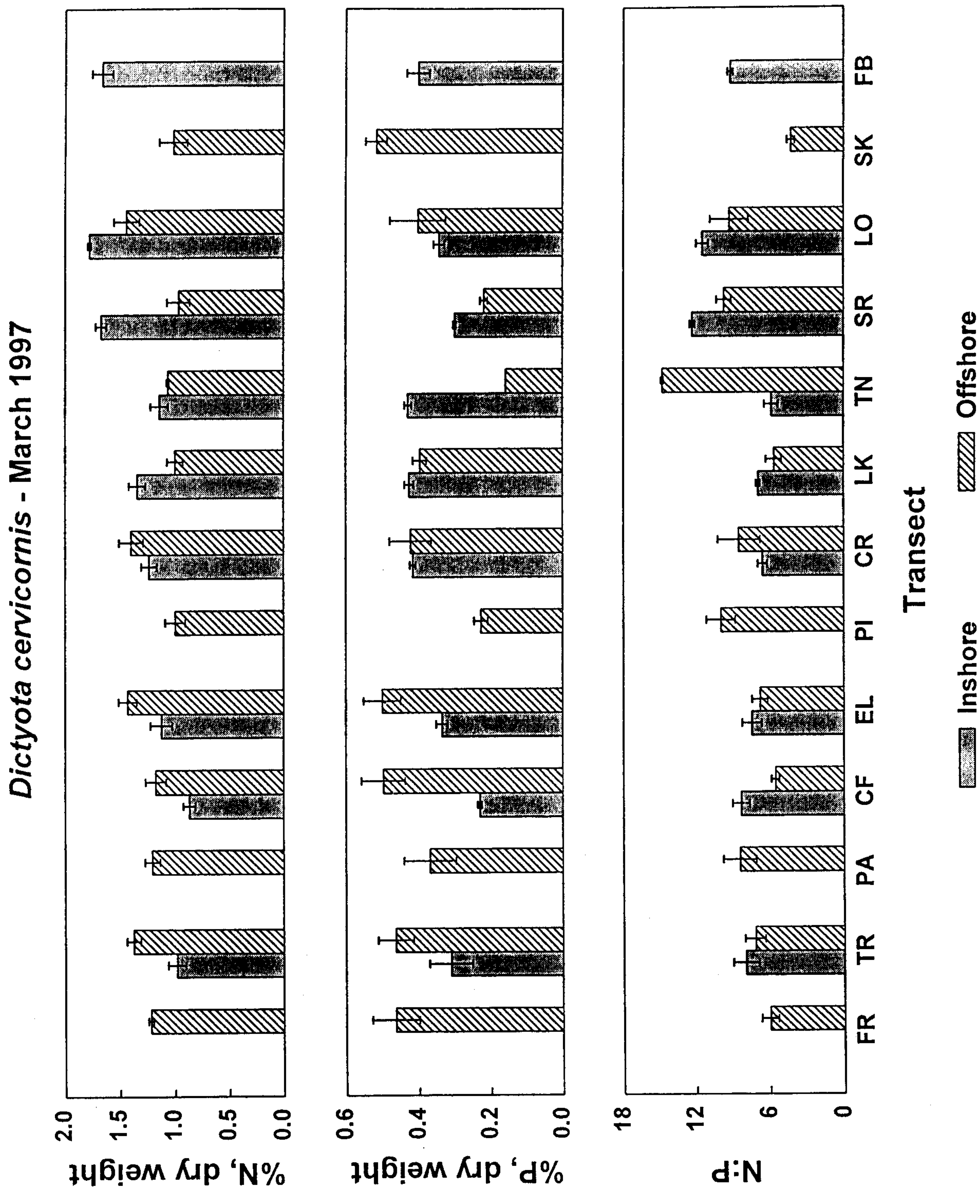

Fig. 10 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Dictyota cervicornis*, March 1997.

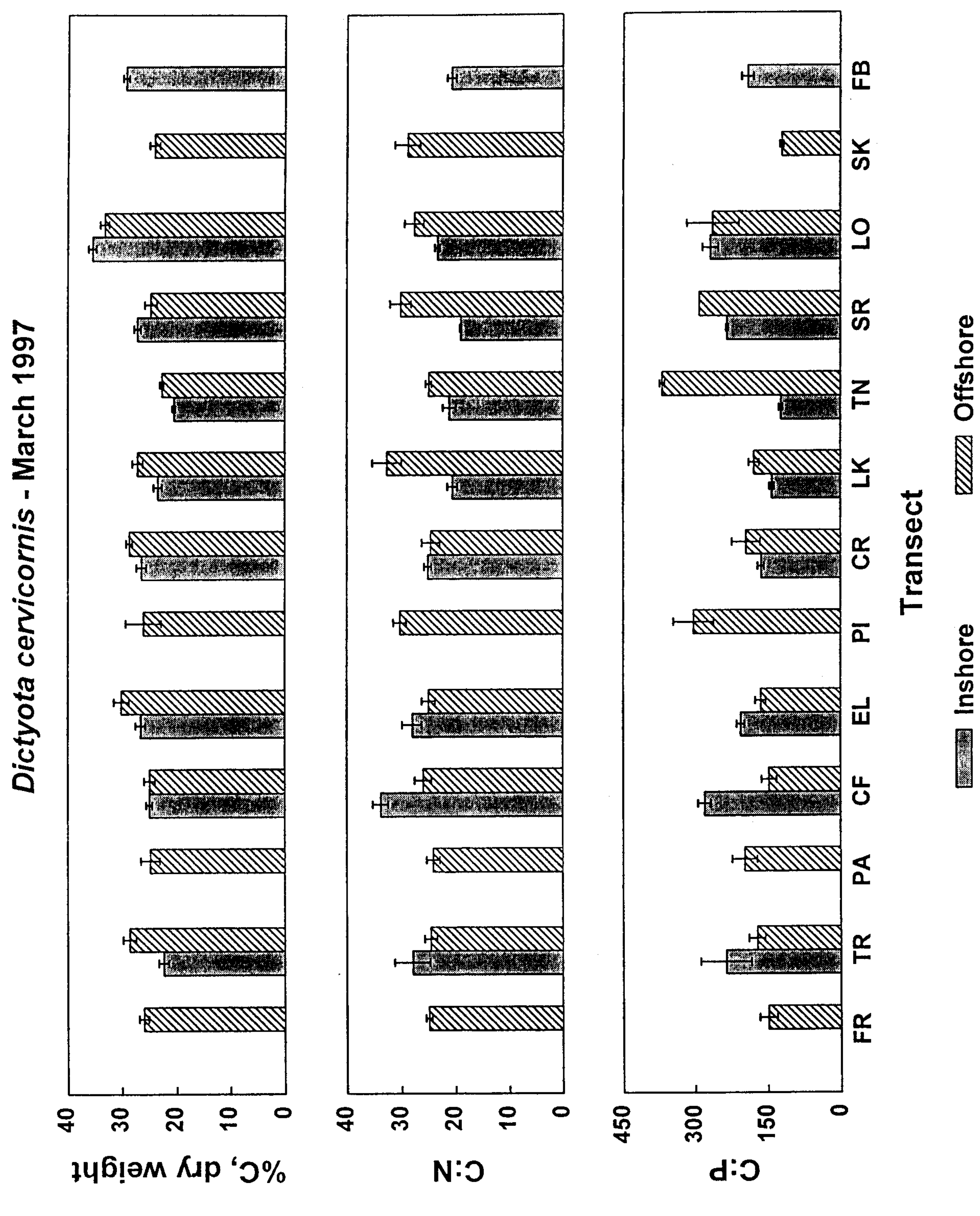

Fig. 11 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Dictyota cervicornis*, March 1997.

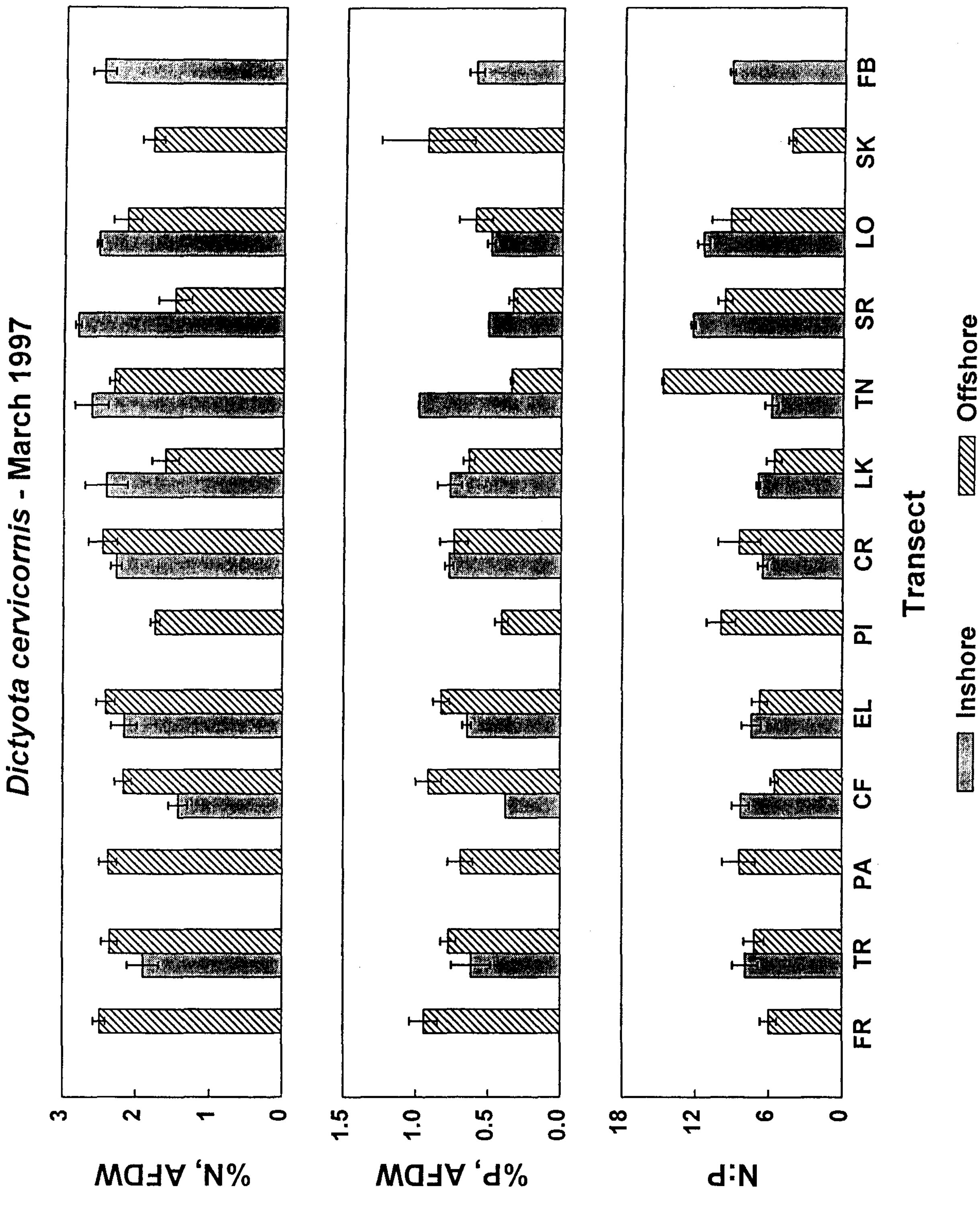

Fig. 12 **Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Dictyota cervicornis*, March 1997.**

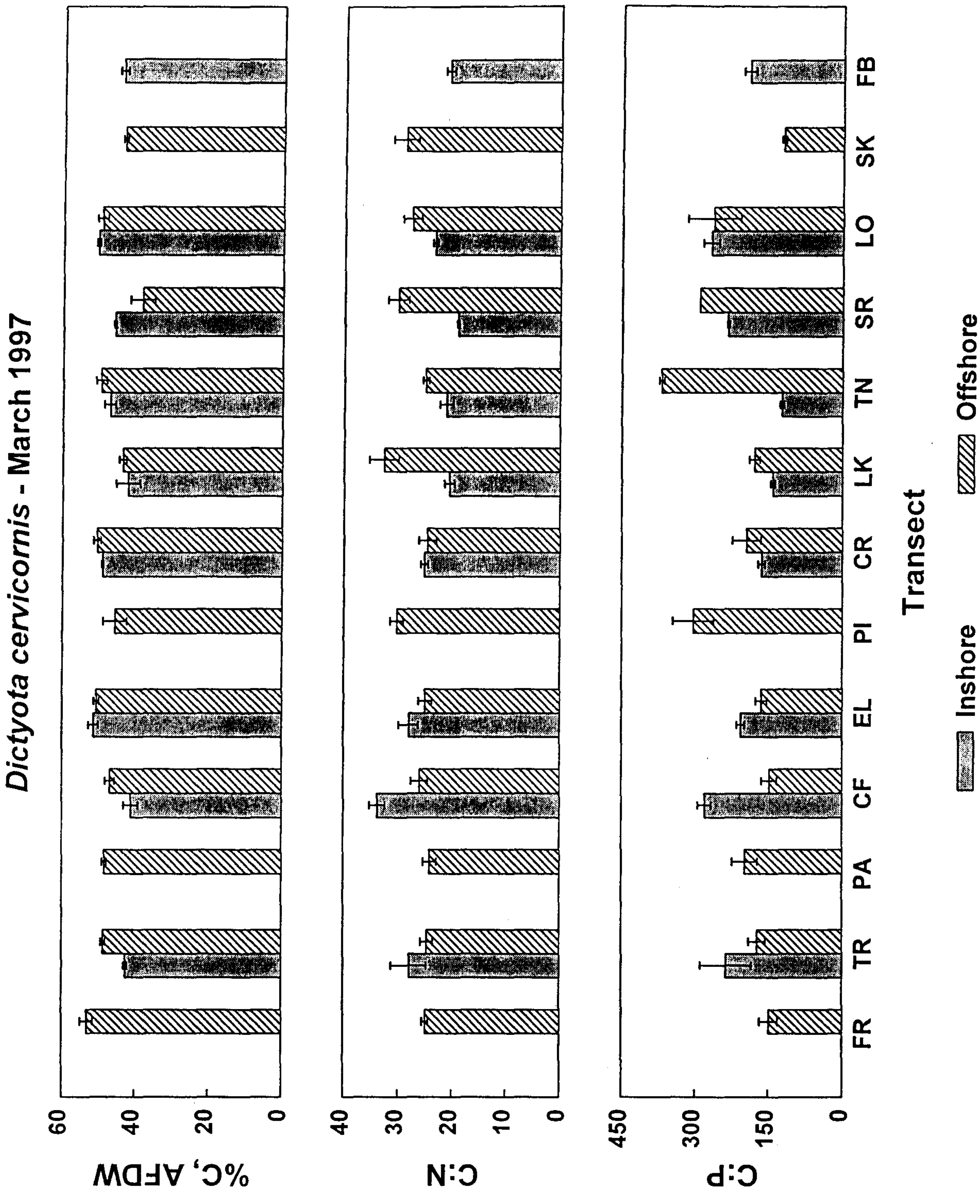

Fig. 13 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Dictyota cervicornis*, March 1997.

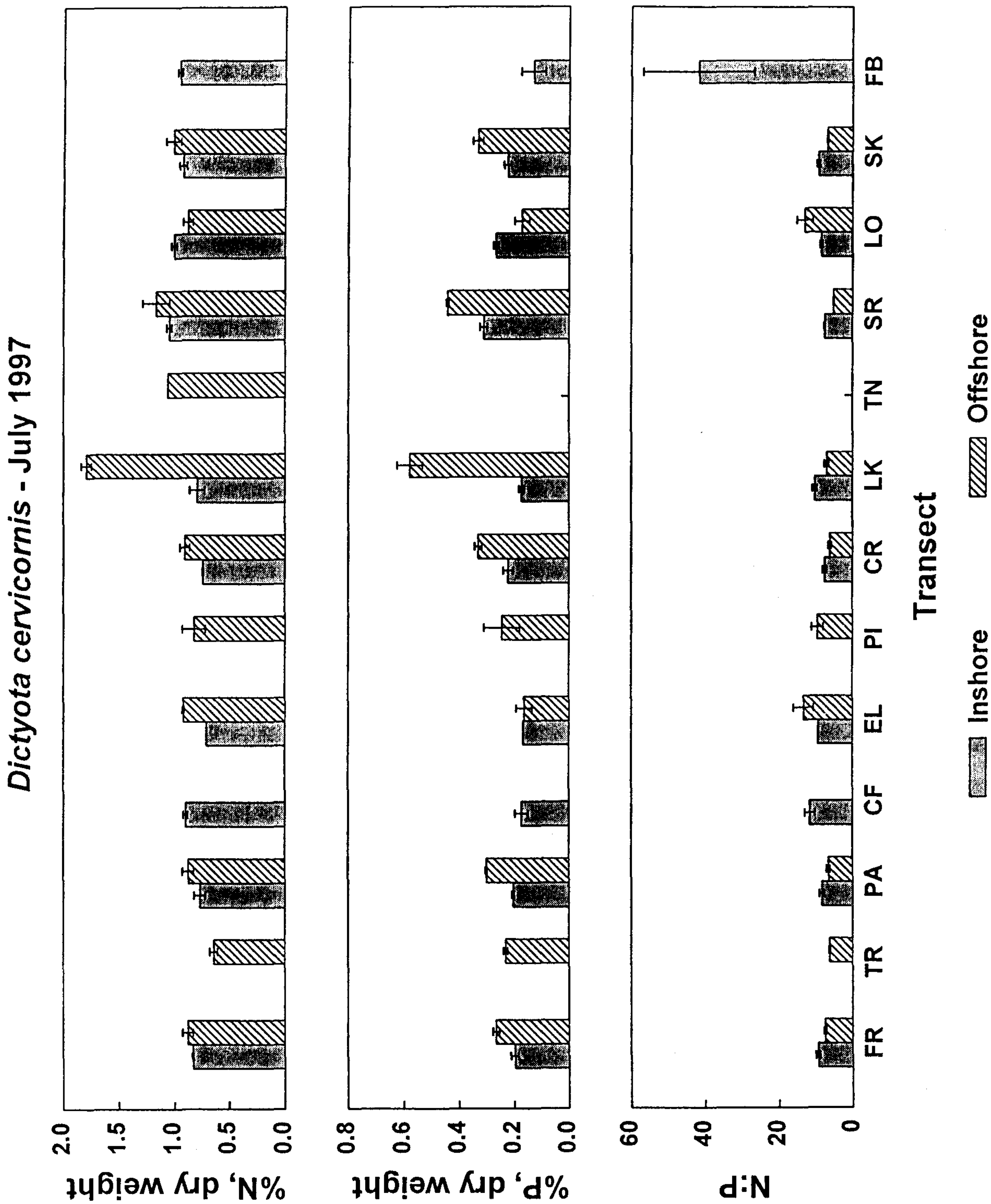

Fig. 14 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Dictyota cervicornis*, July 1997.

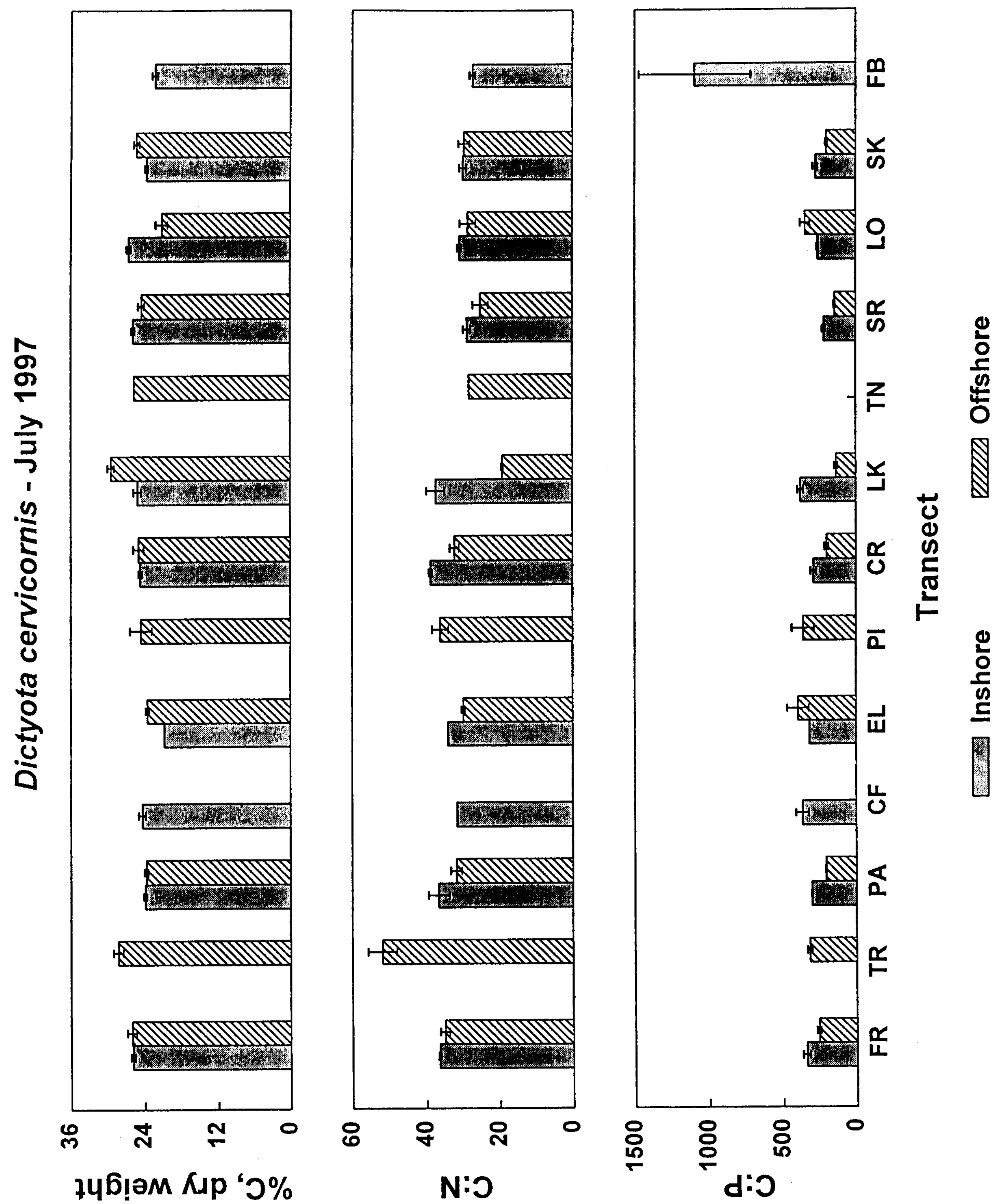

Fig. 15 **Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Dictyota cervicornis*, July 1997.**

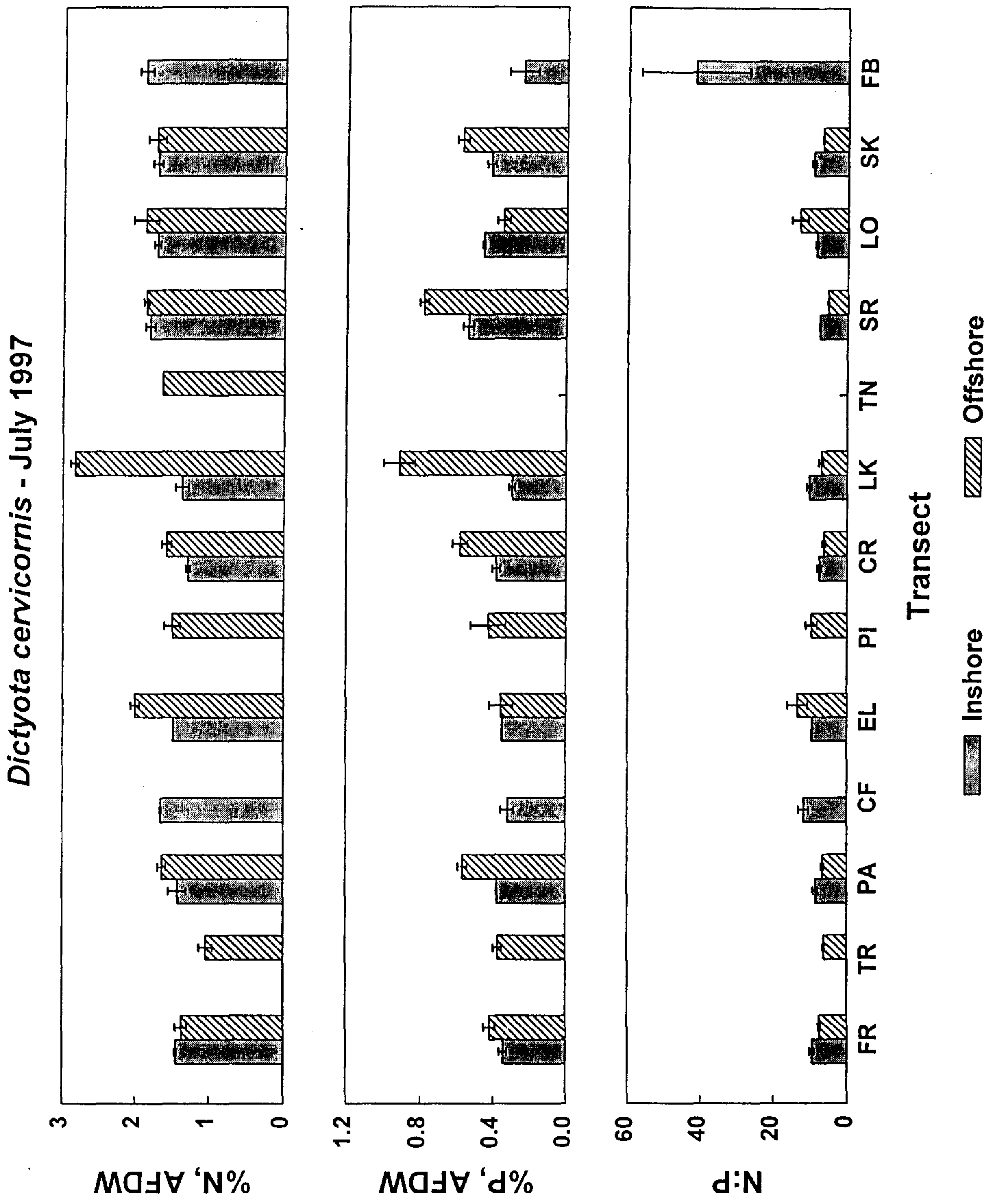

Fig. 16 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Dictyota cervicornis*, July 1997.

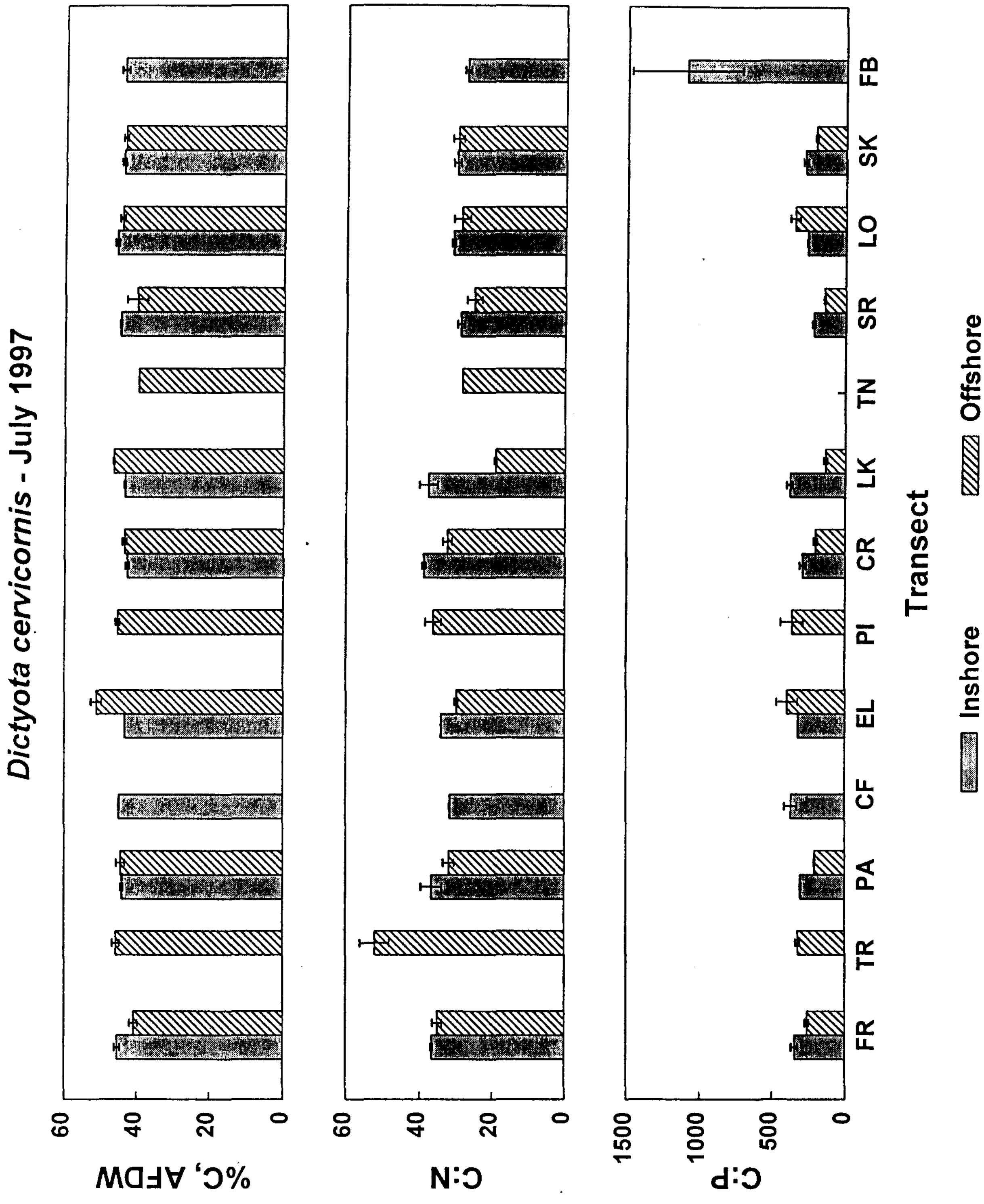

Fig. 17 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Dictyota cervicornis*, July 1997.

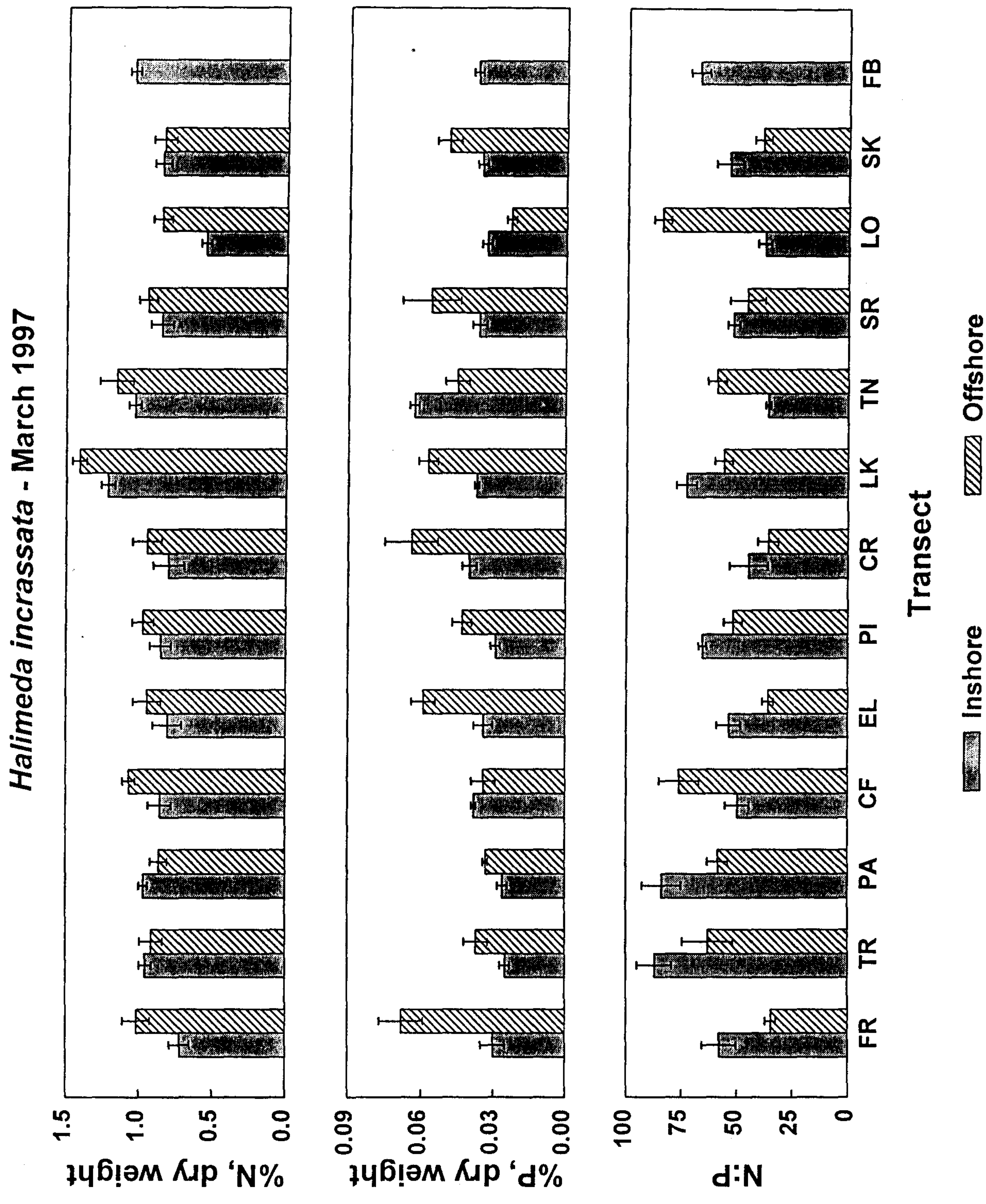

Fig. 18 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda incrassata*, March 1997.

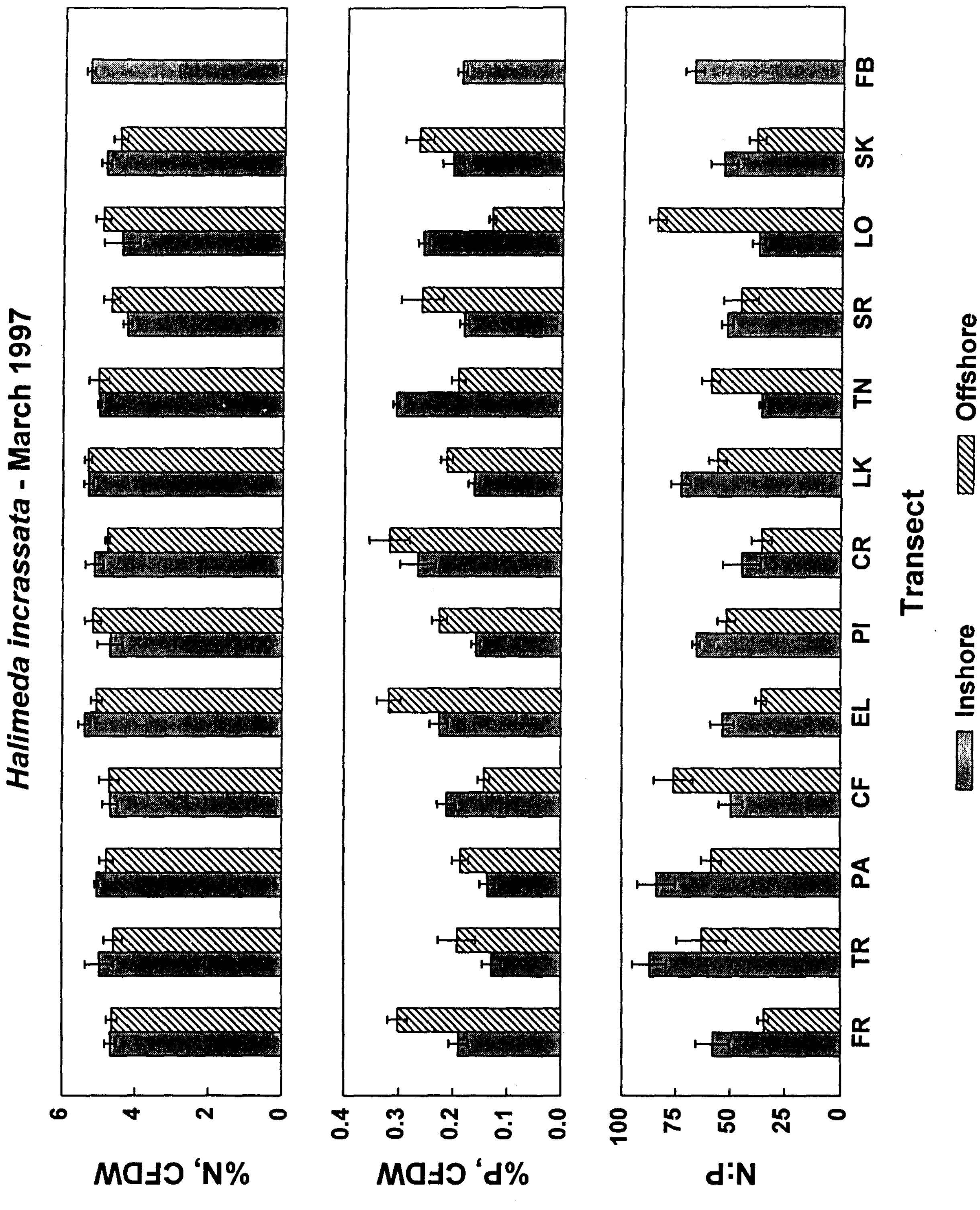

Fig. 19 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda incrassata*, March 1997.

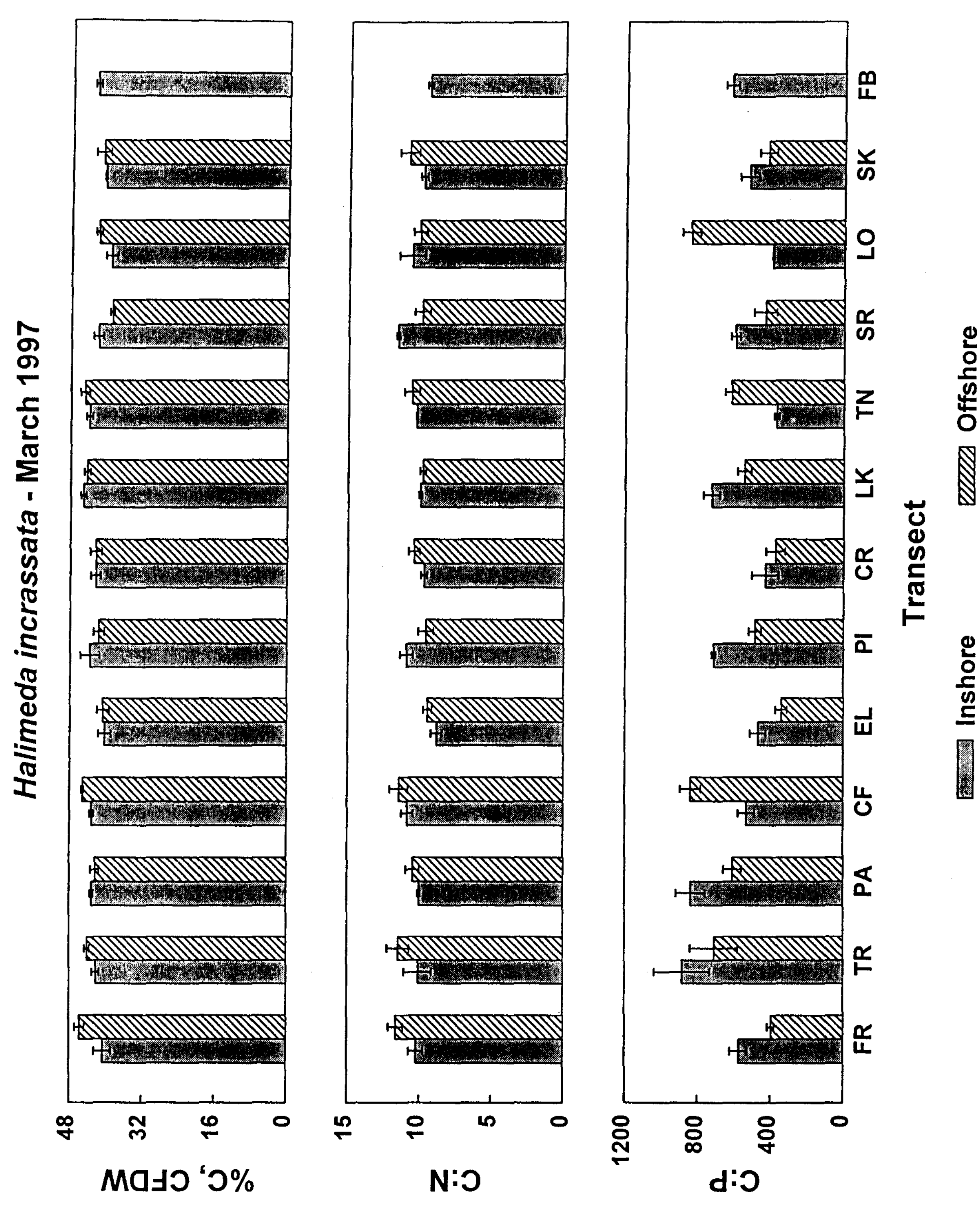

Fig. 20 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda incrassata*, March 1997.

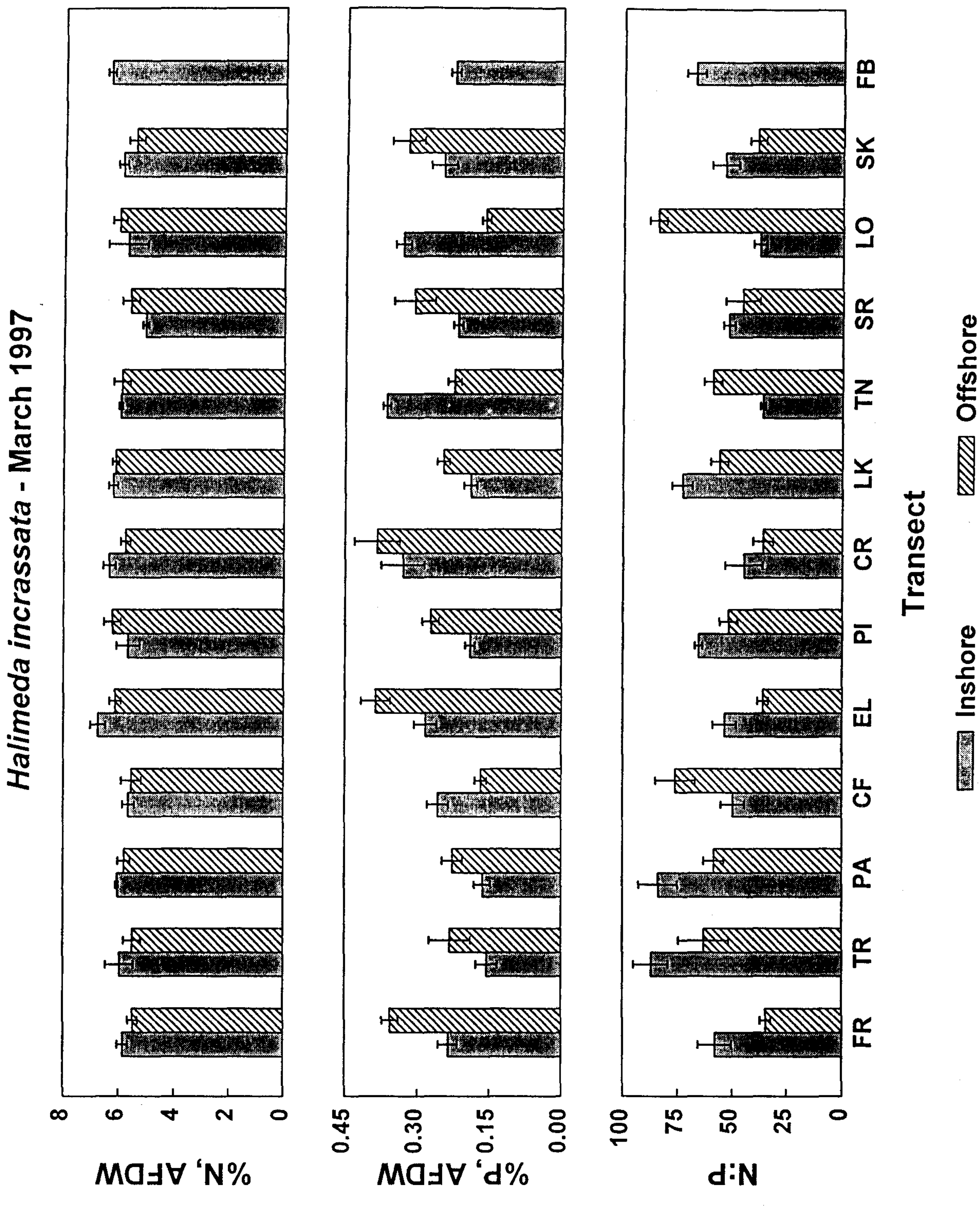

Fig. 21 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda incrassata*, March 1997.

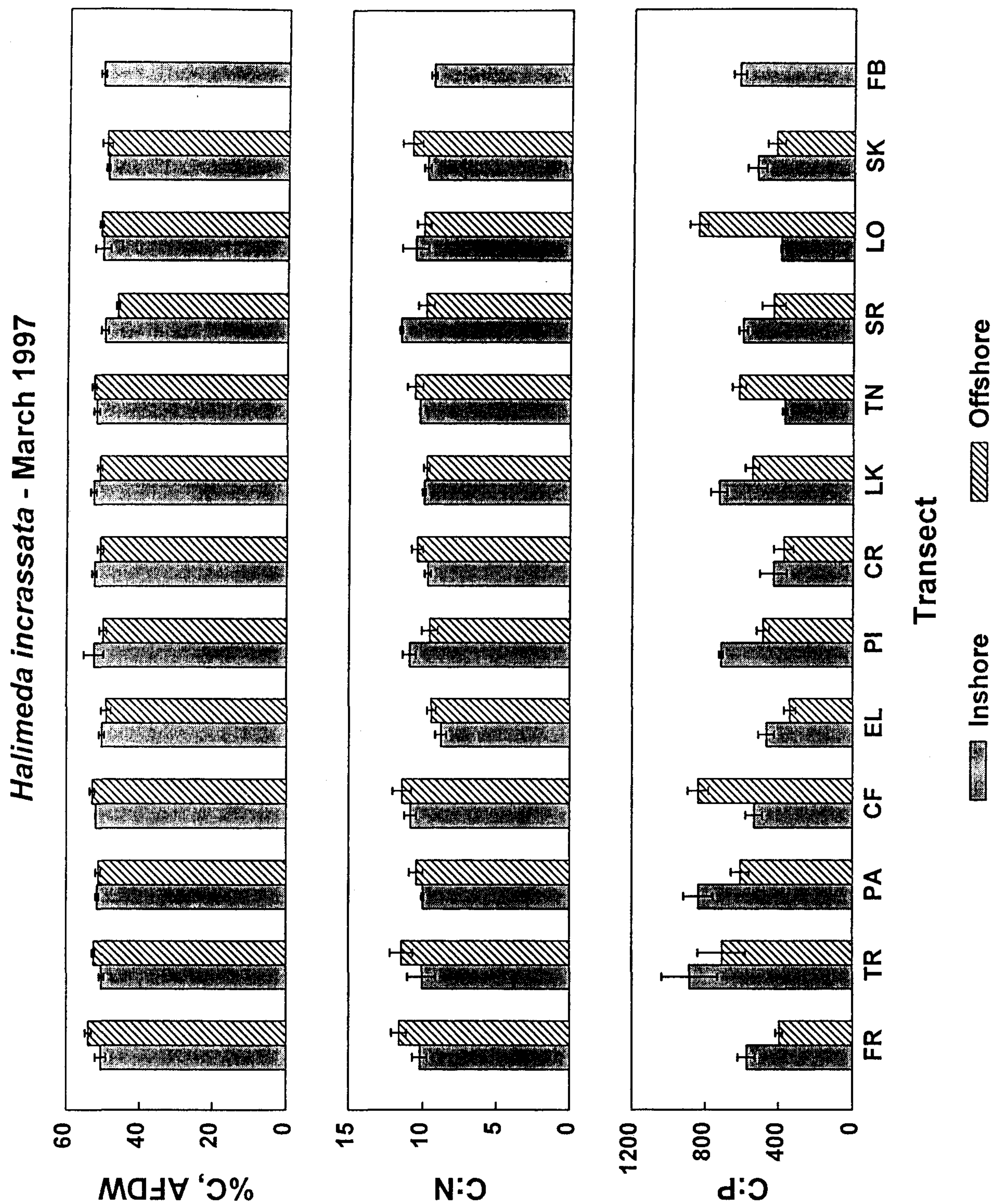

Fig. 22 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda incrassata*, March 1997.

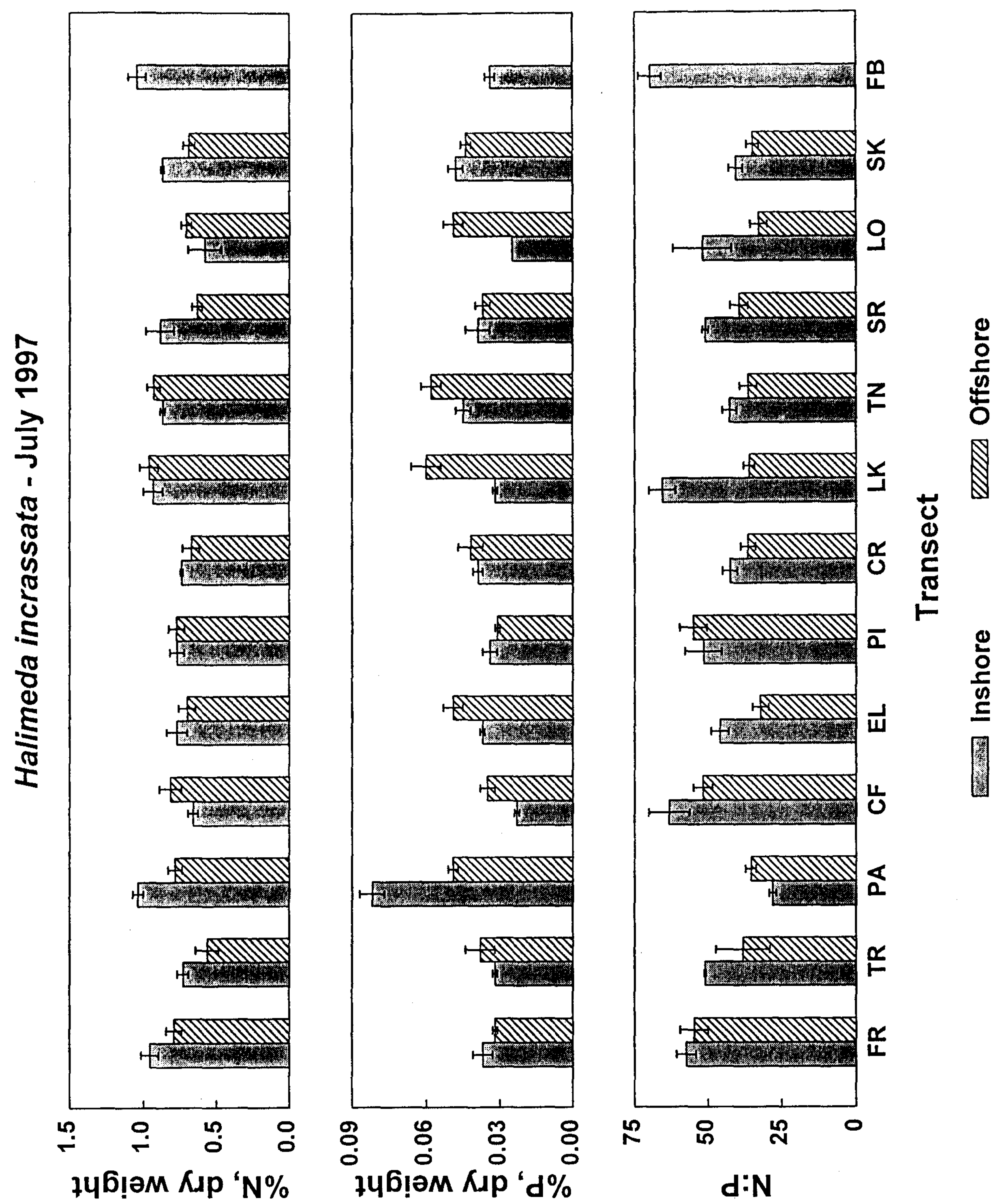

Fig. 23 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda incrassata*, July 1997.

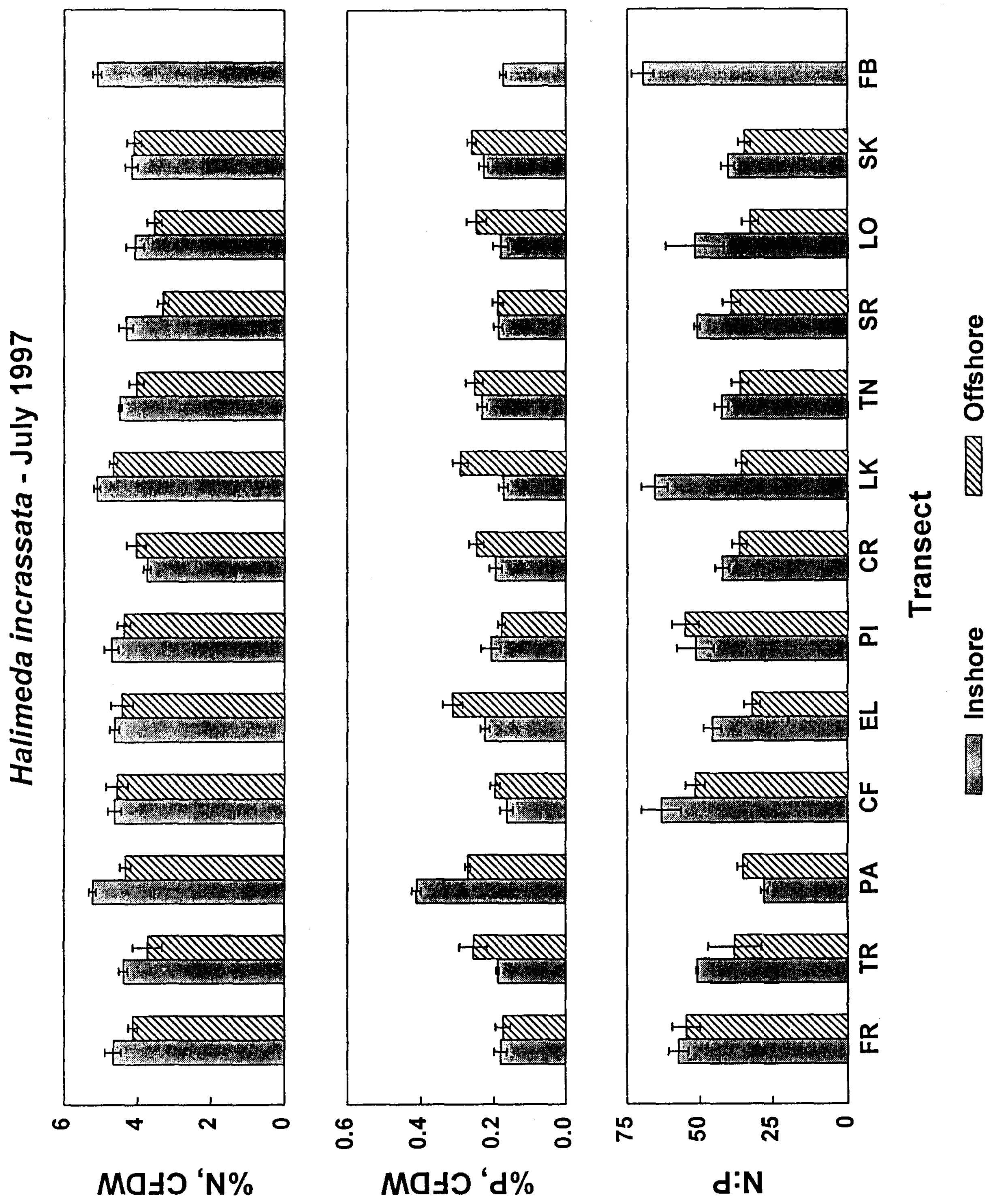

Fig. 24 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda incrassata*, July 1997.

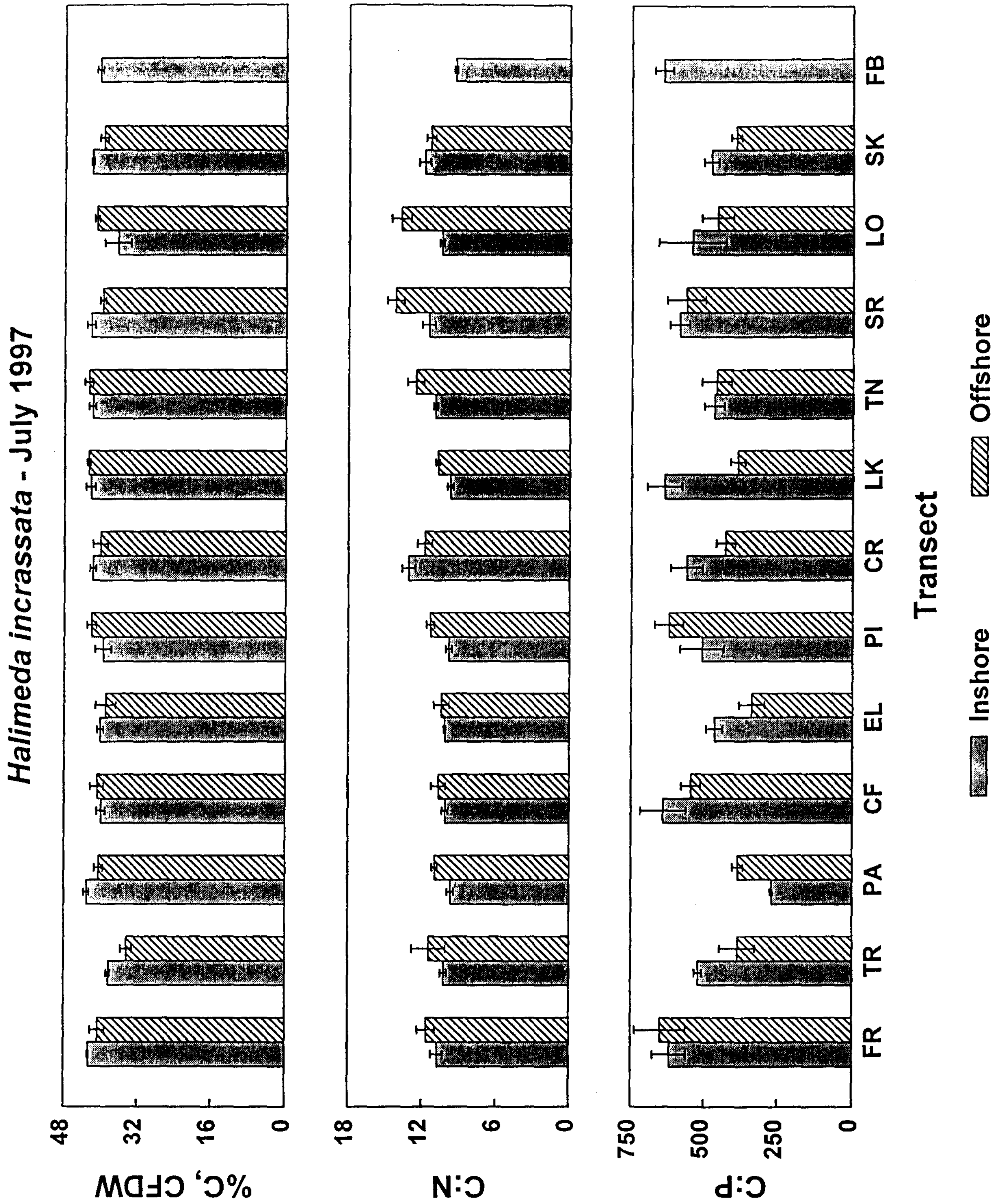

Fig. 25 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda incrassata*, July 1997.

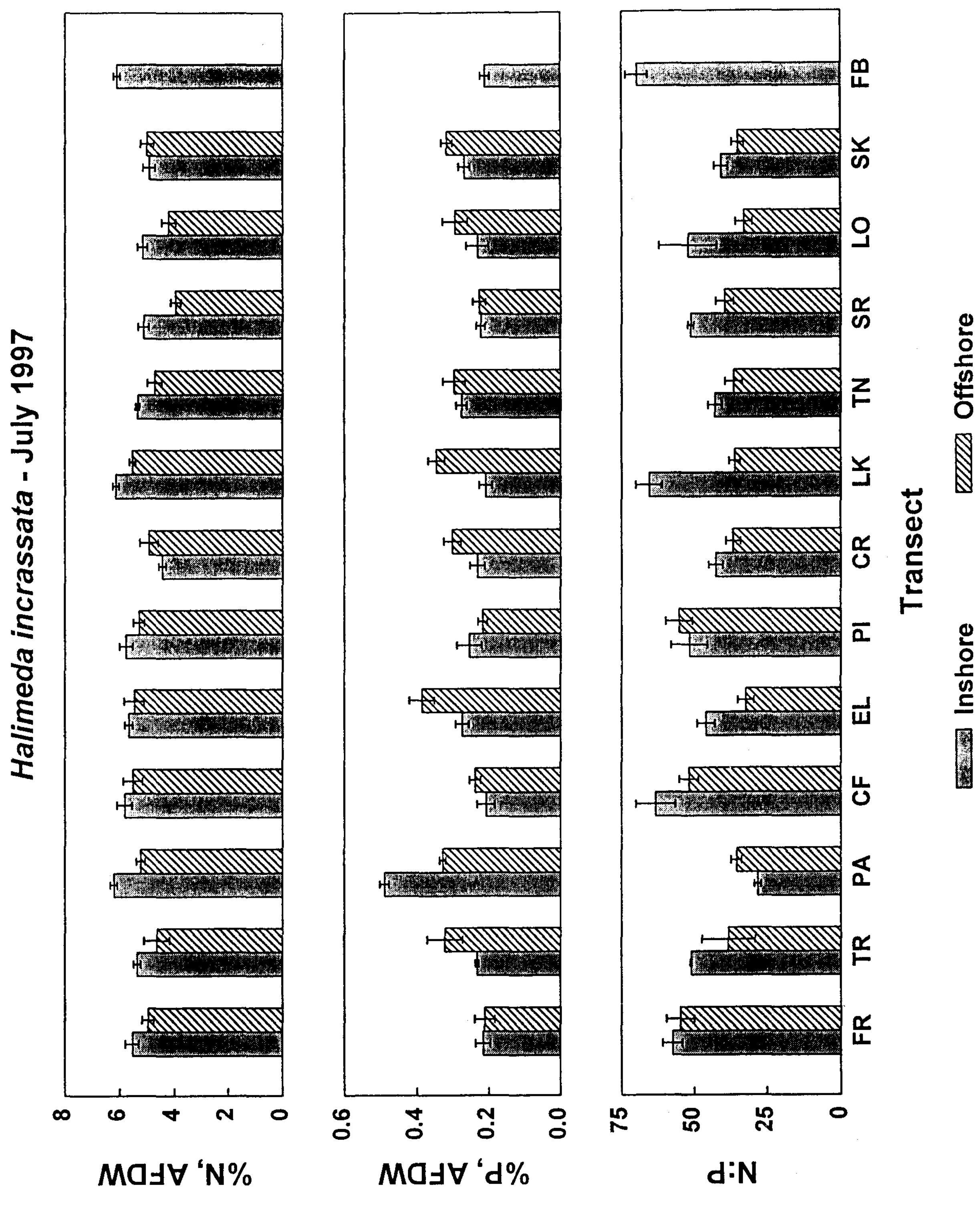

Fig. 26 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda incrassata*, July 1997.

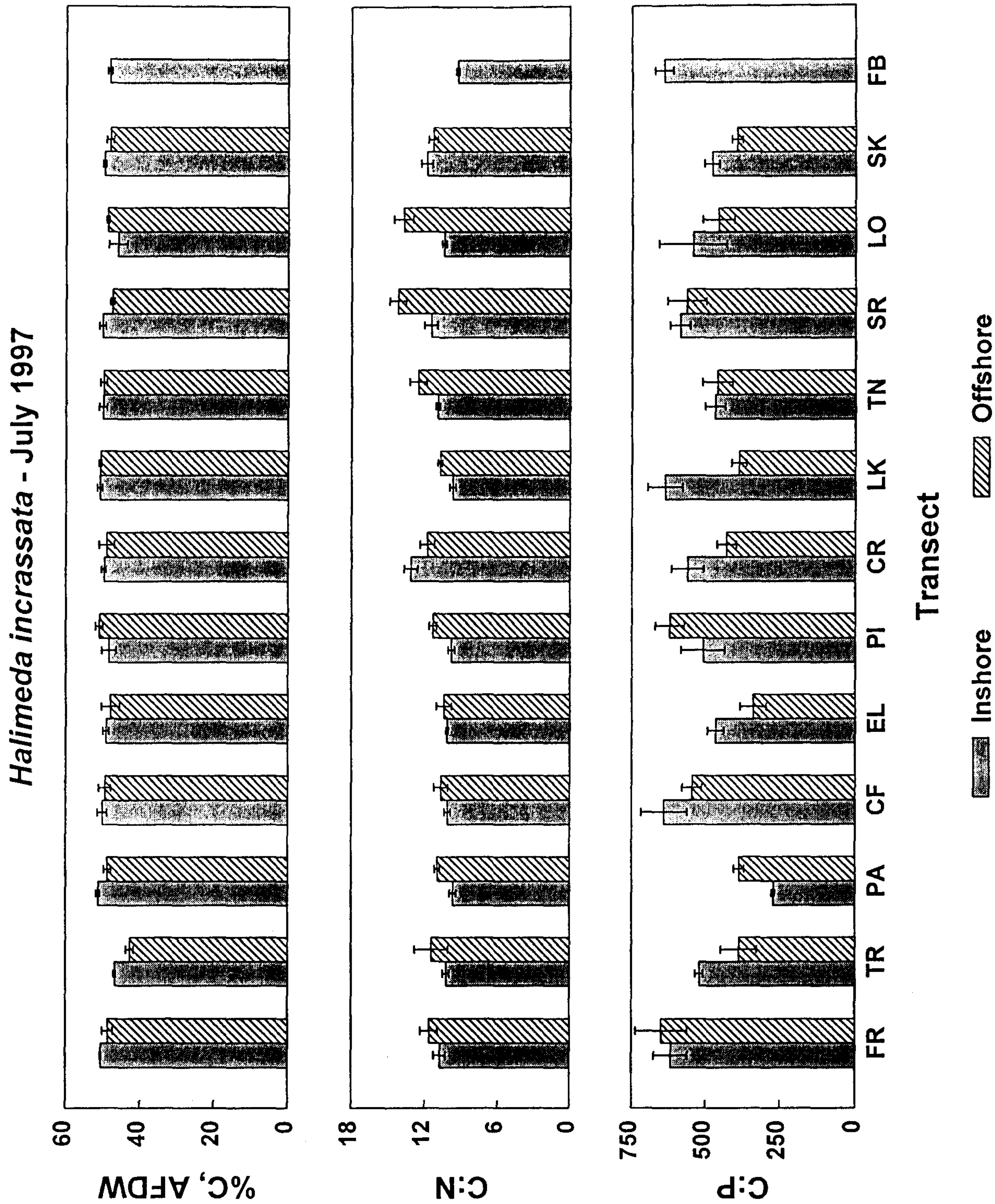

Fig. 27 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda incrassata*, July 1997.

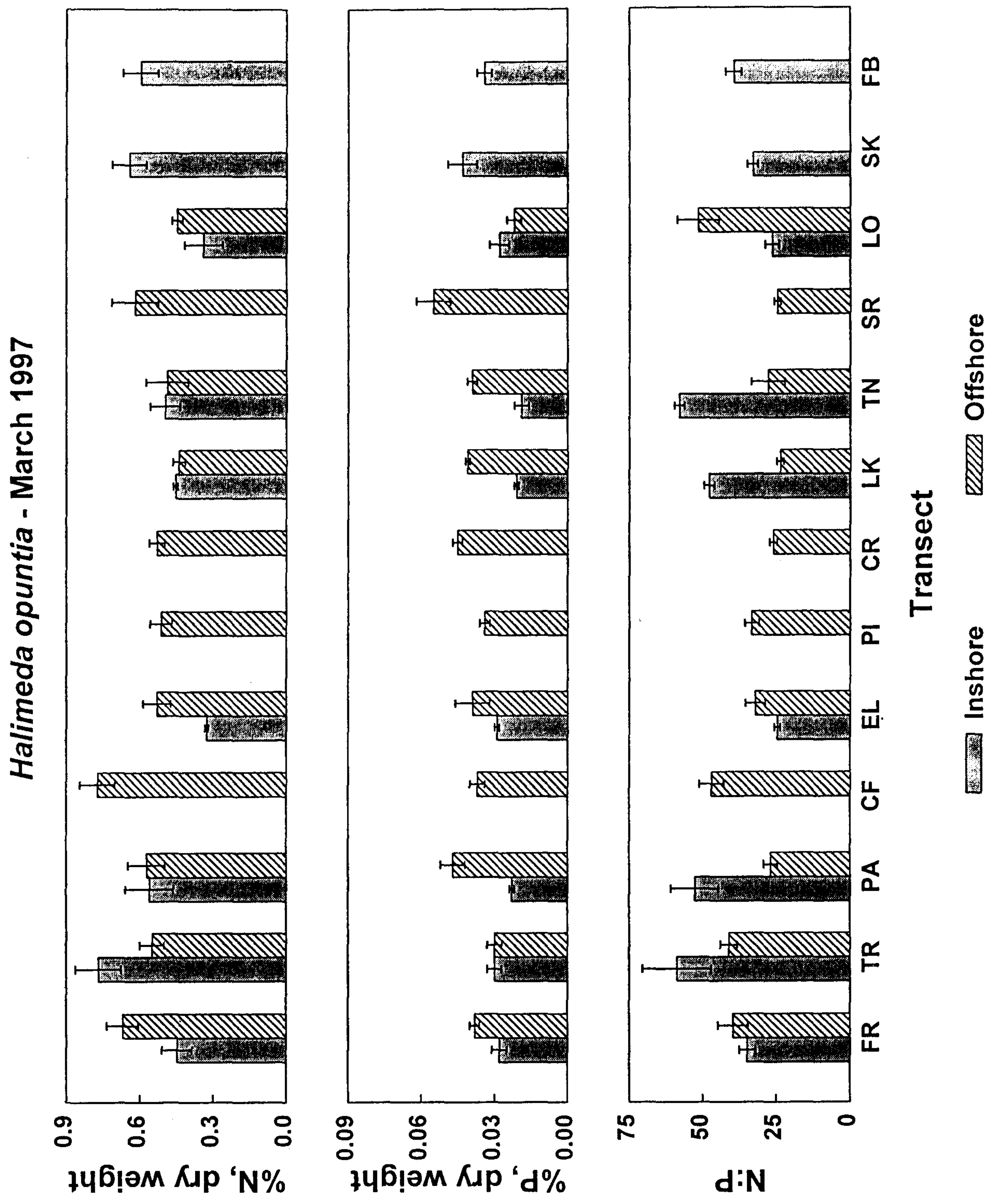

Fig. 28 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda opuntia*, March 1997.

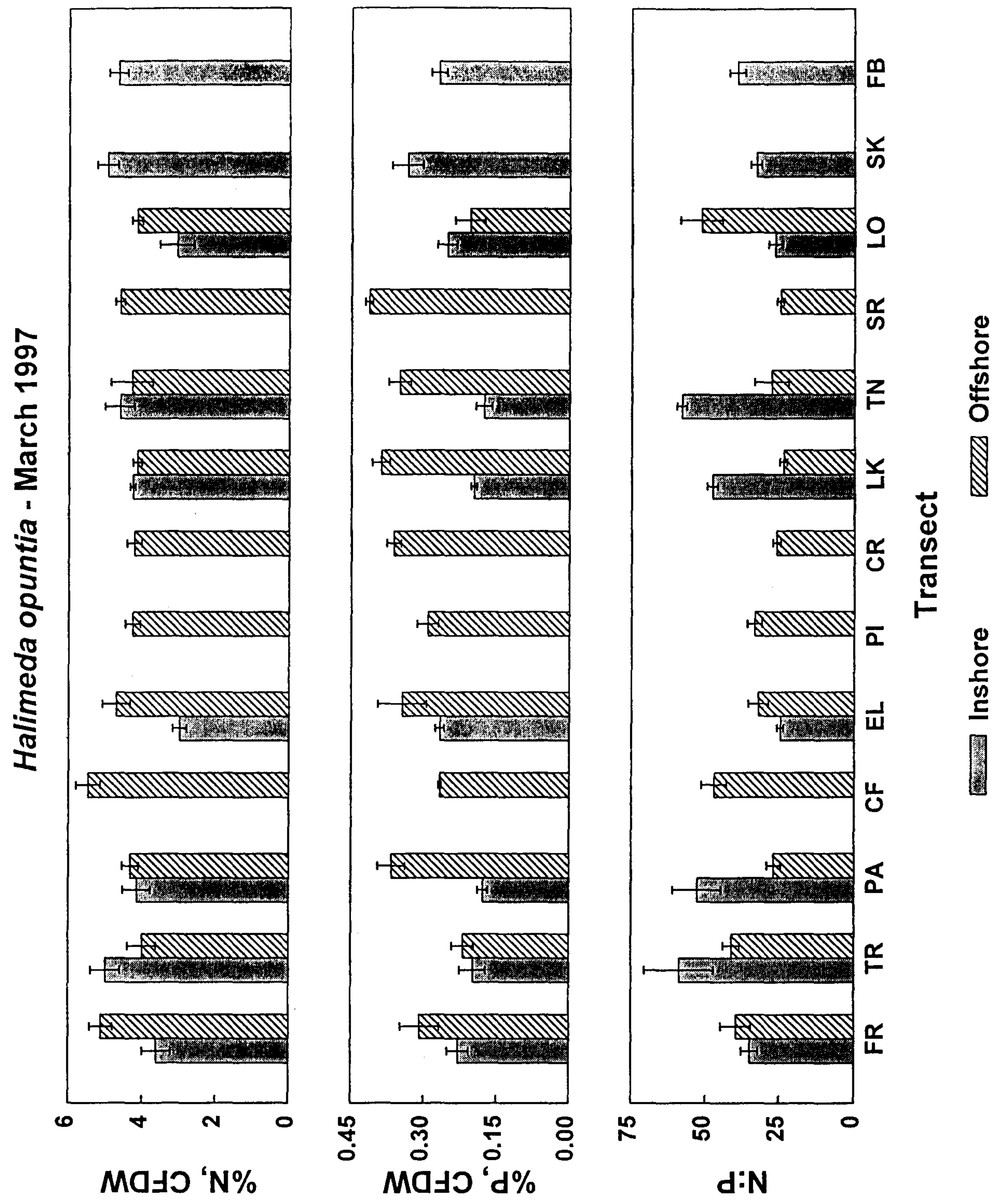

Fig. 29 **Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda opuntia*, March 1997.**

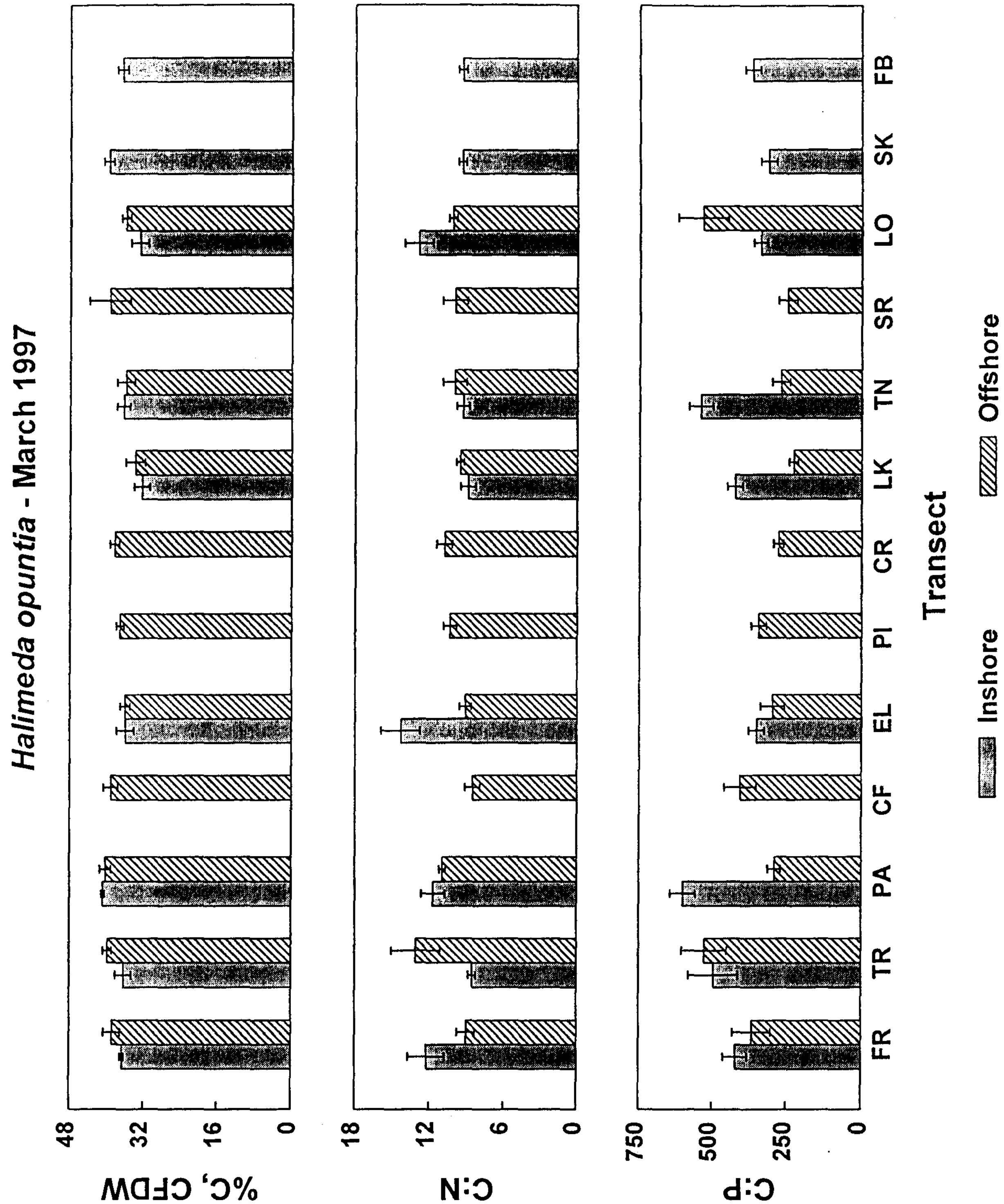

Fig. 30 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda opuntia*, March 1997.

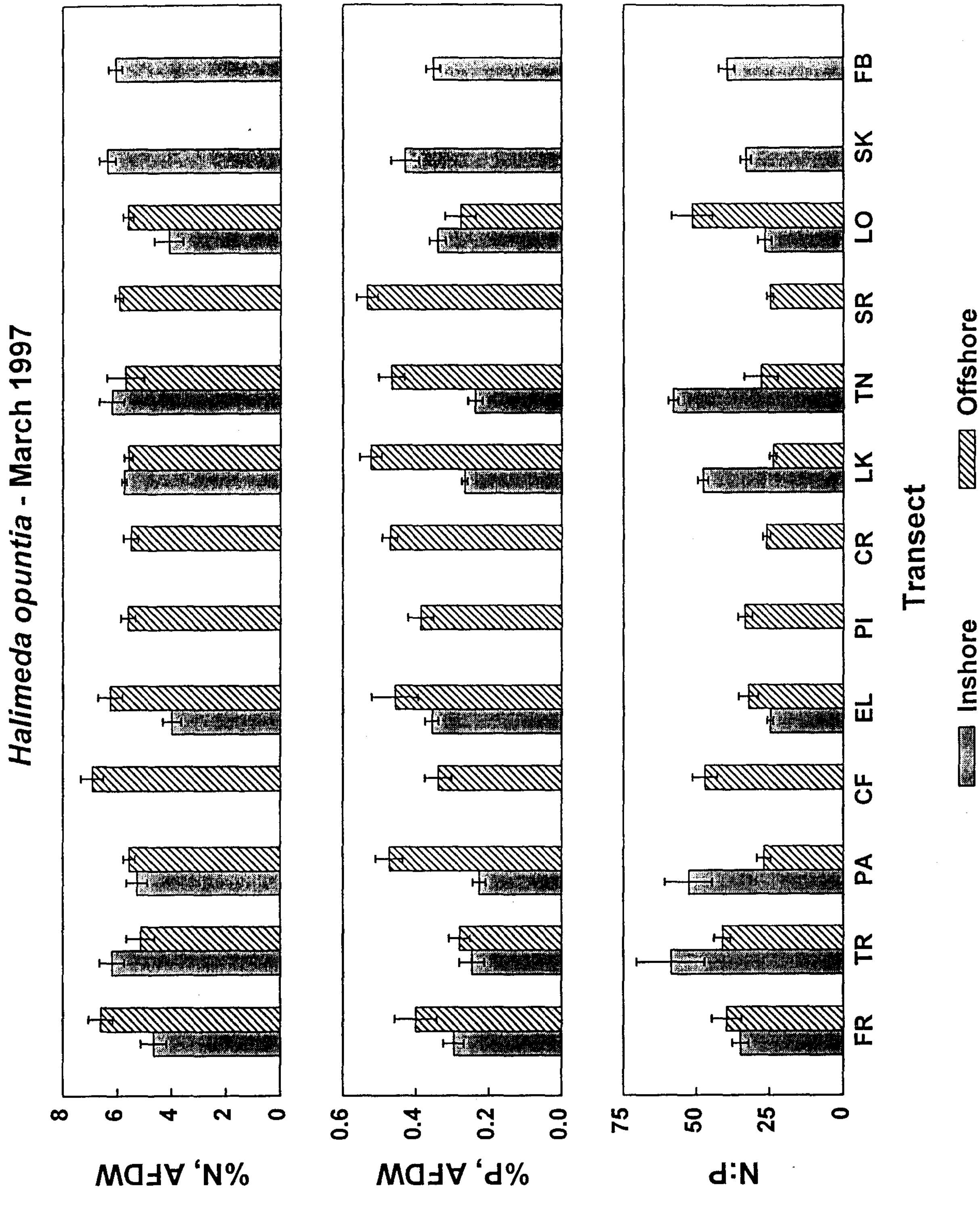

Fig. 31 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda opuntia*, March 1997.

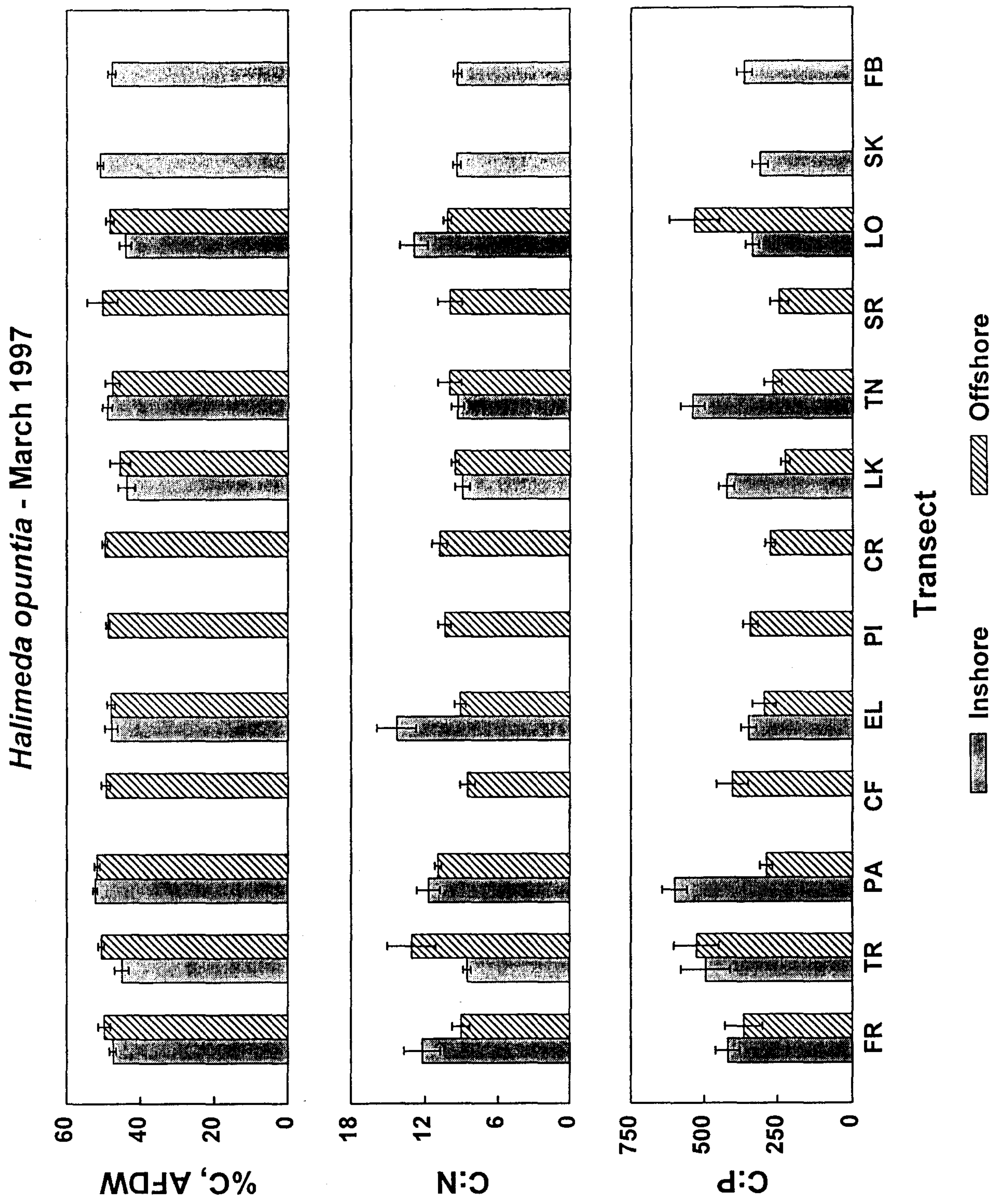

Fig. 32 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda opuntia*, March 1997.

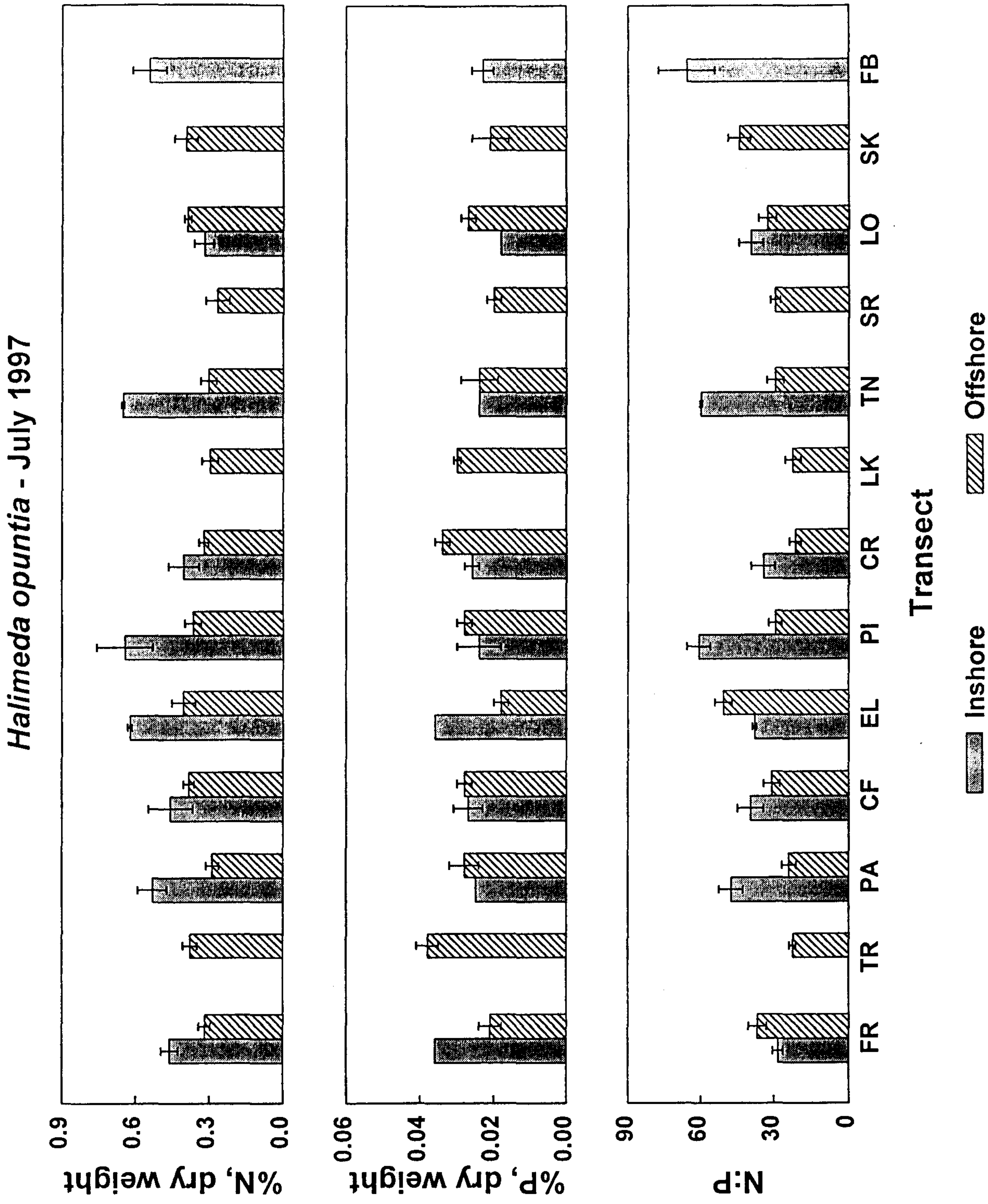

Fig. 33 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda opuntia*, July 1997.

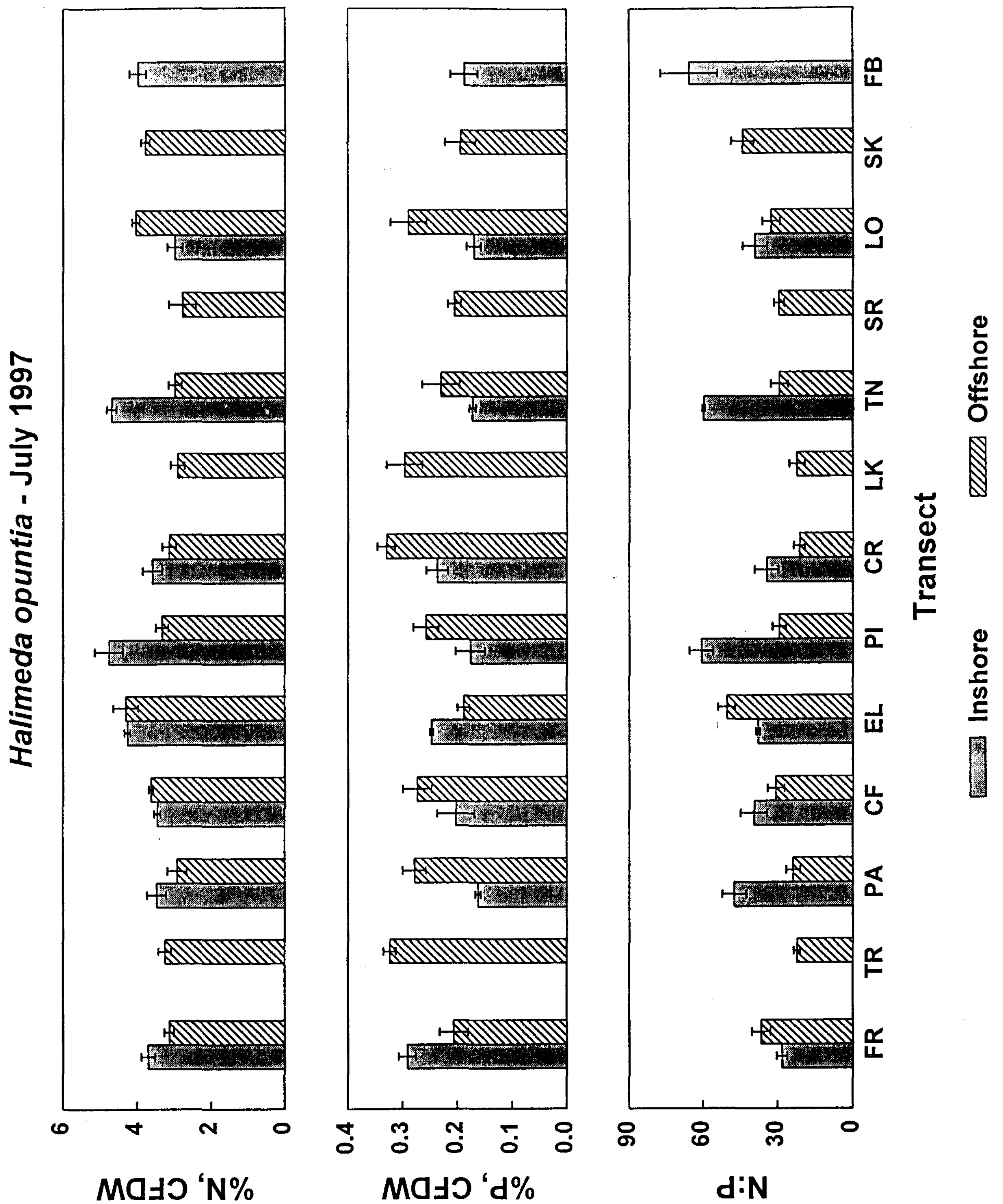

Fig. 34 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda opuntia*, July 1997.

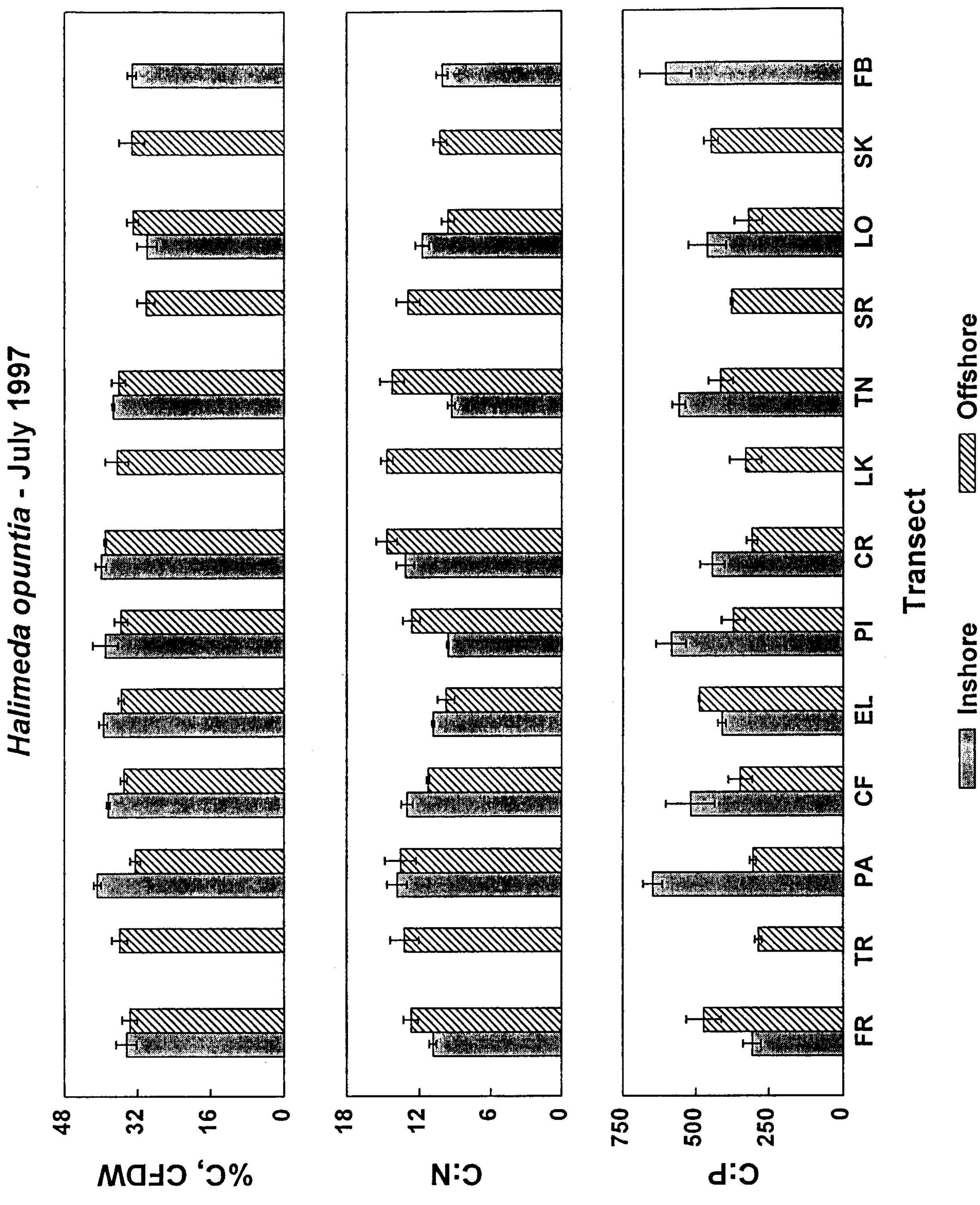

Fig. 35 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda opuntia*, July 1997.

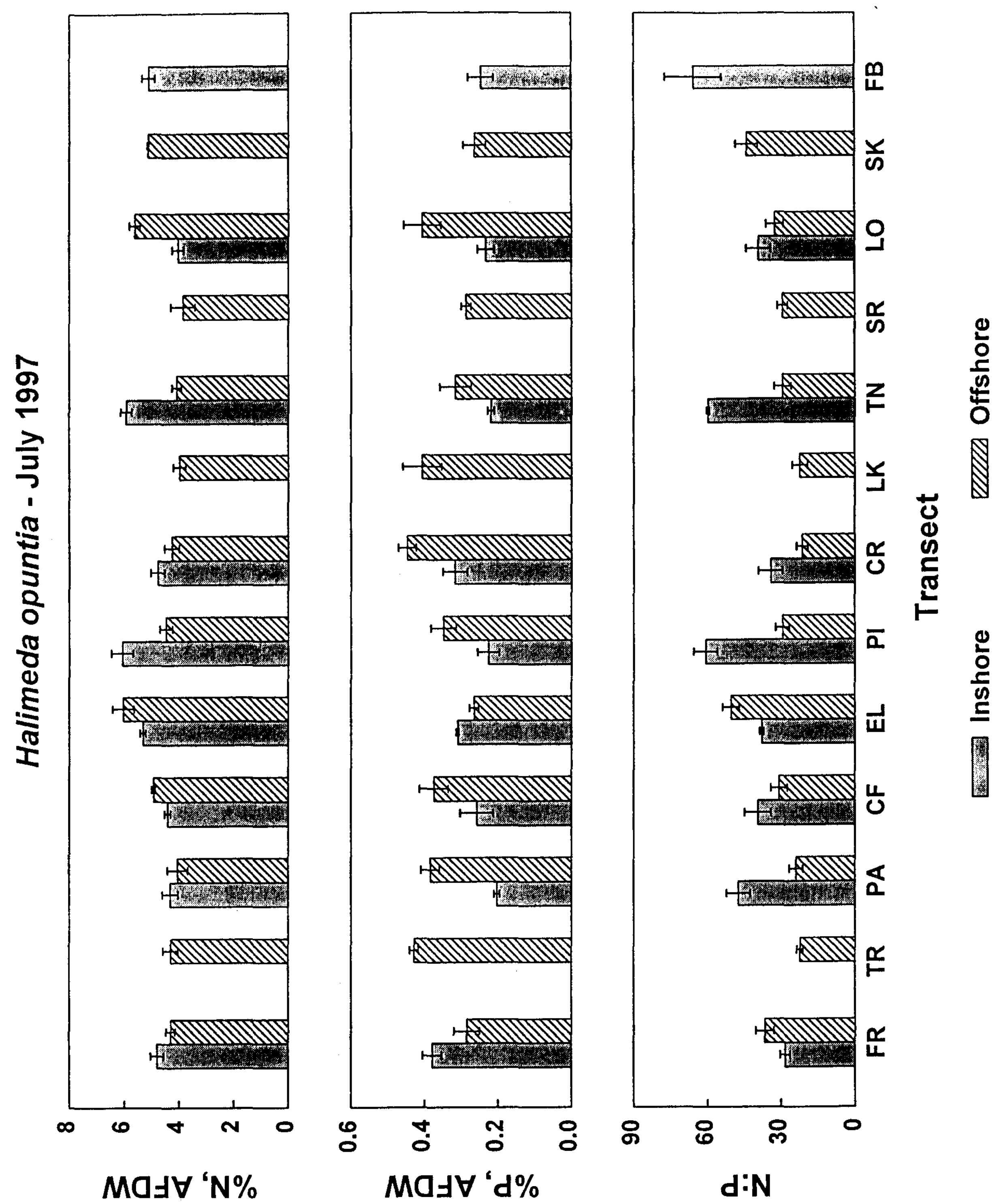

Fig. 36 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda opuntia*, July 1997.

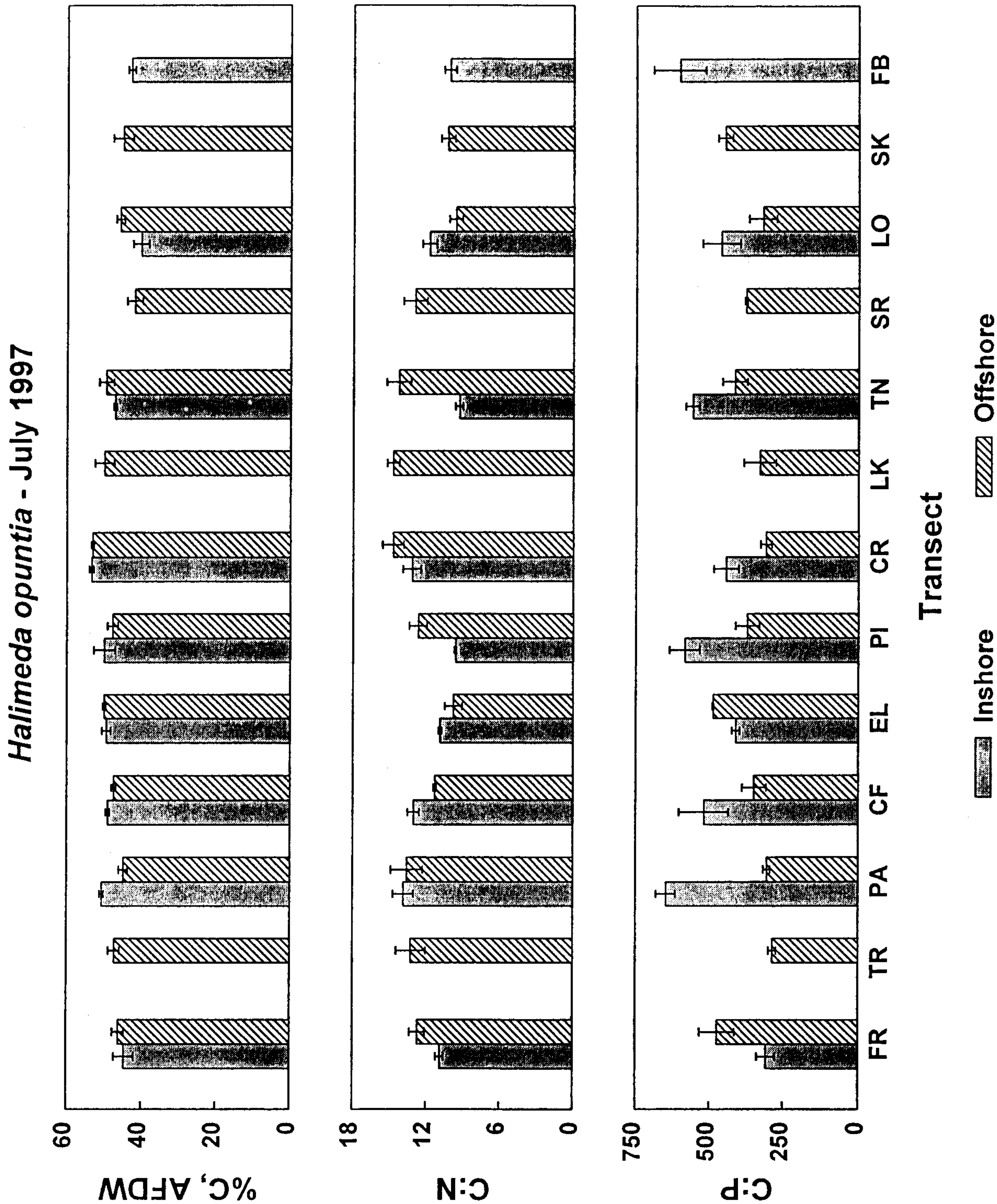

Fig. 37 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda opuntia*, July 1997.

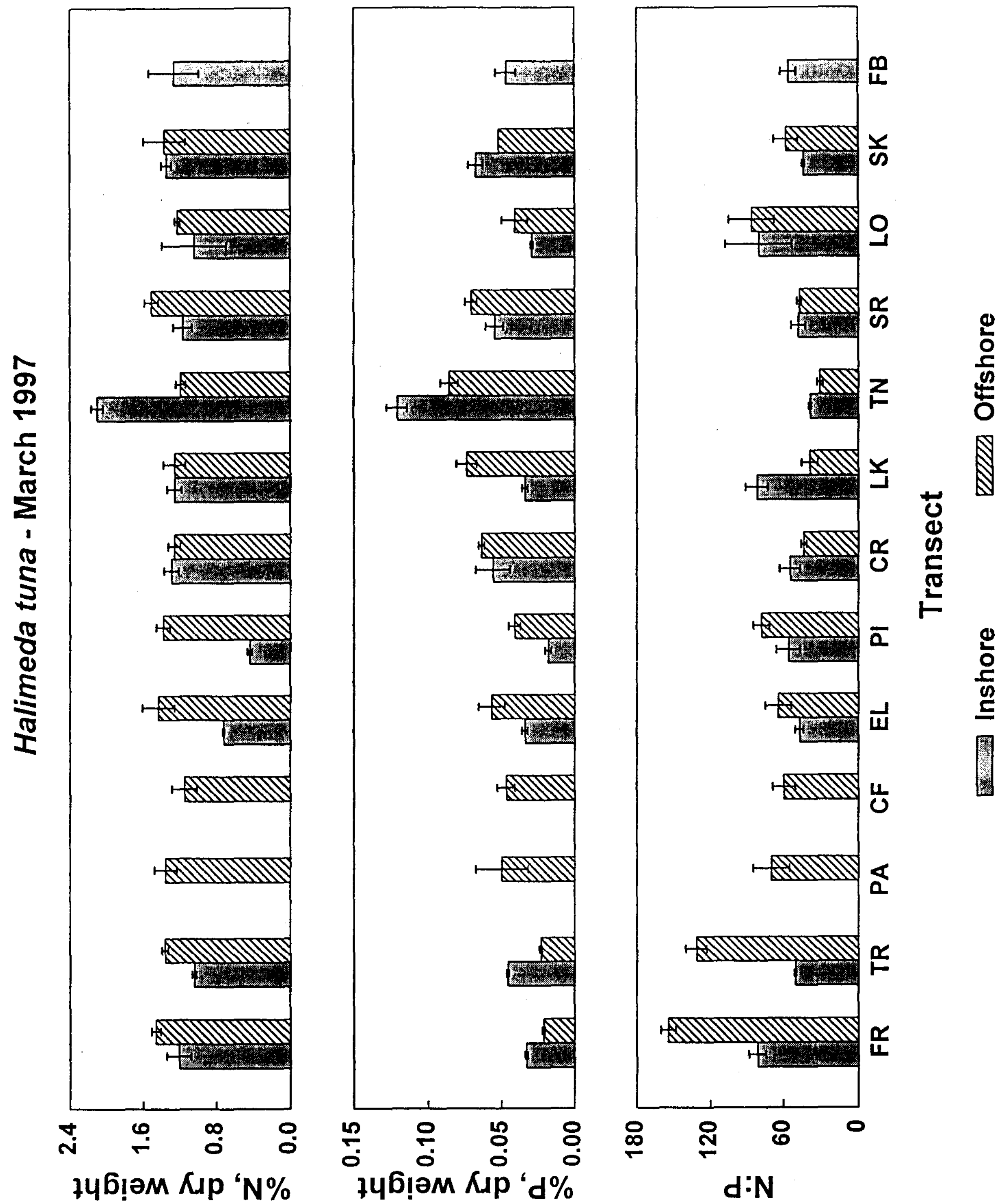

Fig. 38 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda tuna,* March 1997.

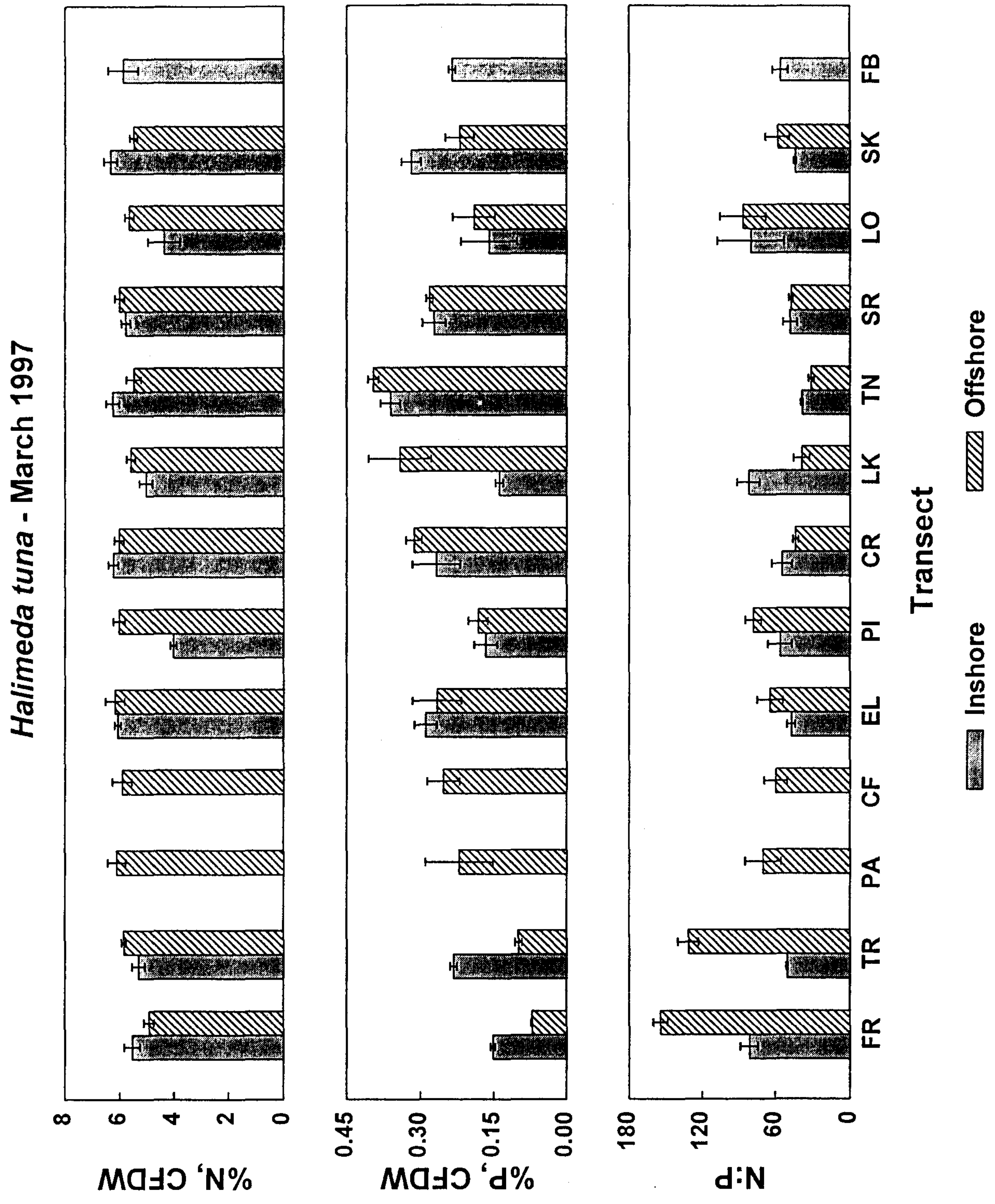

Fig. 39 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda tuna*, March 1997.

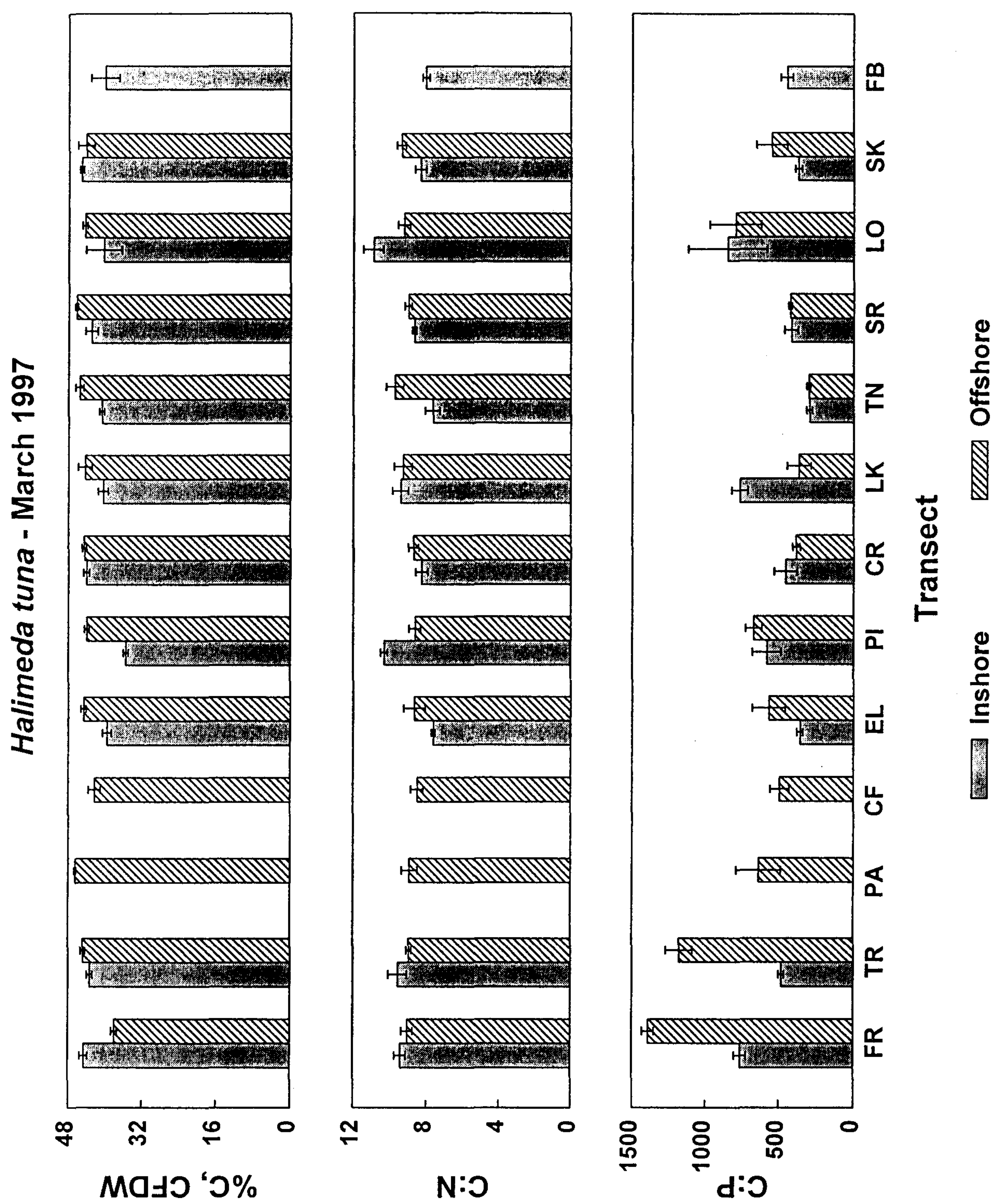

Fig. 40 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda tuna*, March 1997.

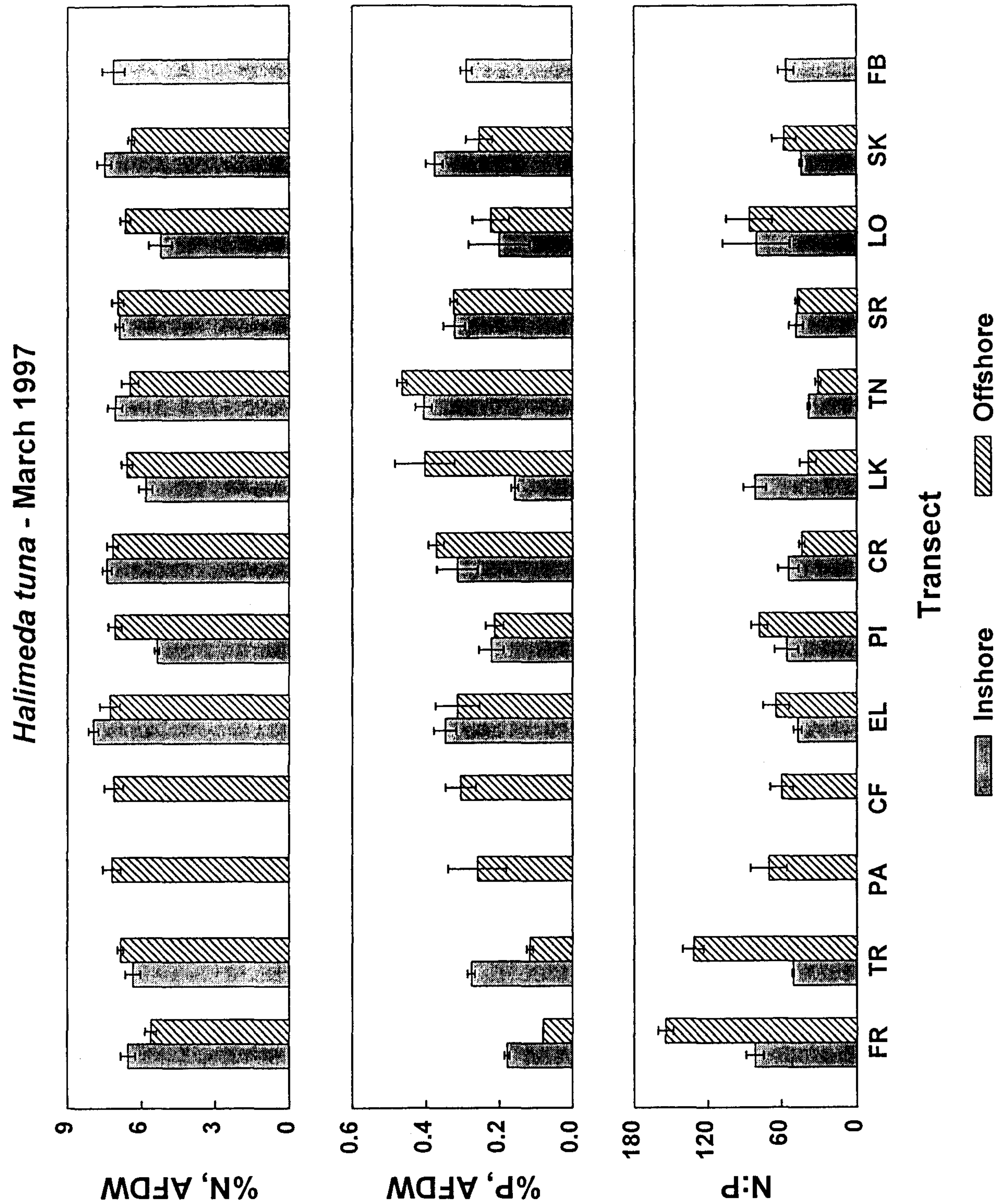

Fig. 41 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda tuna*, March 1997.

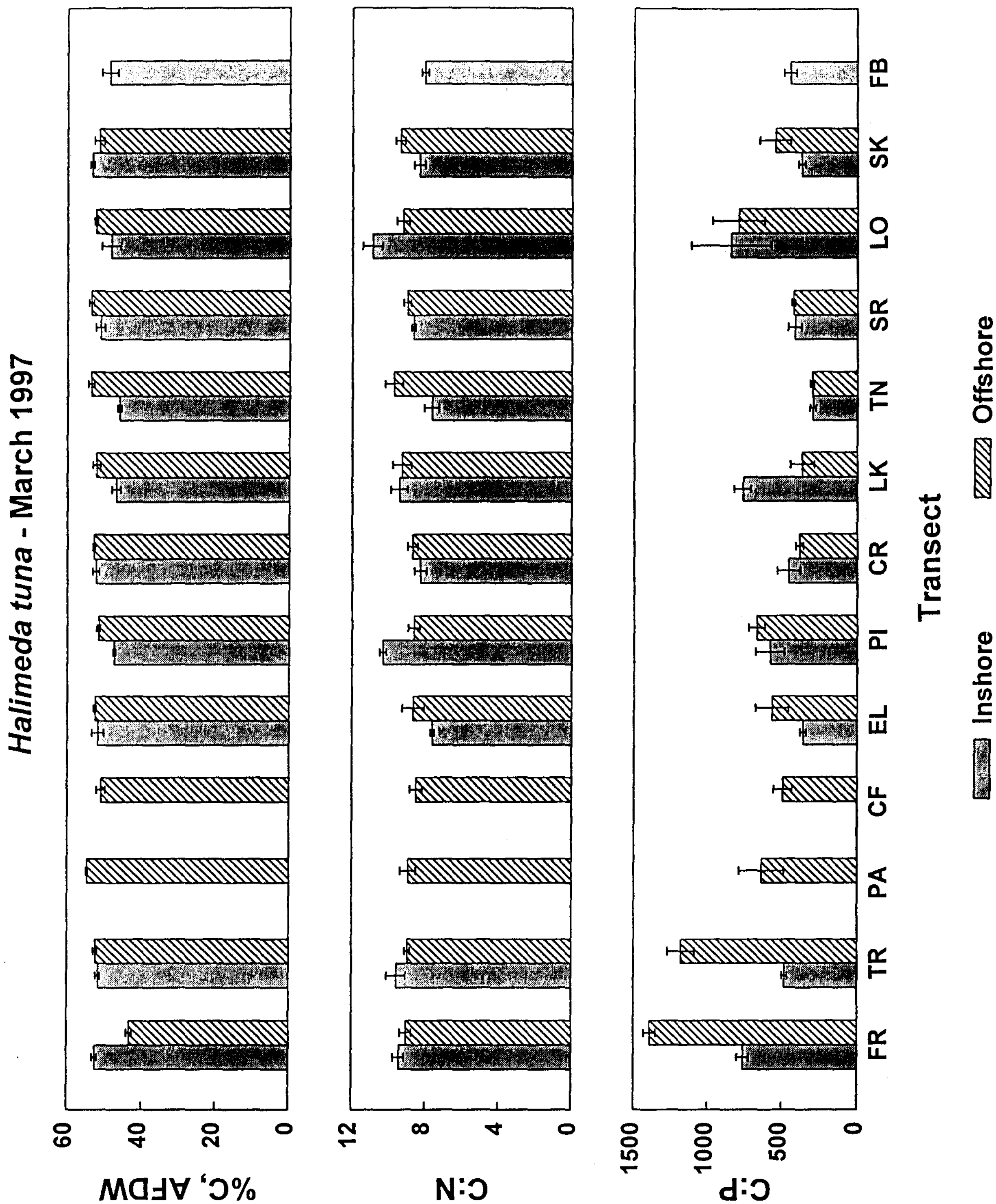

Fig. 42 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda tuna*, March 1997.

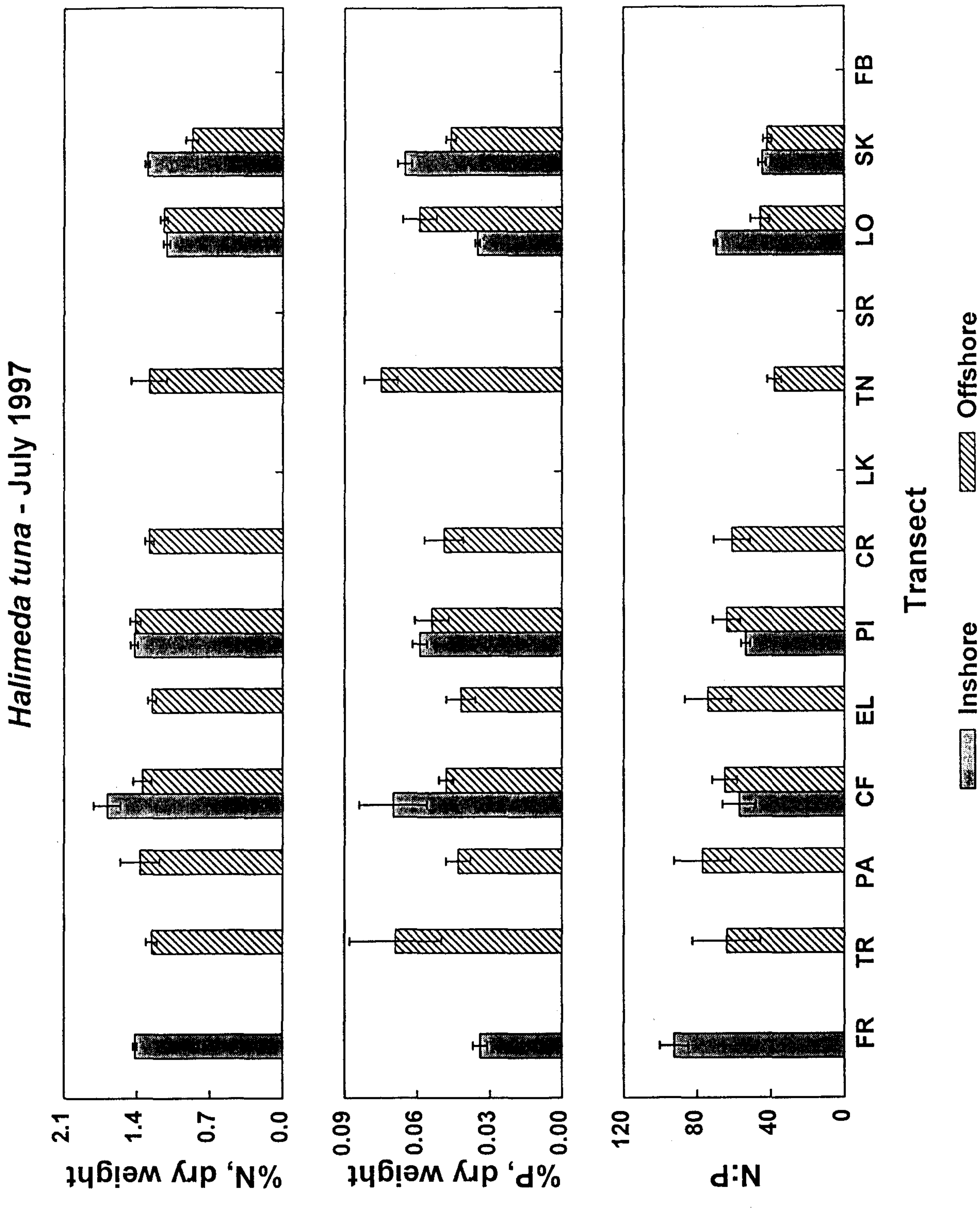

Fig. 43 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda tuna*, July 1997.

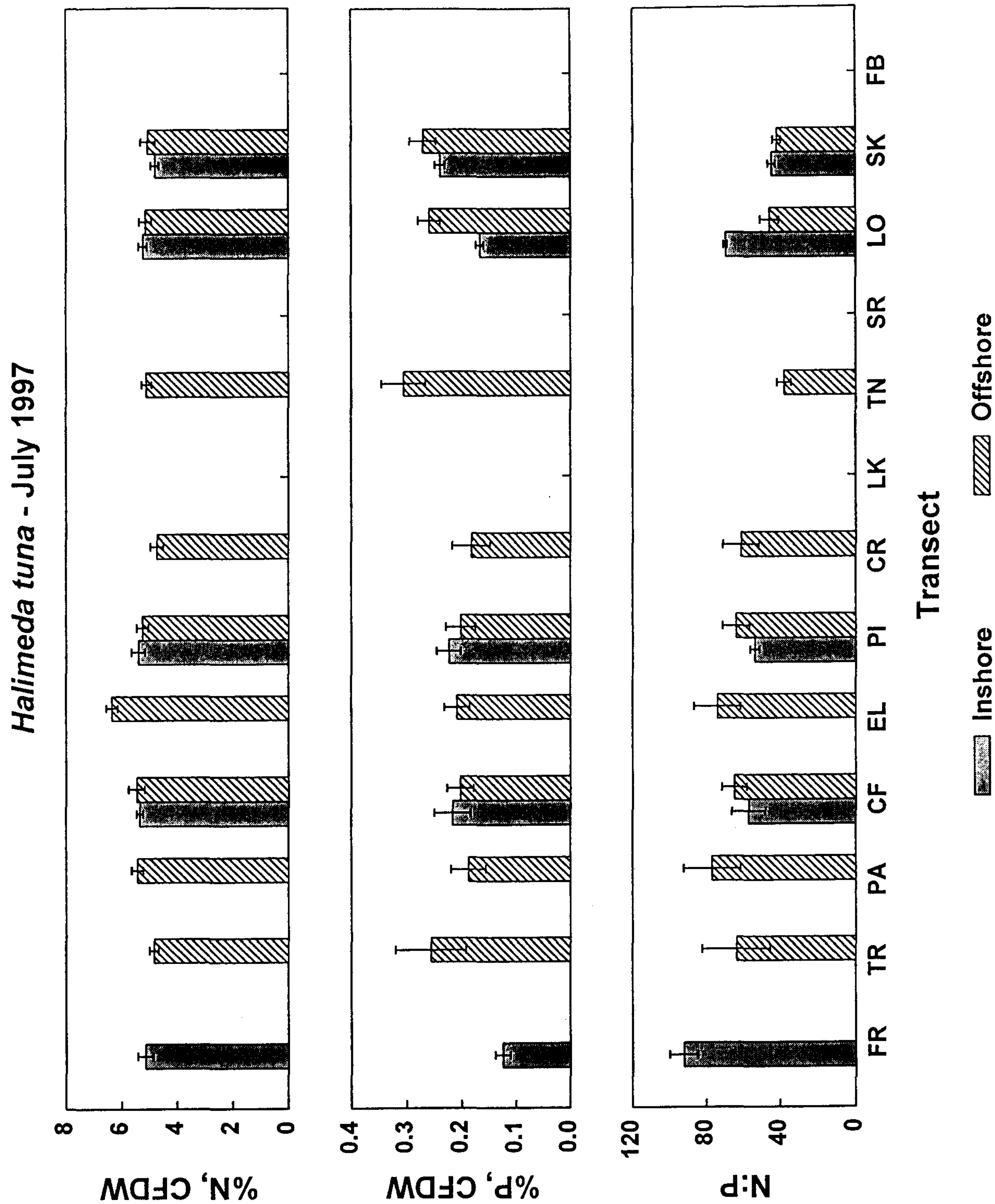

Fig. 44 **Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda tuna*, July 1997.**

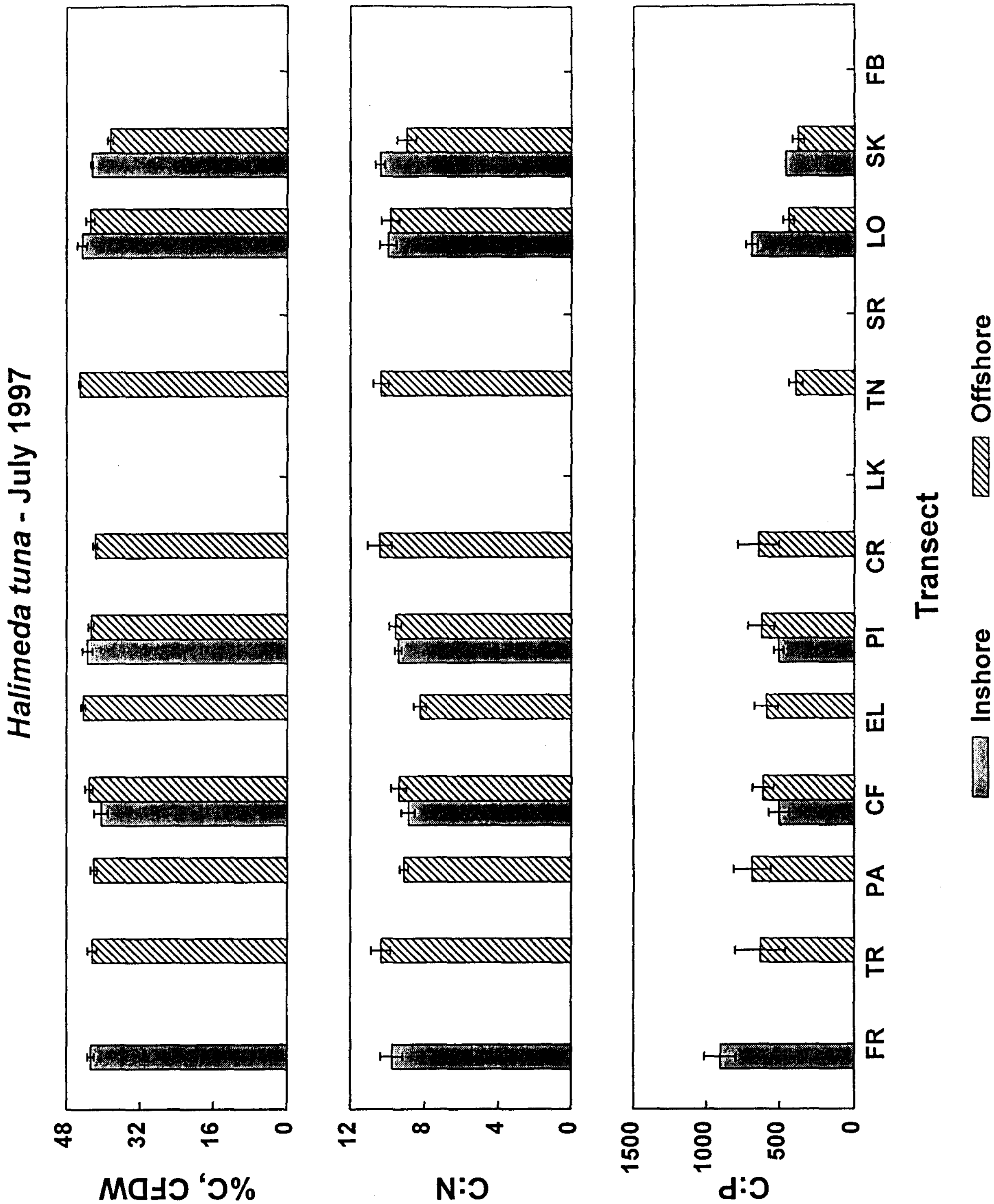

Fig. 45 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda tuna*, July 1997.

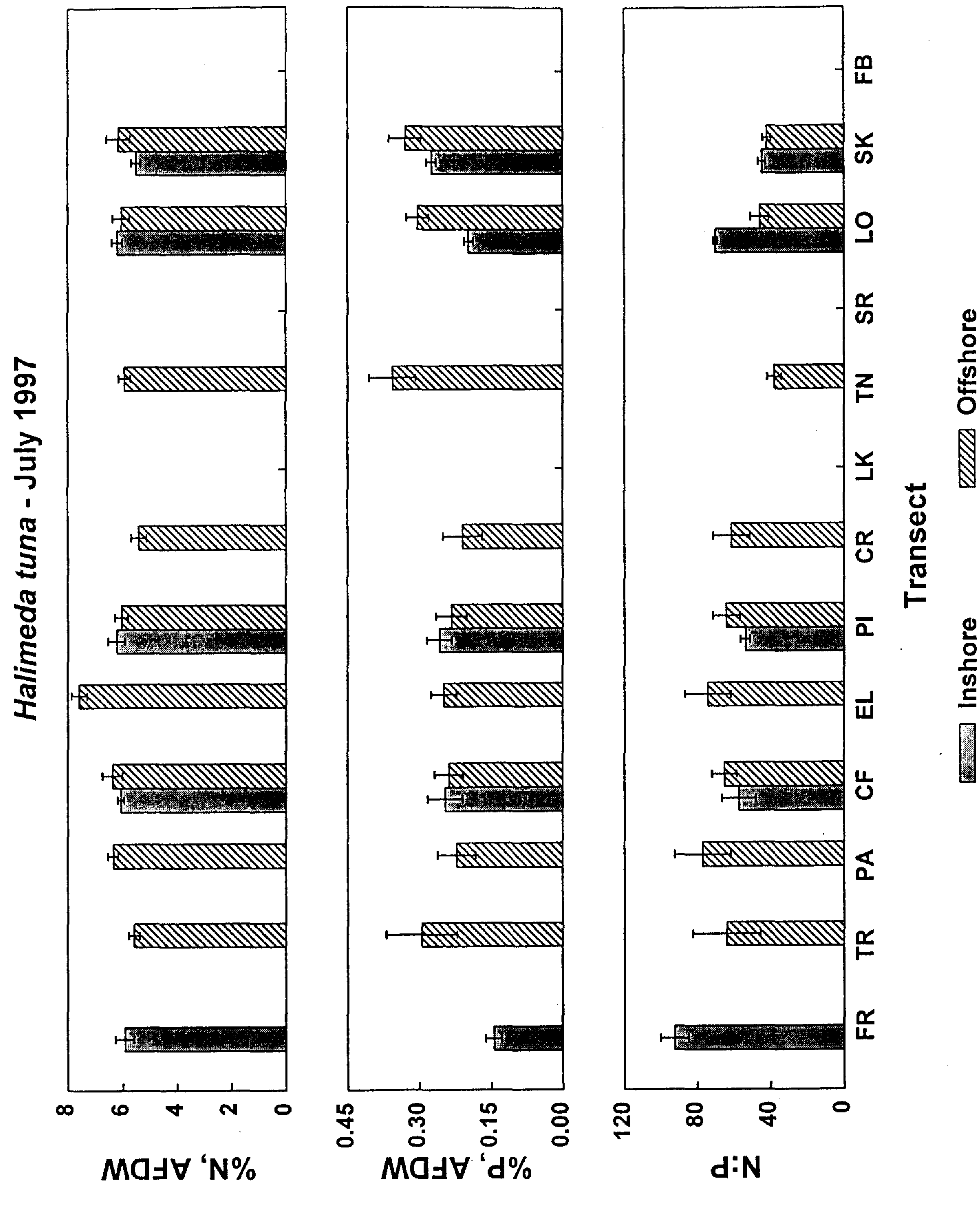

Fig. 46 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda tuna*, July 1997.

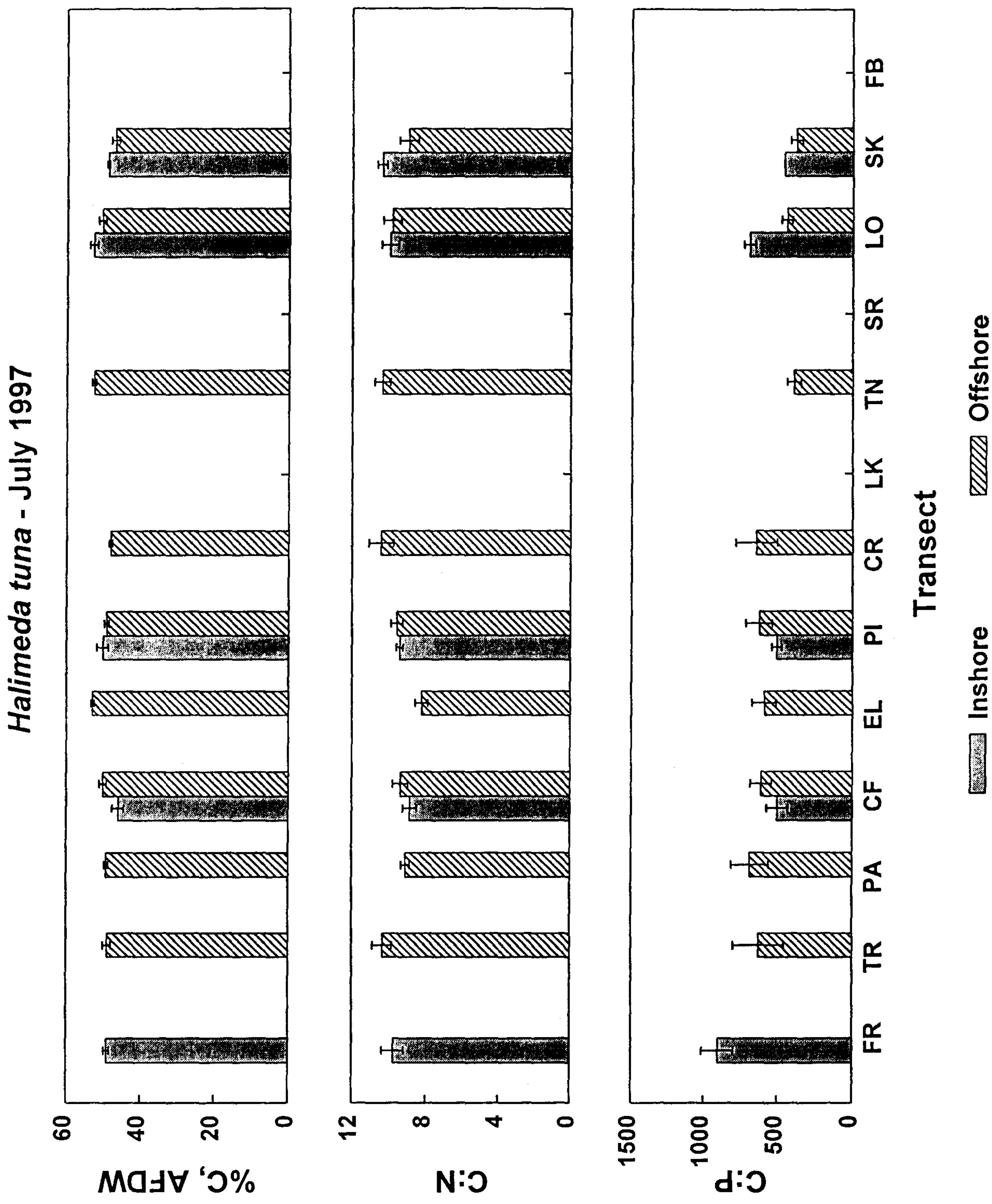

Fig. 47 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda tuna*, July 1997.

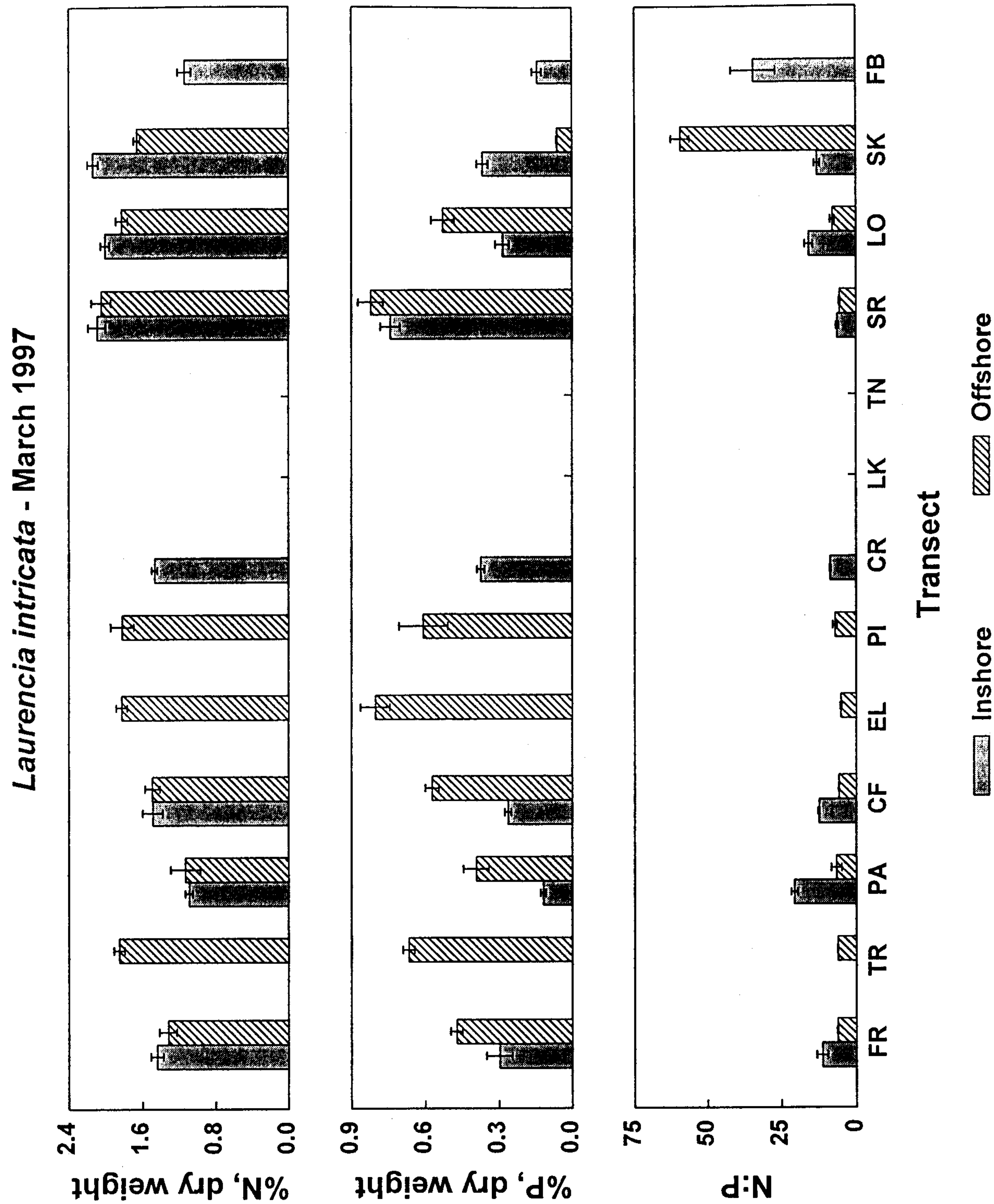

Fig. 48 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia intricata*, March 1997.

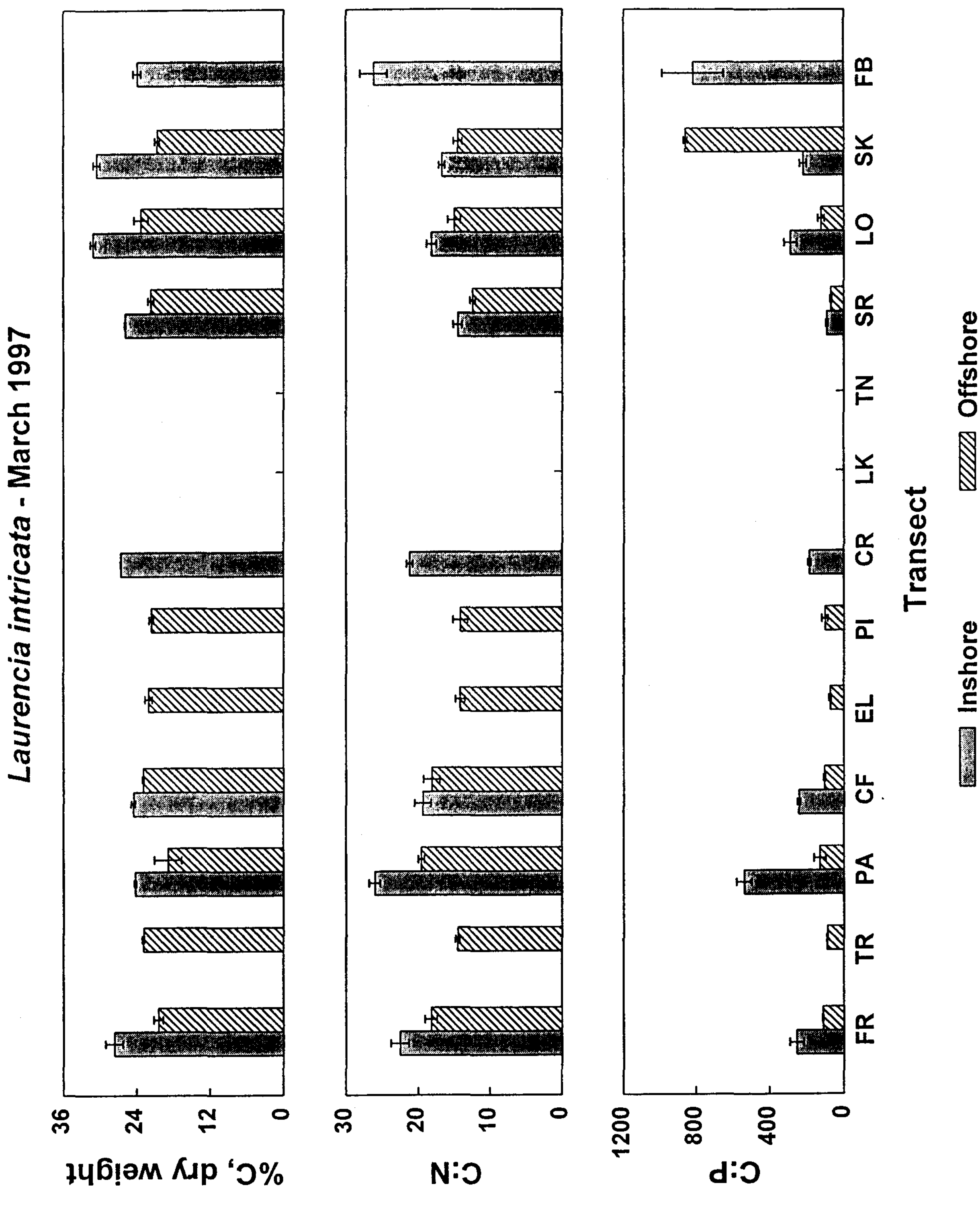

Fig. 49 **Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia intricata*, March 1997.**

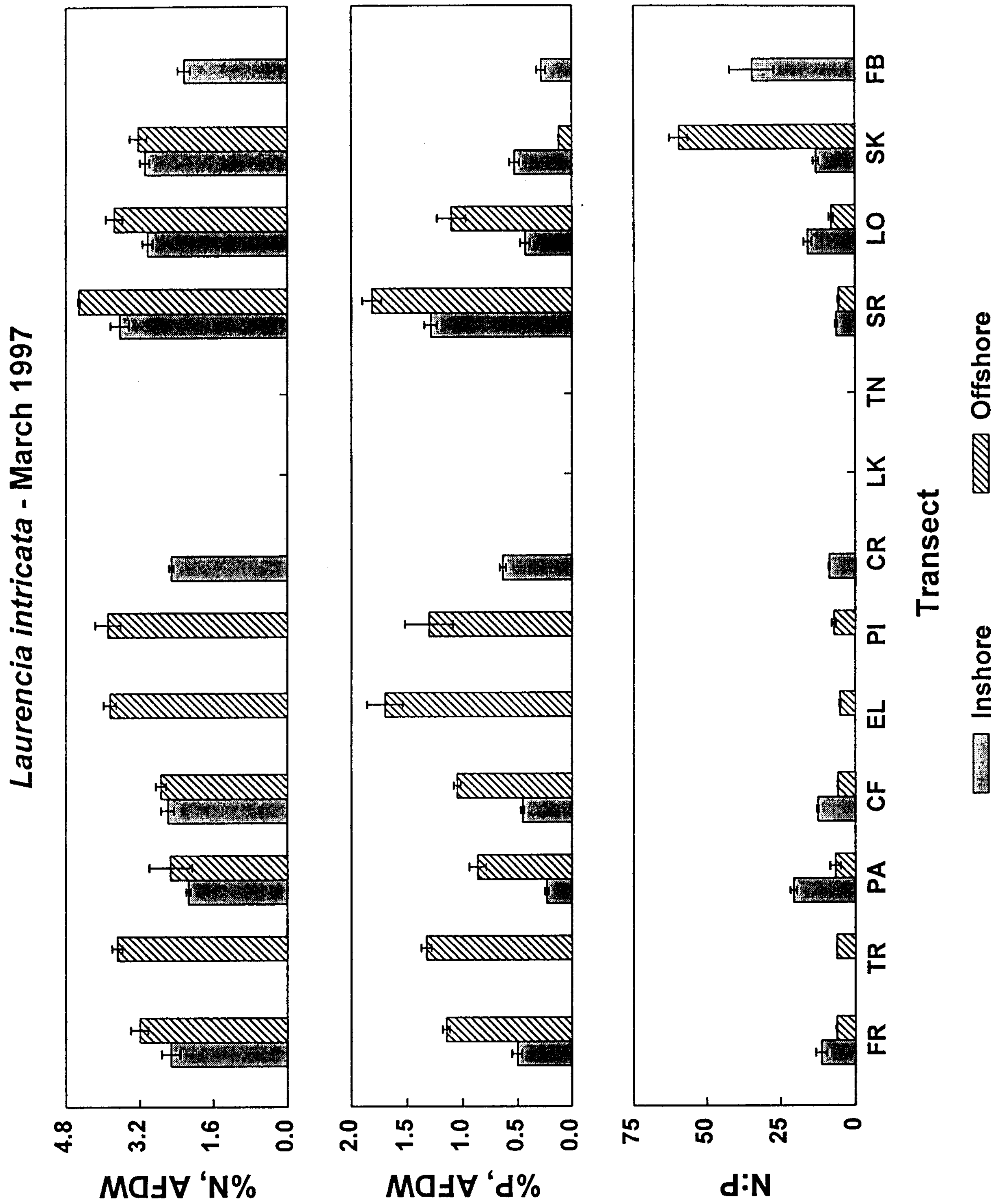

Fig. 50 **Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia intricata*, March 1997.**

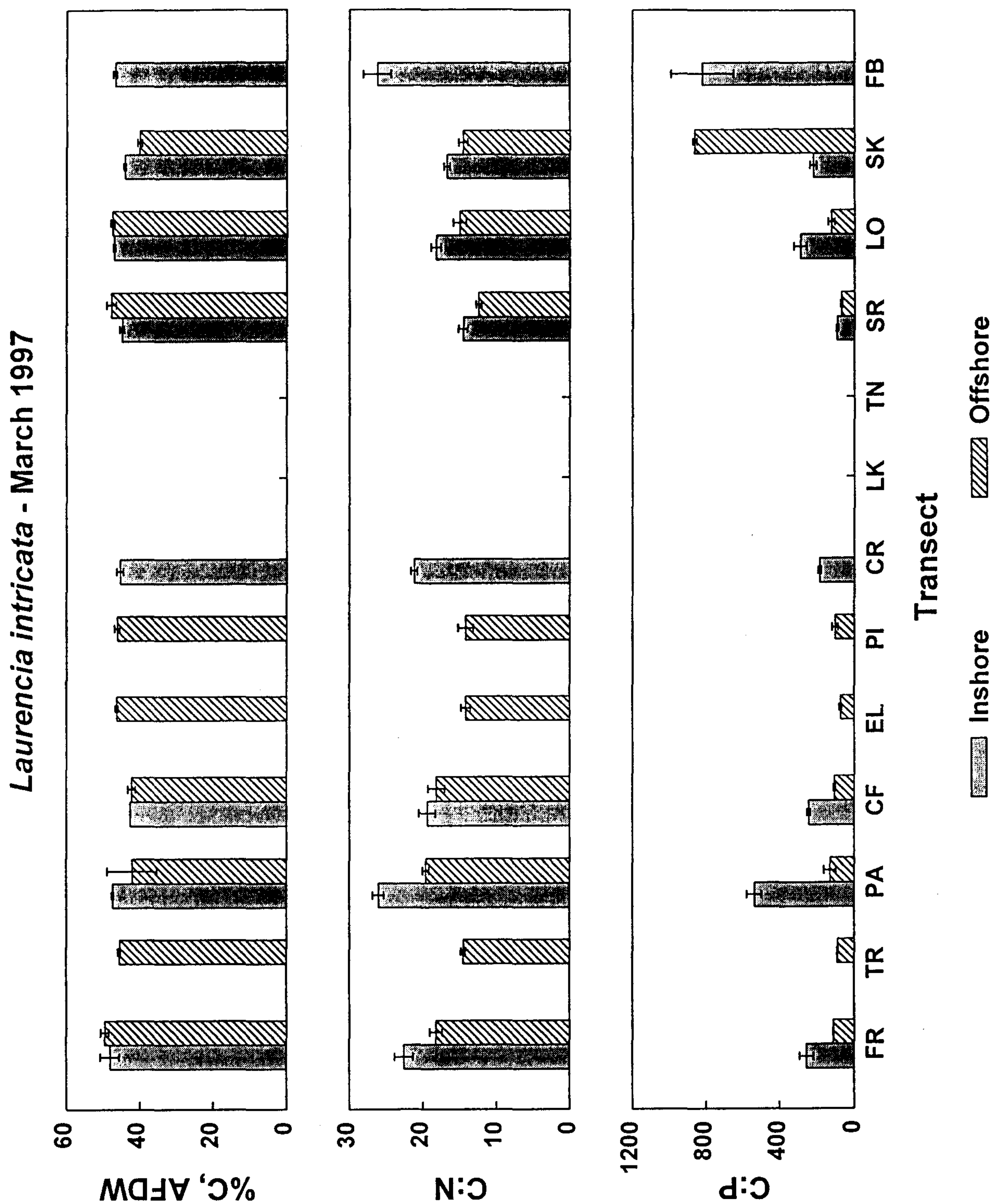

Fig. 51 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia intricata*, March 1997.

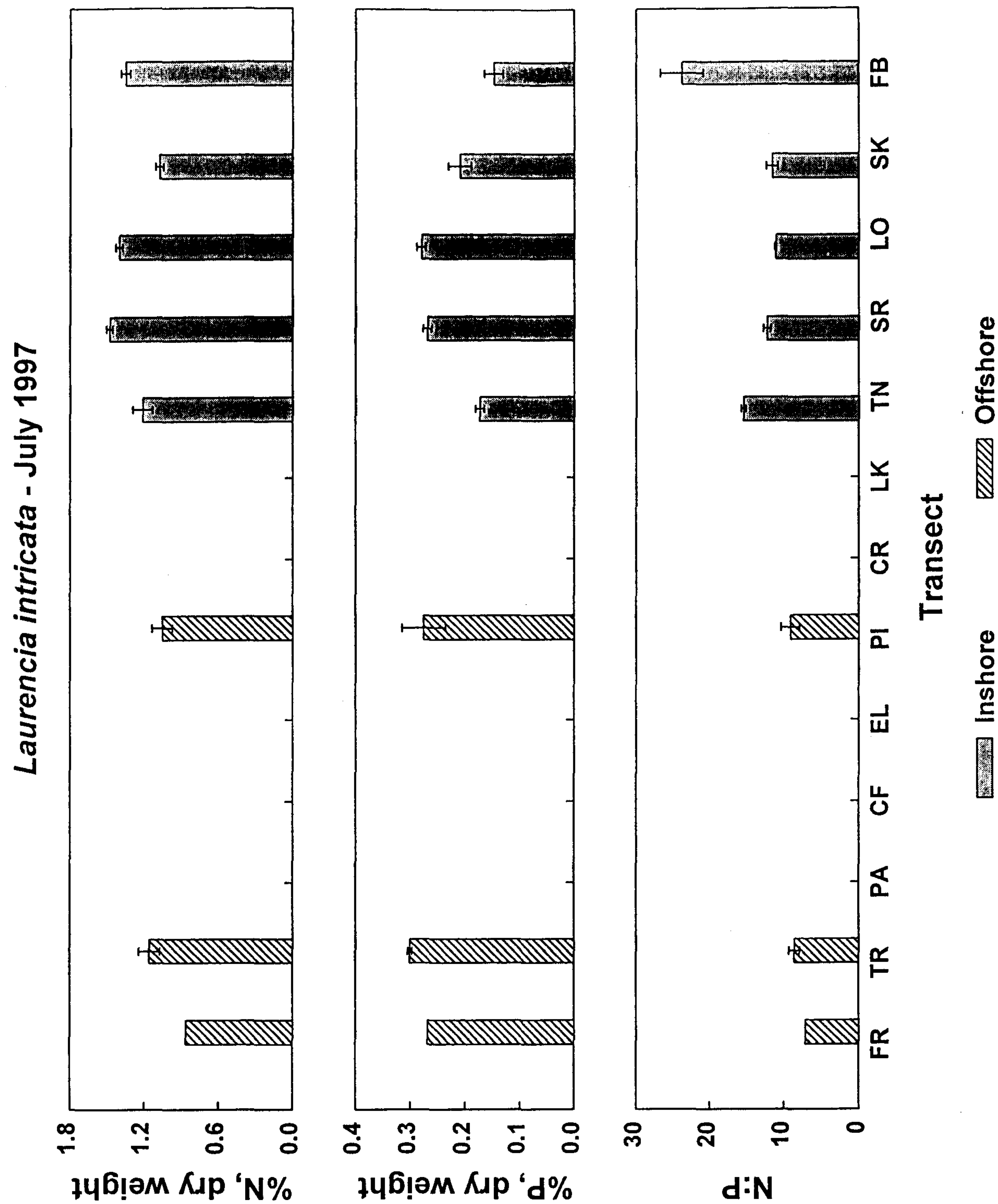

Fig. 52 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia intricata*, July 1997.

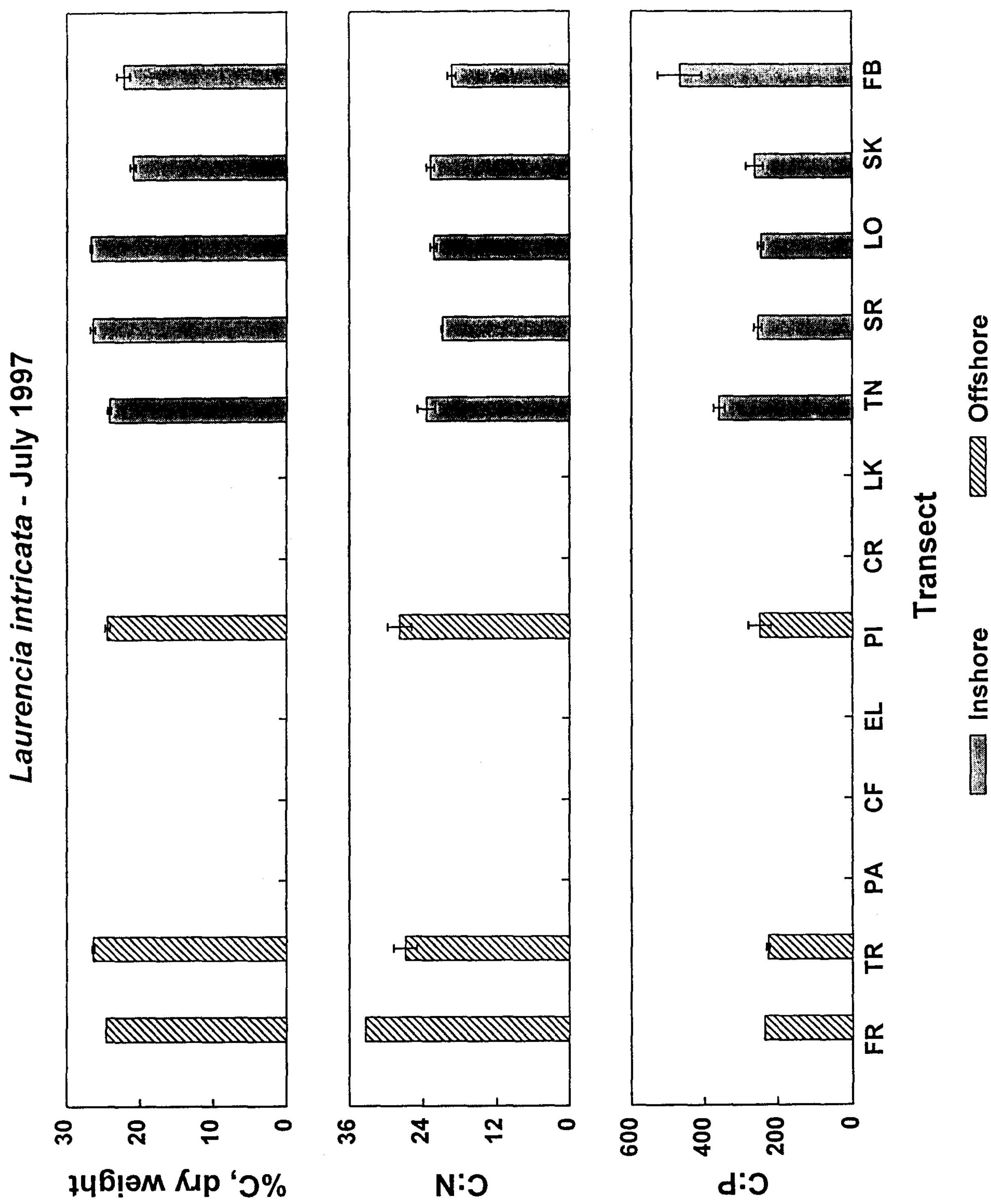

Fig. 53 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia intricata*, July 1997.

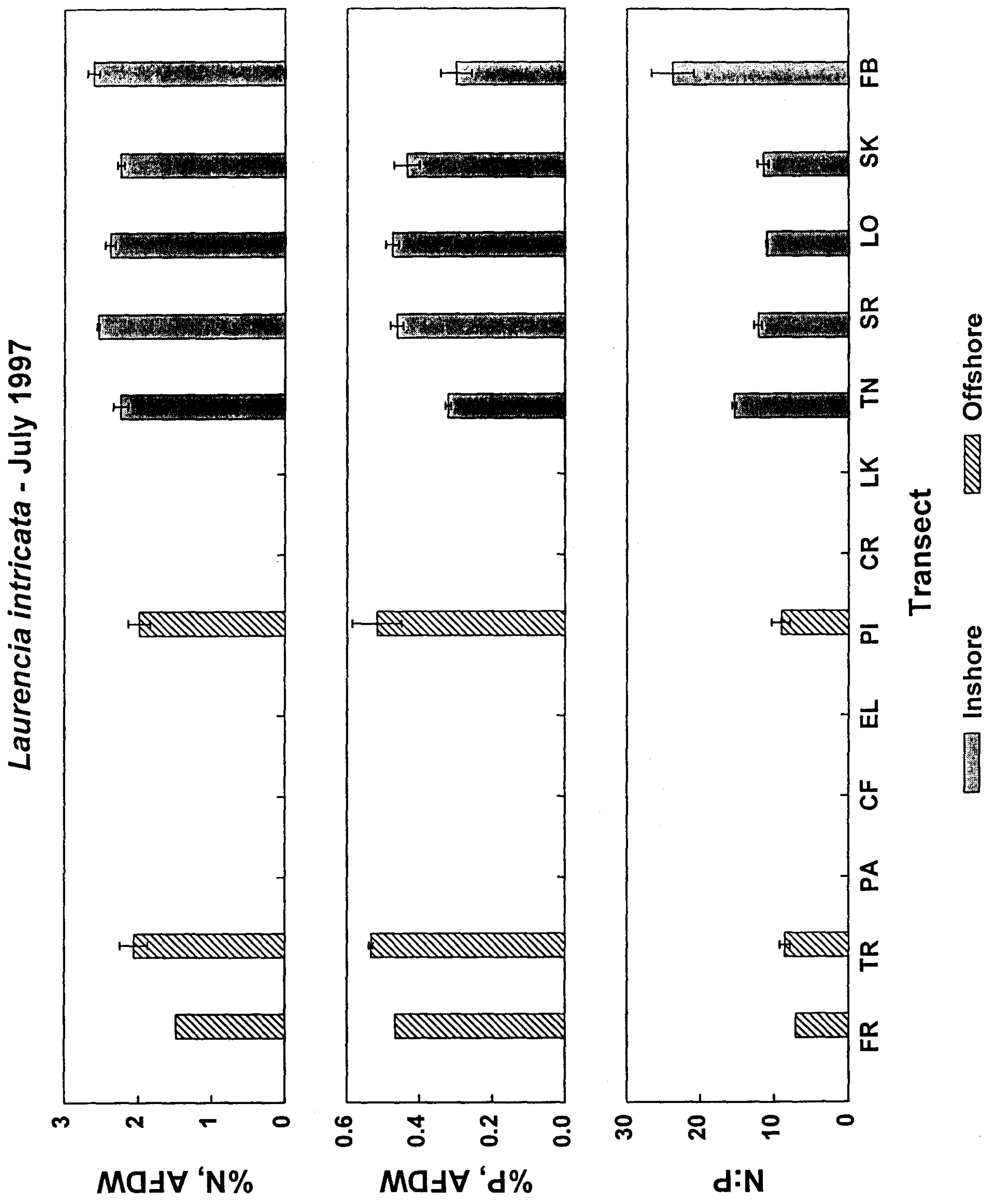

Fig. 54 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia intricata*, July 1997.

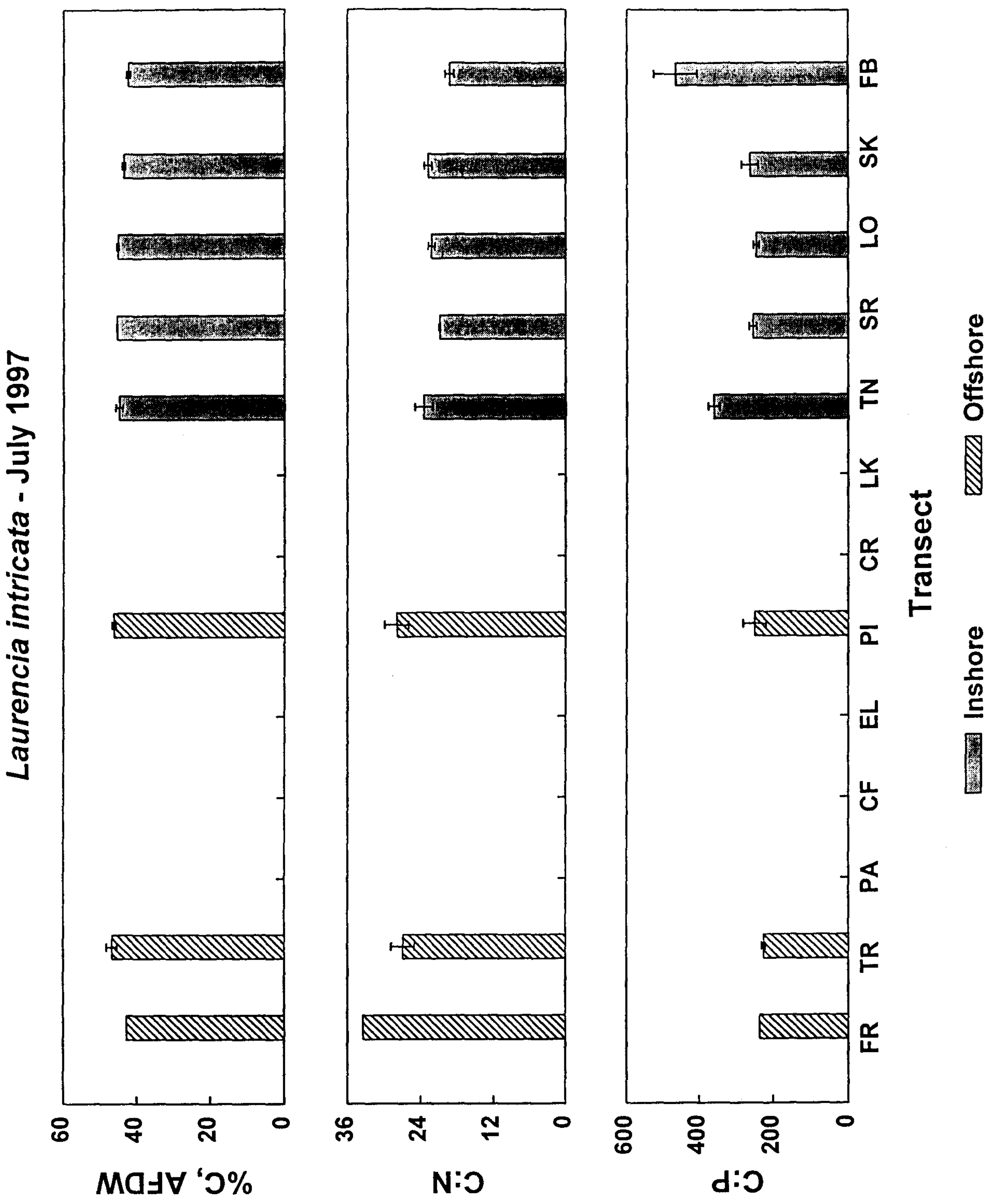

Fig. 55 **Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia intricata*, July 1997.**

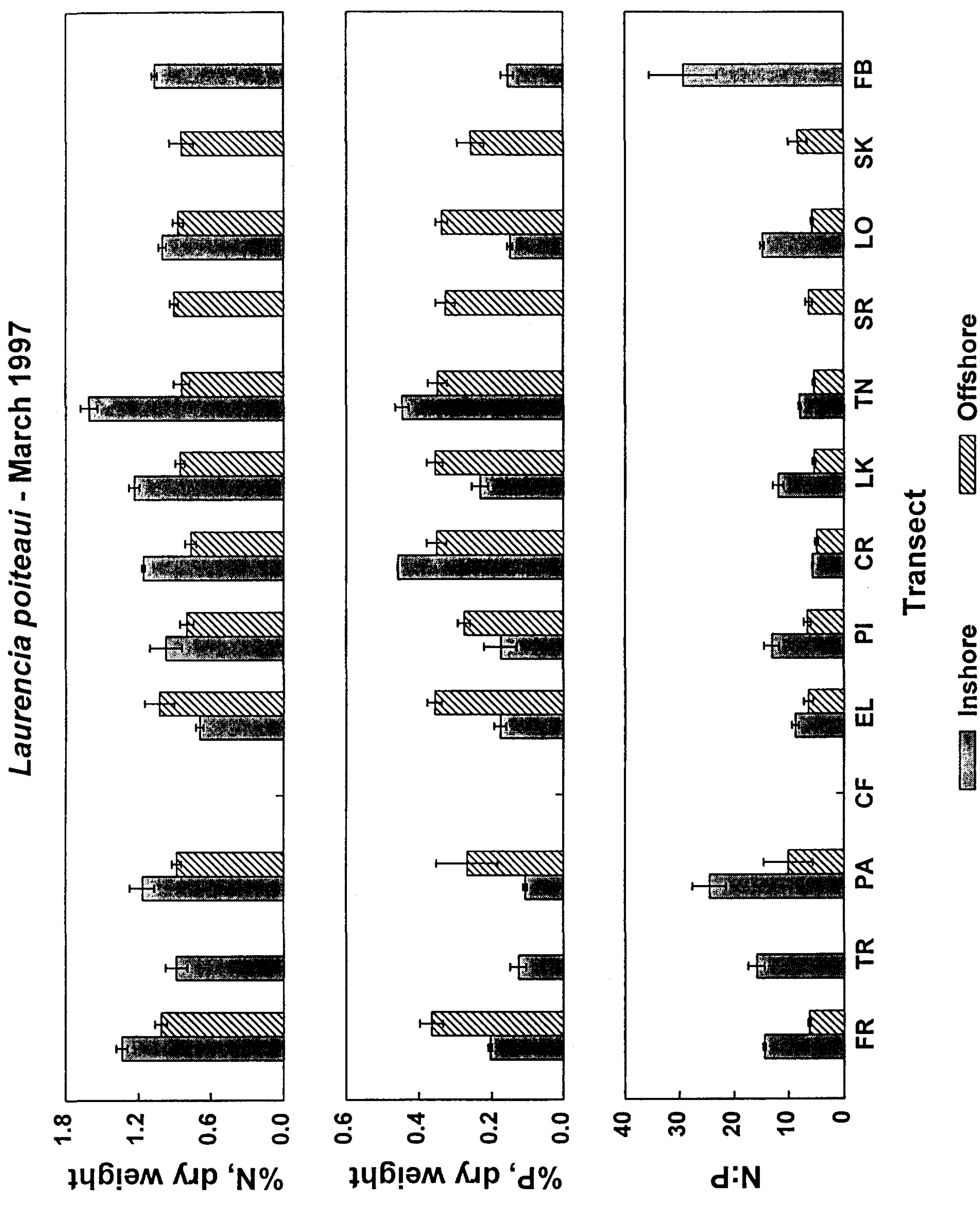

Fig. 56 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia poiteaui*, March 1997.

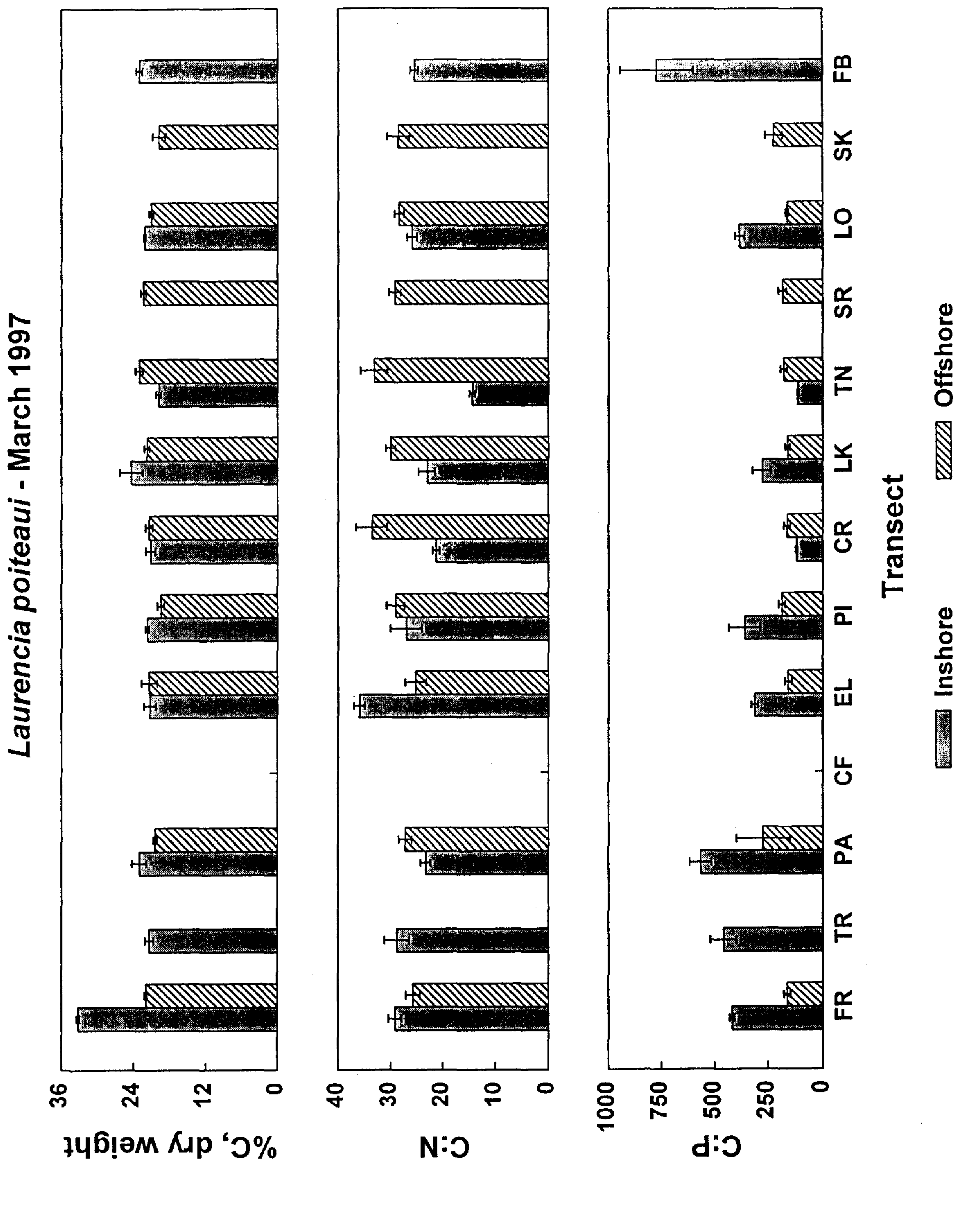

Fig. 57 **Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia poiteaui*, March 1997.**

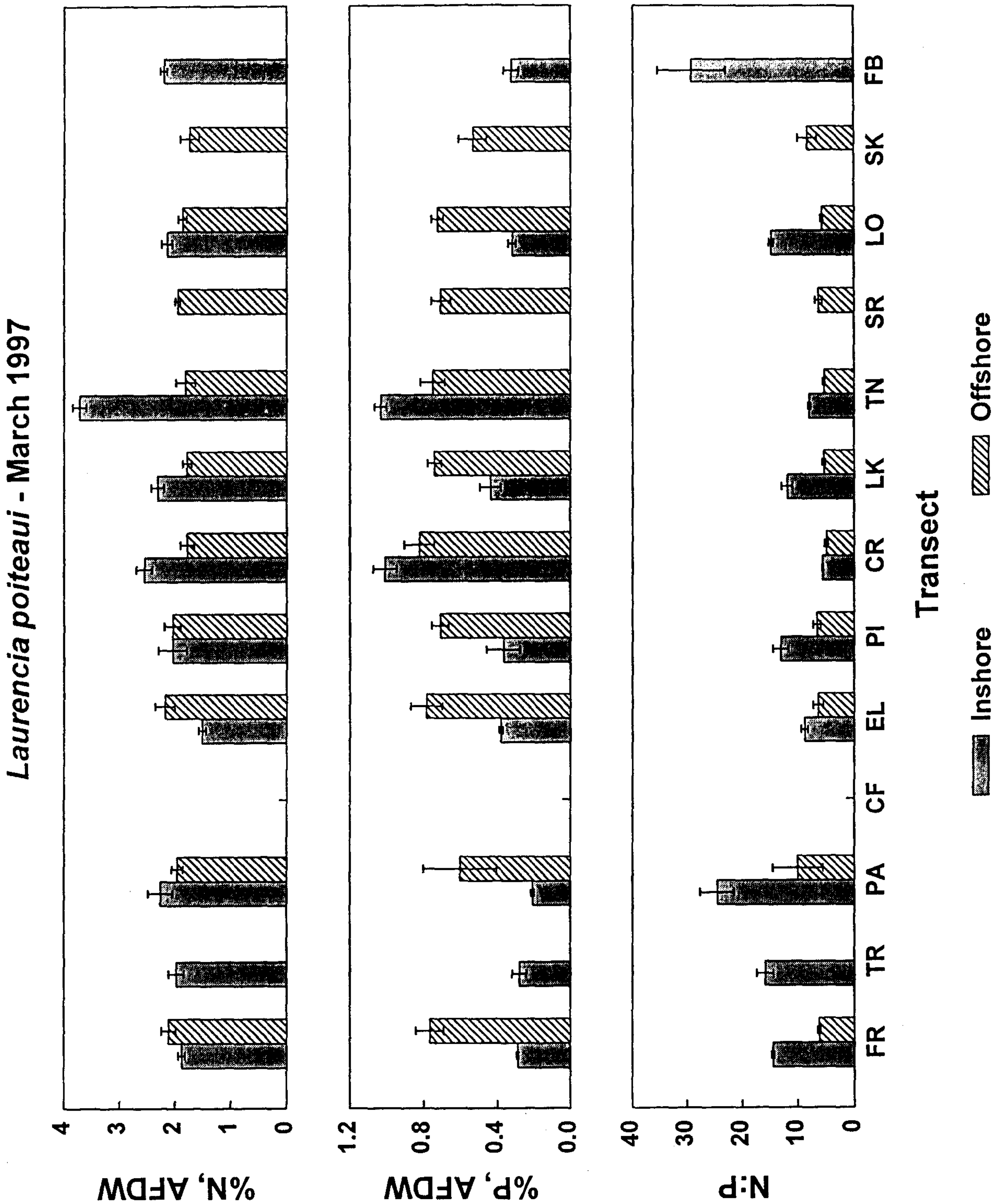

Fig. 58 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia poiteaui*, March 1997.

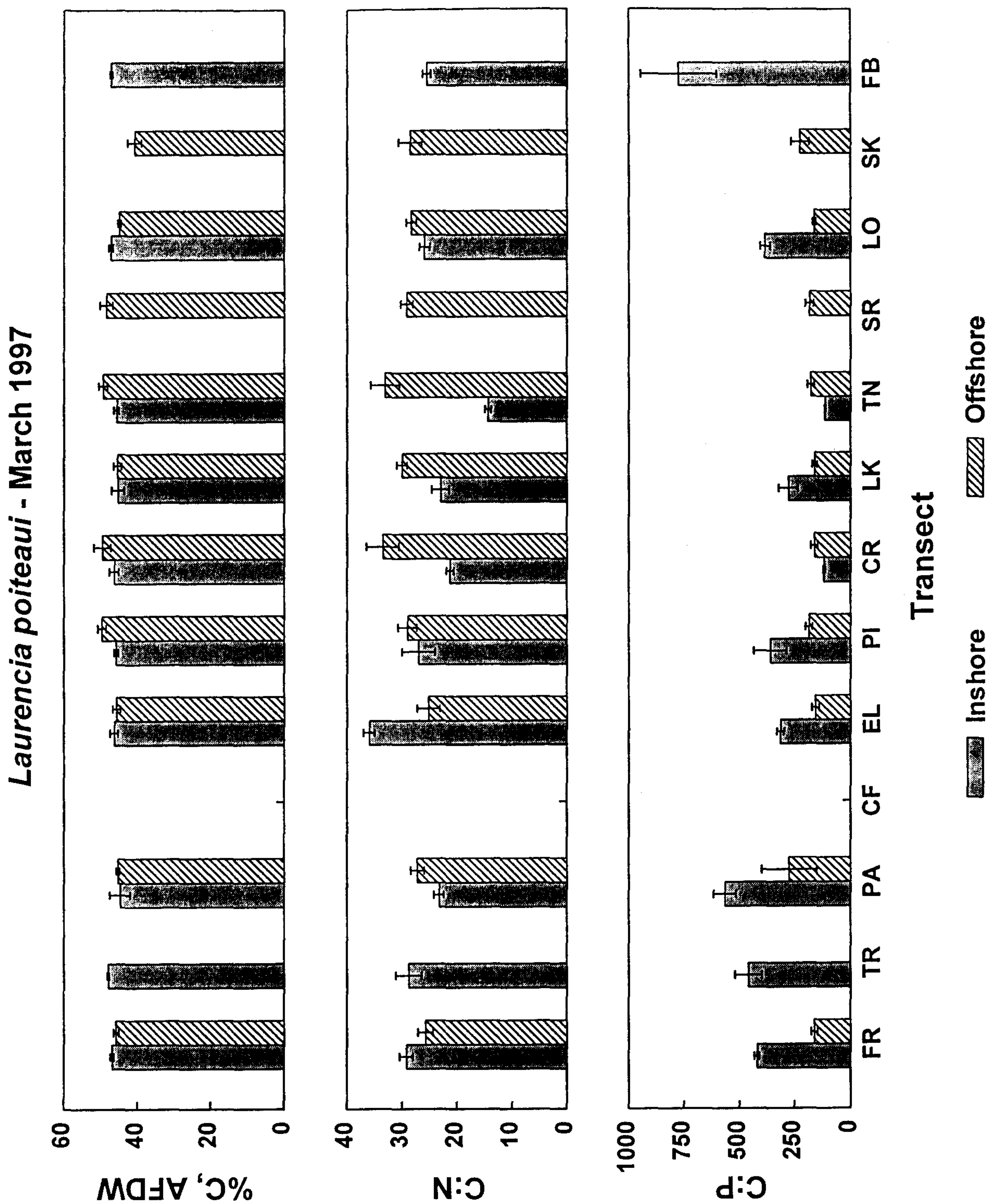

Fig. 59 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia poiteaui*, March 1997.

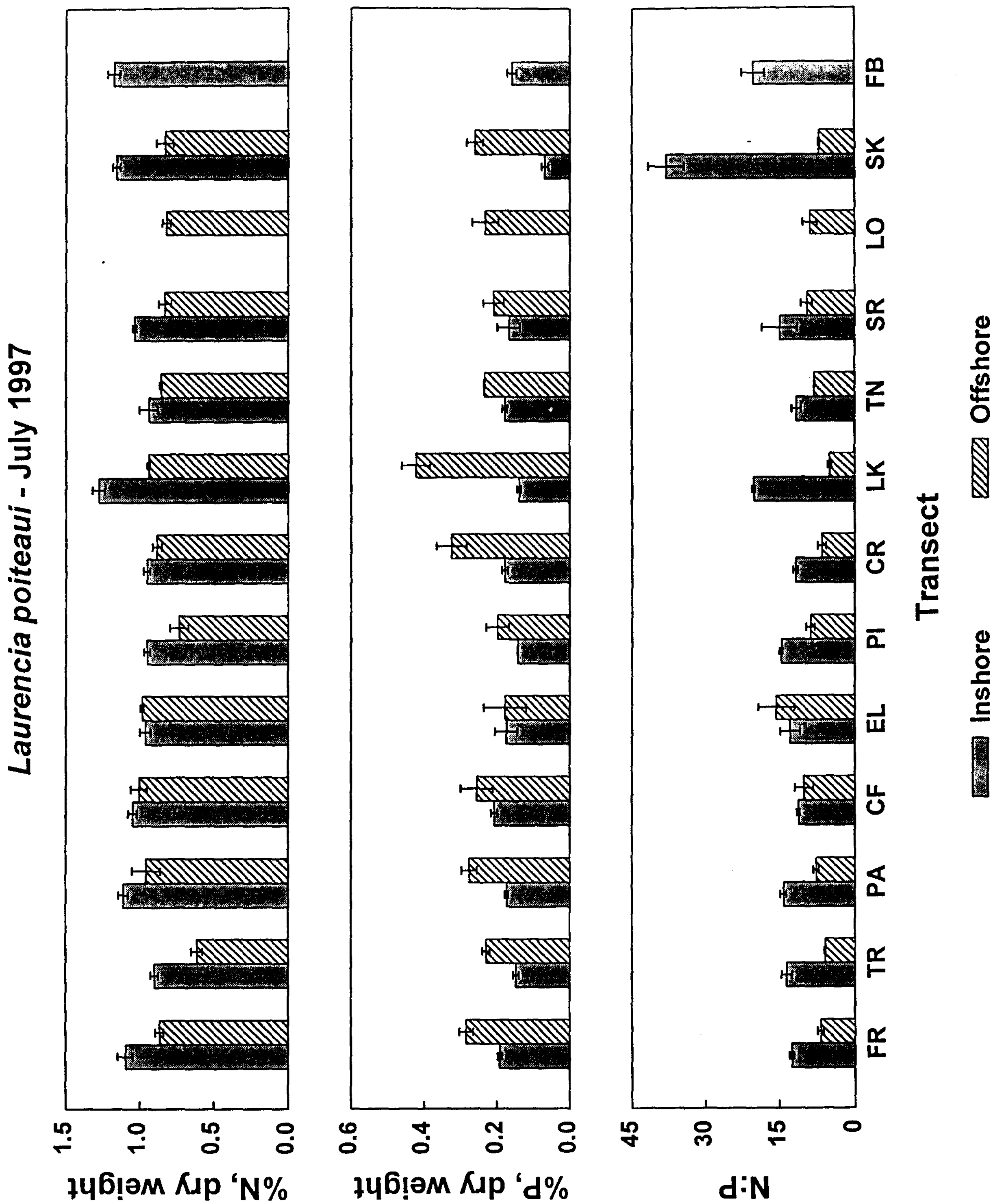

Fig. 60 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia poiteaui*, July 1997.

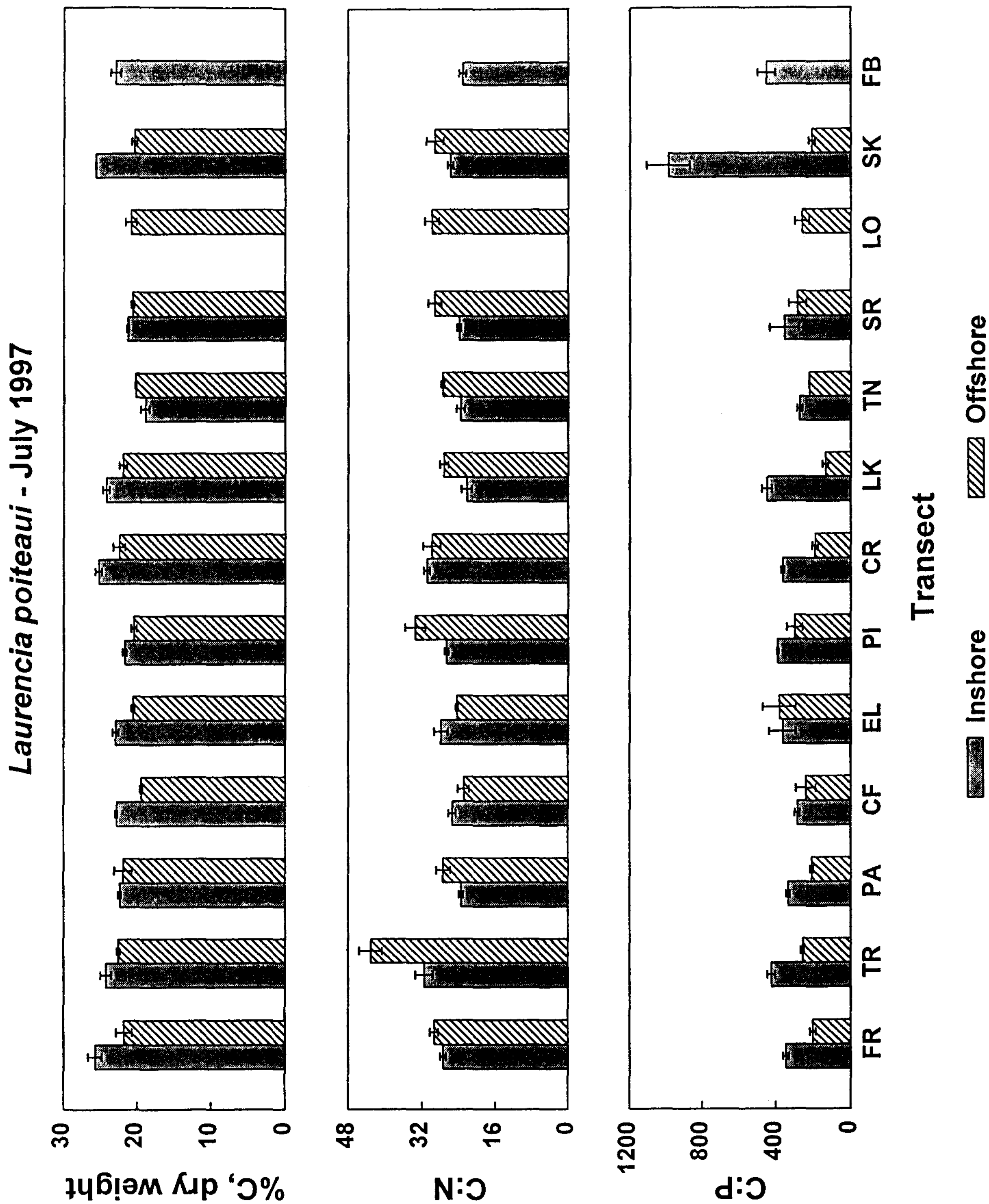

Fig. 61 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia poiteaui*, July 1997.

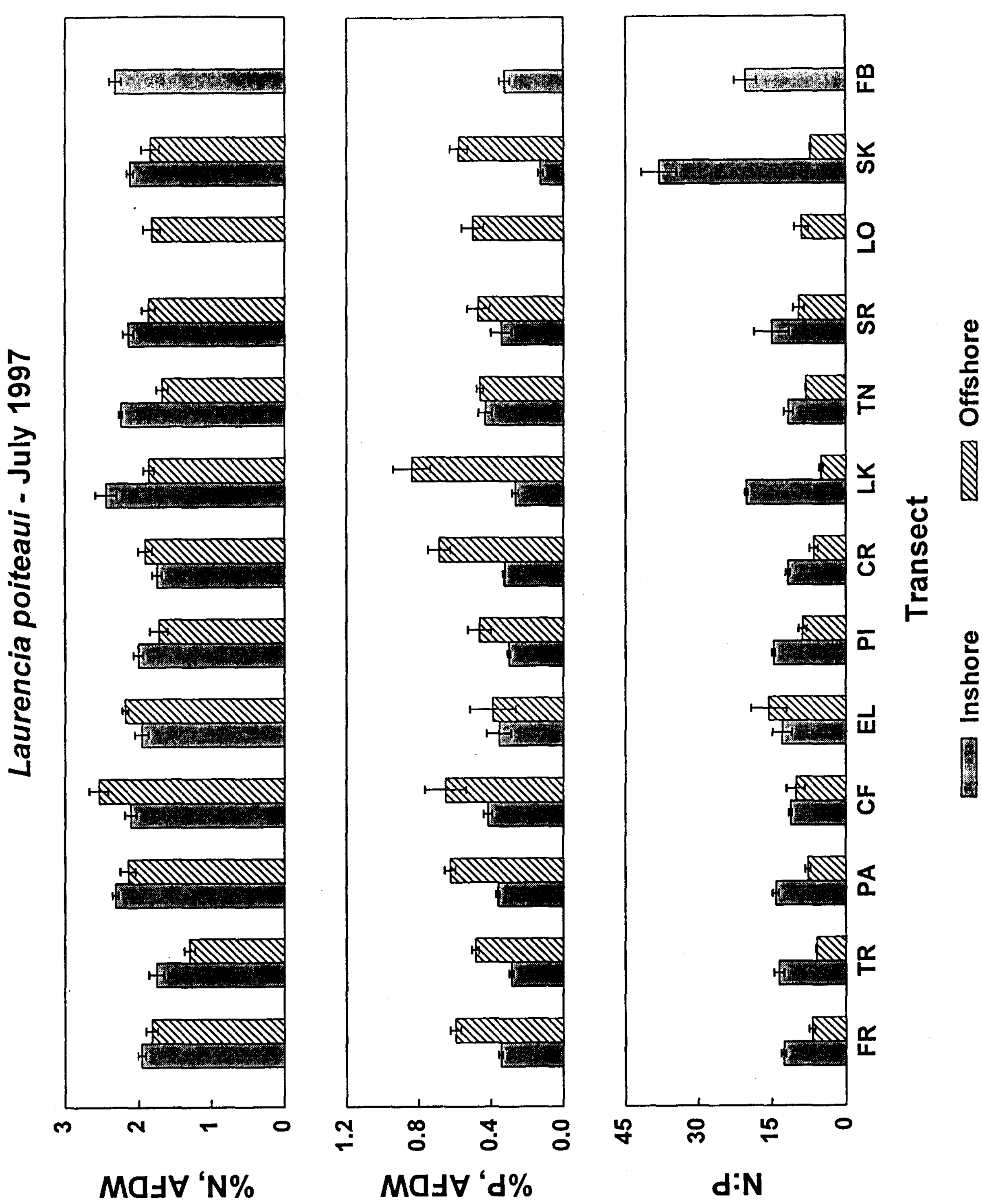

Fig. 62 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia poiteaui*, July 1997.

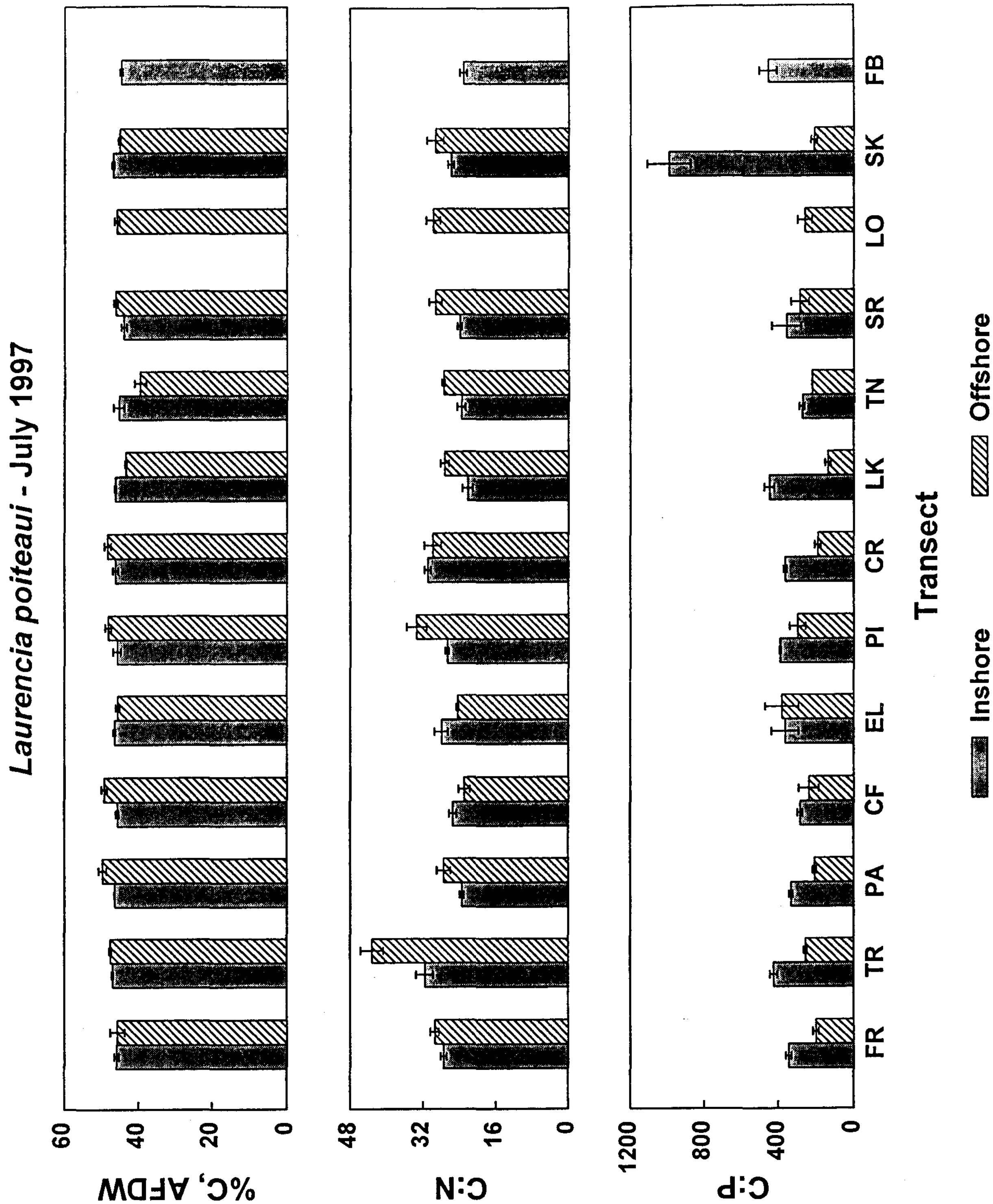

Fig. 63 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia poiteaui*, July 1997.

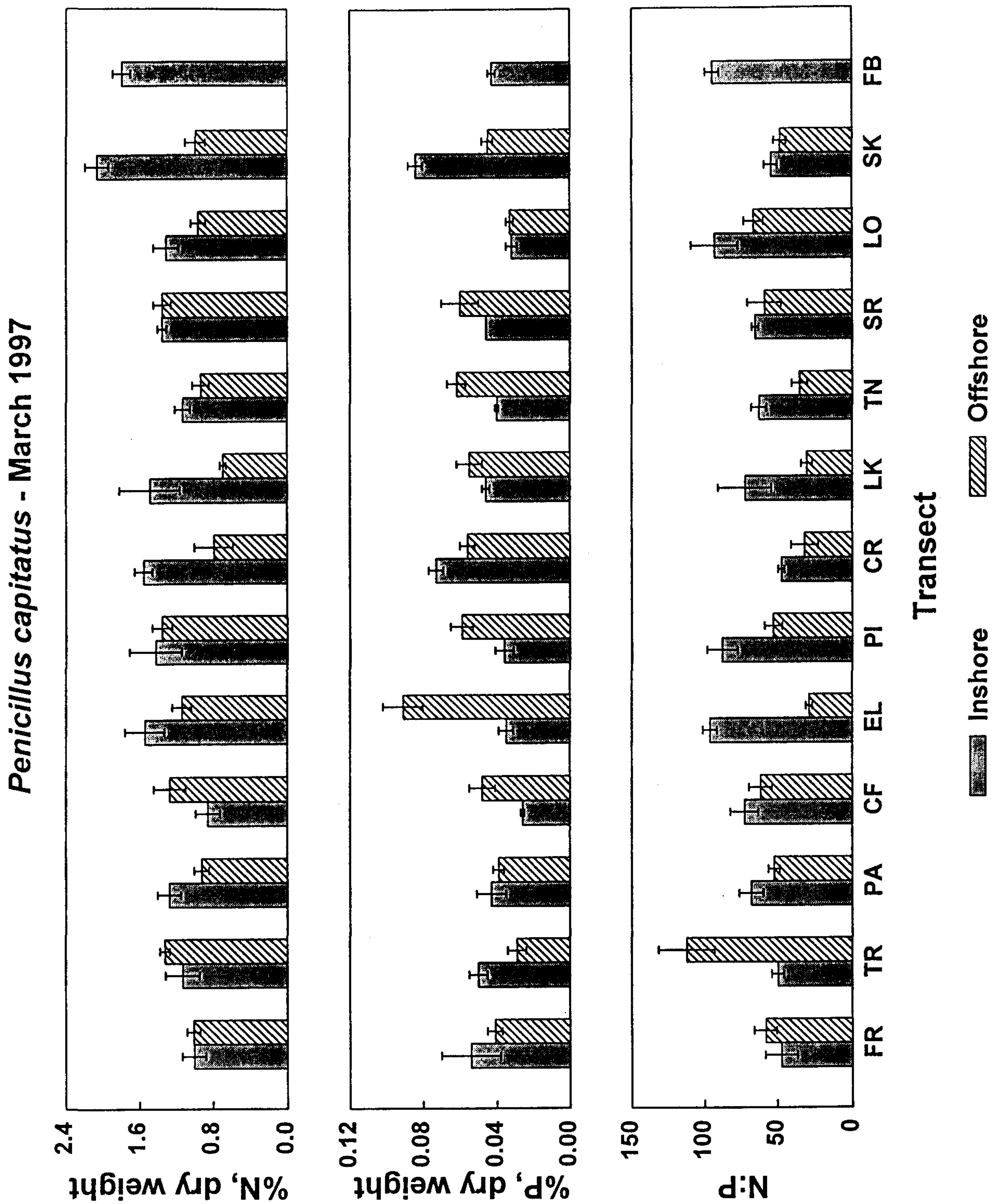

Fig. 64 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Penicillus capitatus*, March 1997.

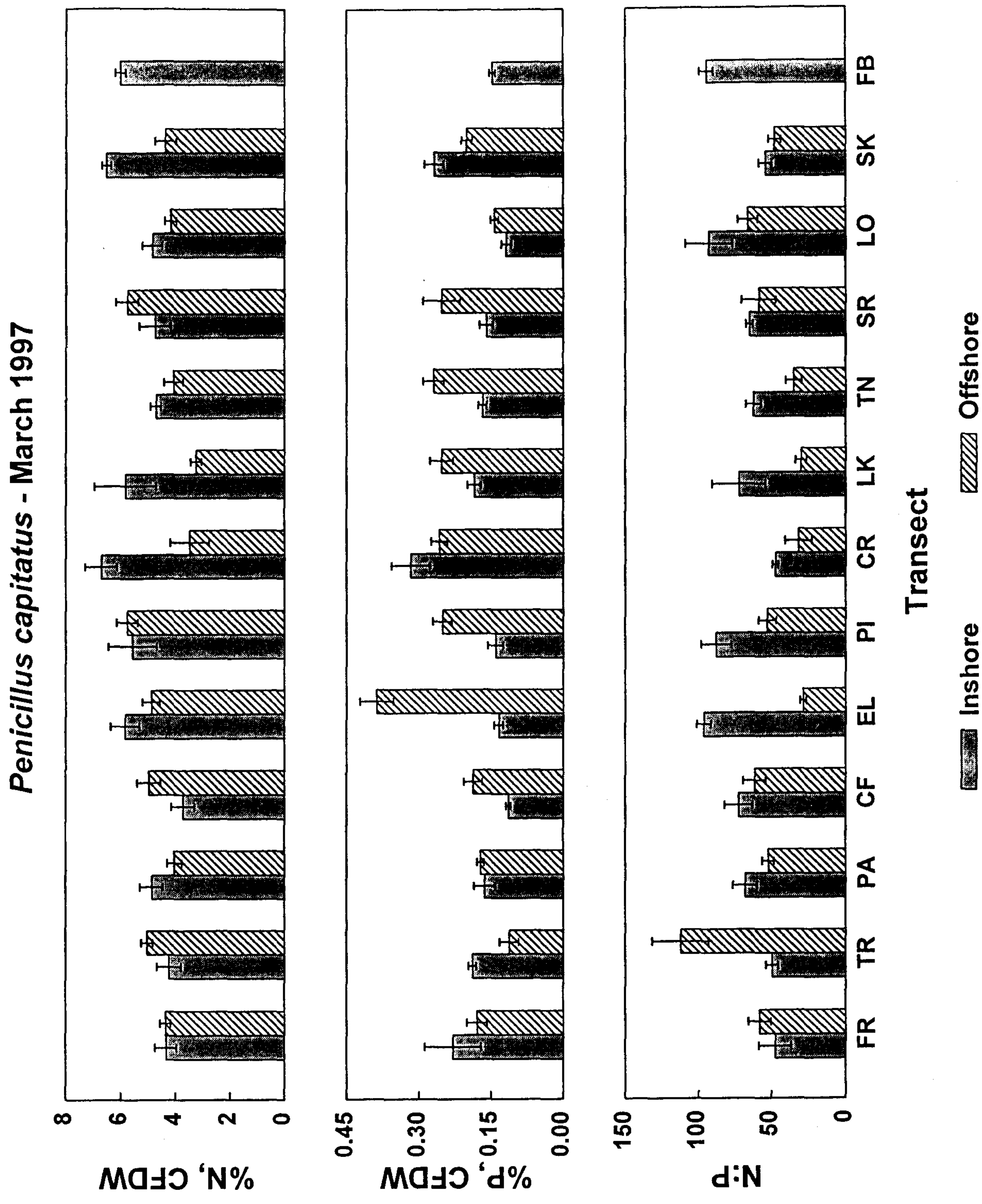

Fig. 65 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus capitatus*, March 1997.

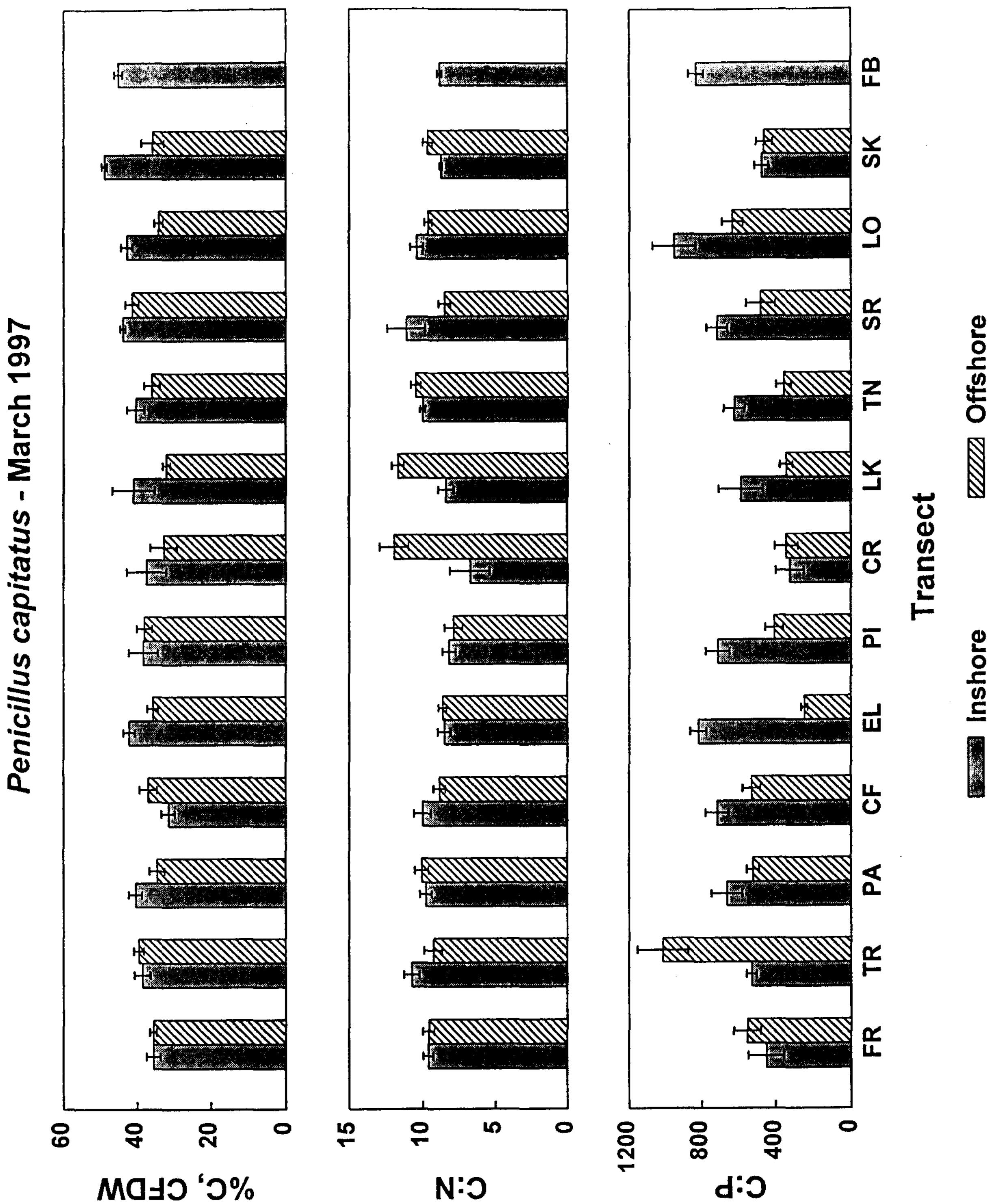

Fig. 66 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus capitatus*, March 1997.

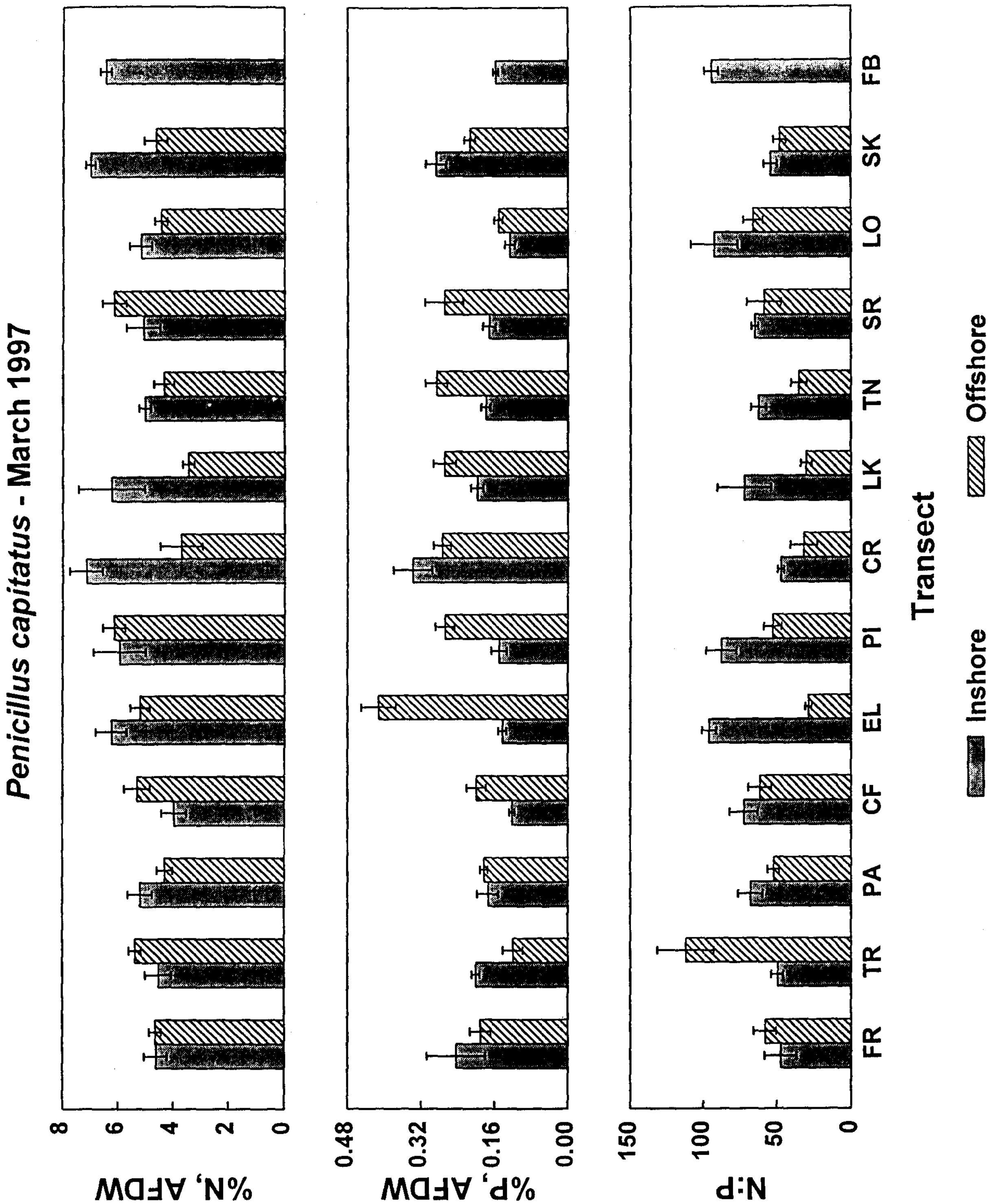

Fig. 67 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus capitatus*, March 1997.

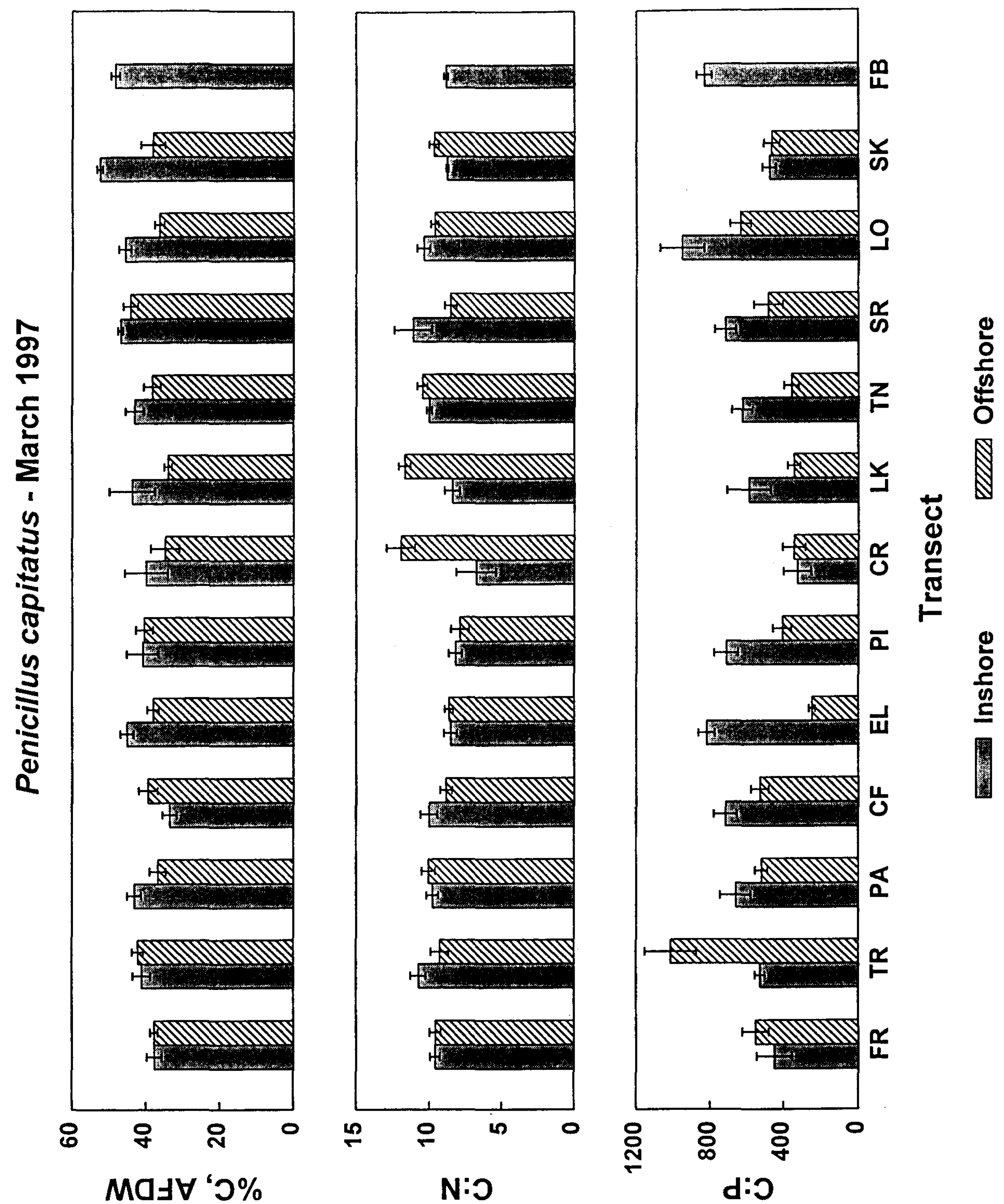

Fig. 68 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus capitatus*, March 1997.

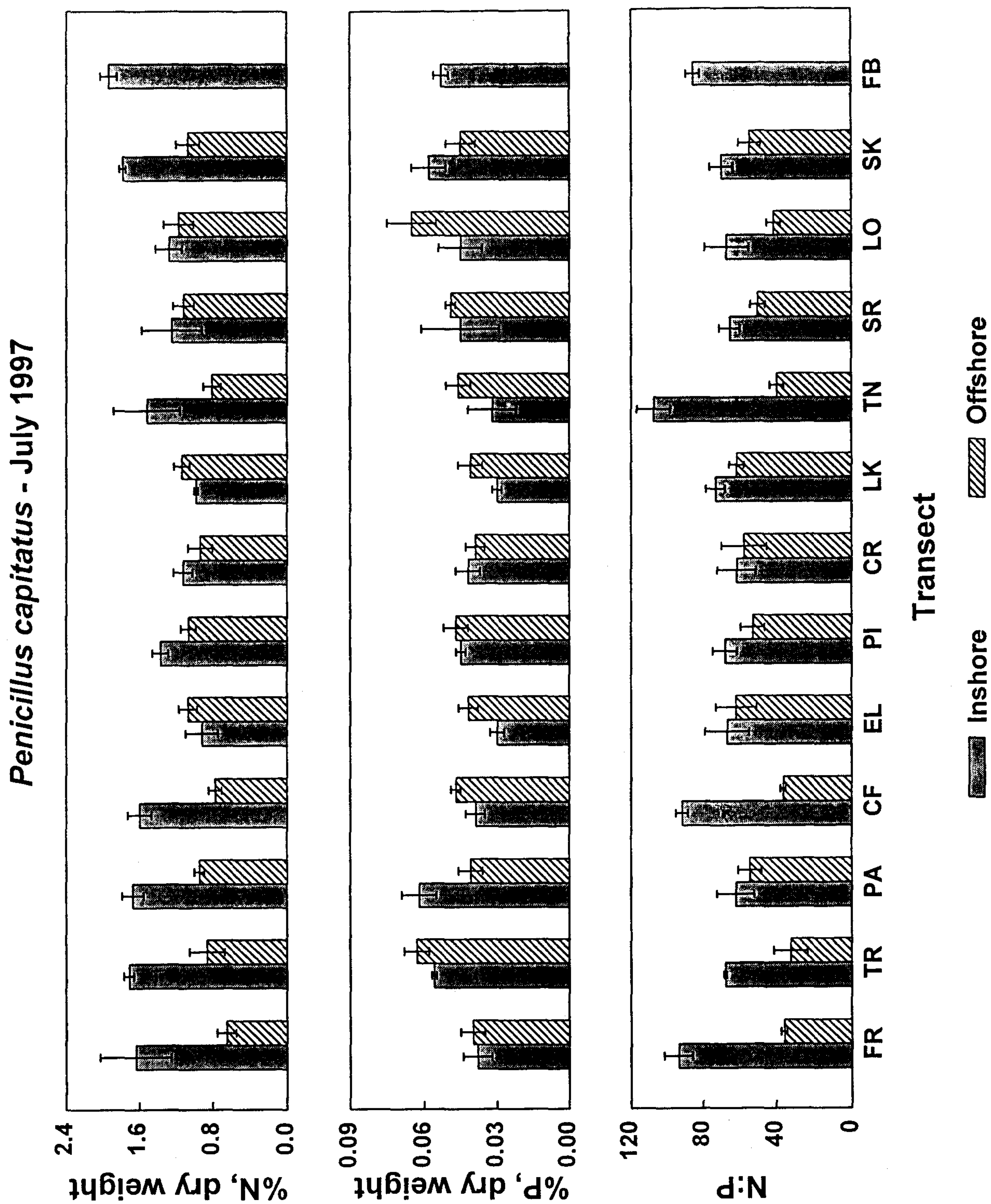

Fig. 69 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Penicillus capitatus*, July 1997.

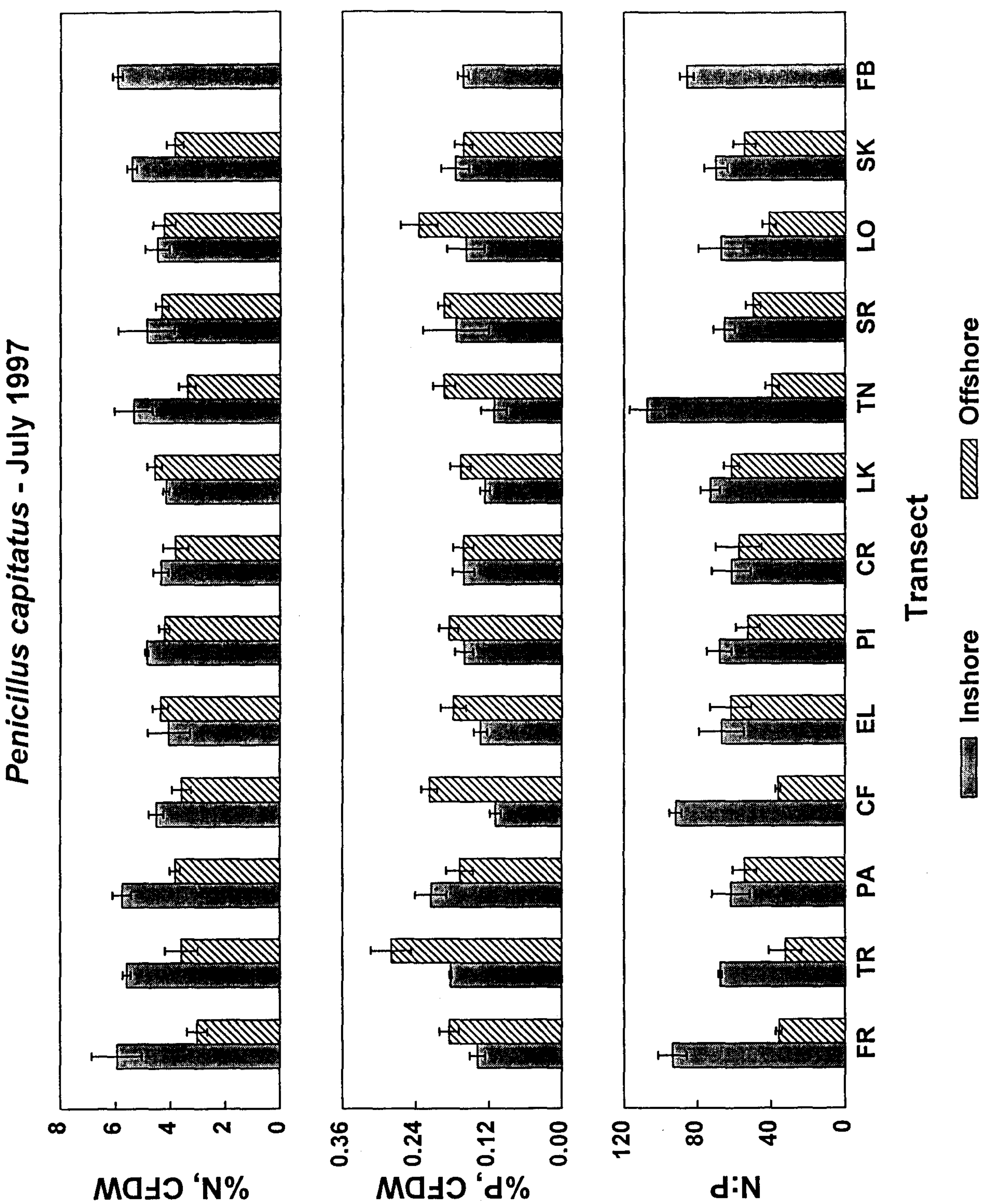

Fig. 70 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus capitatus*, July 1997.

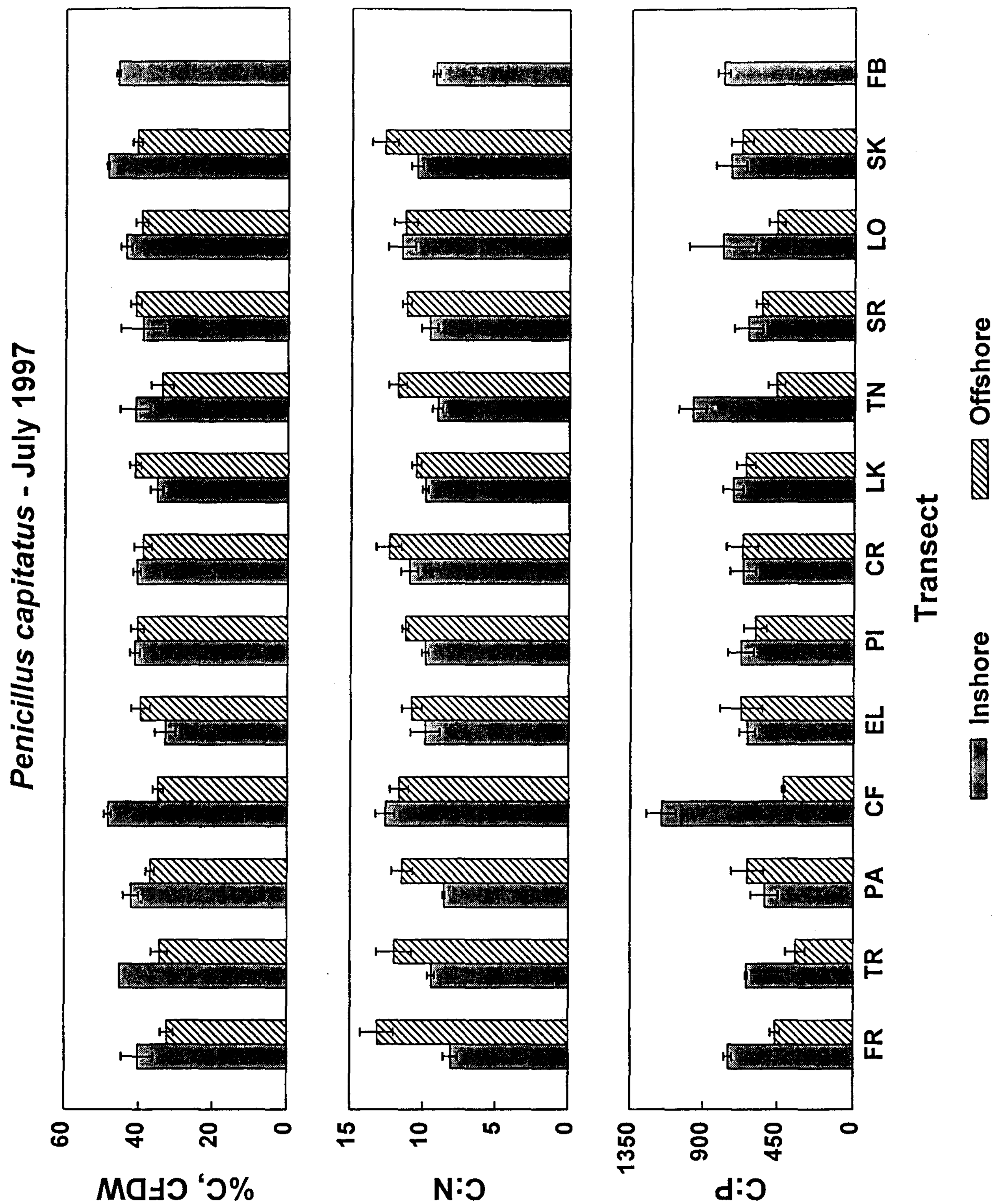

Fig. 71 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus capitatus*, July 1997.

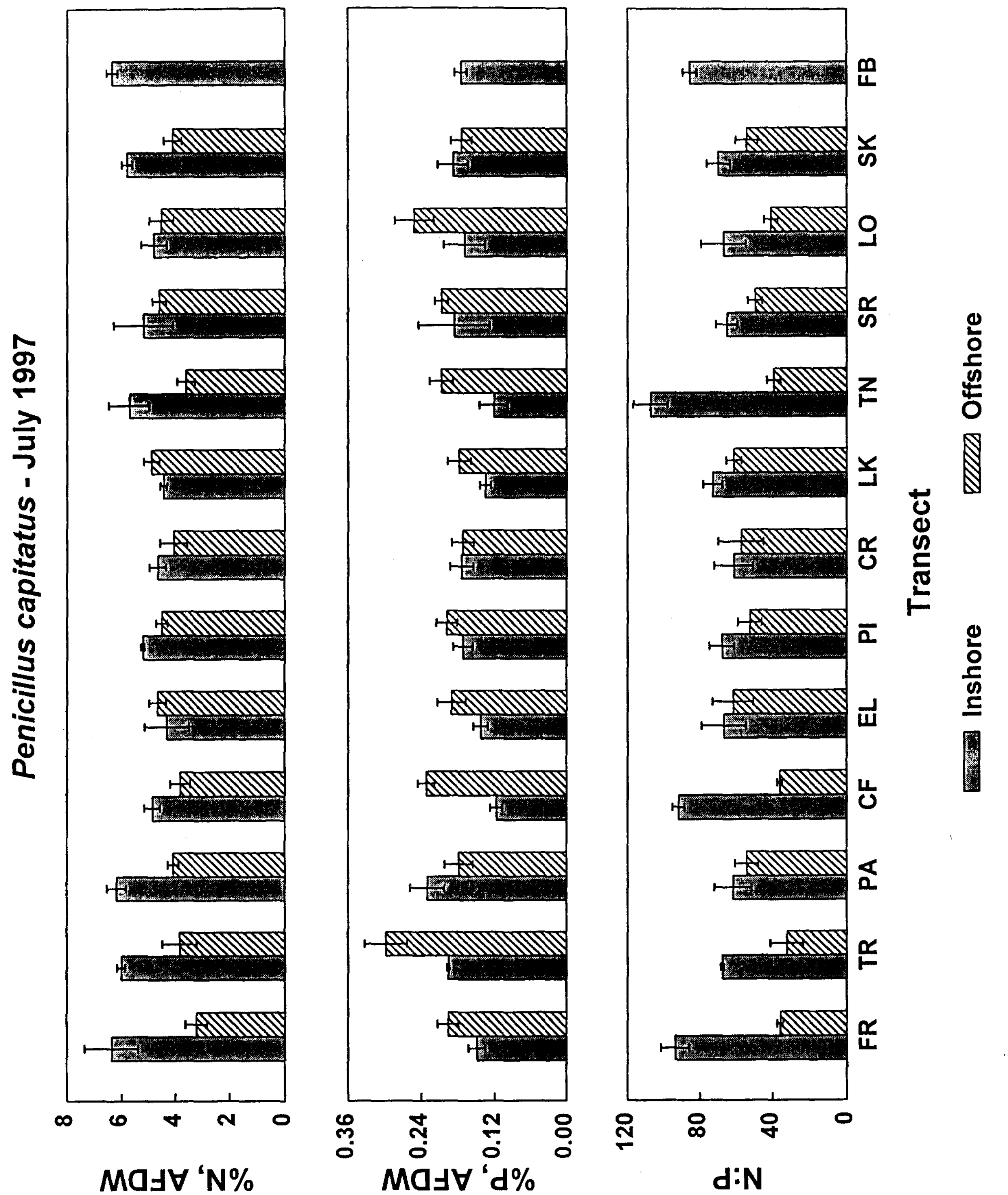

Fig. 72 **Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus capitatus*, July 1997.**

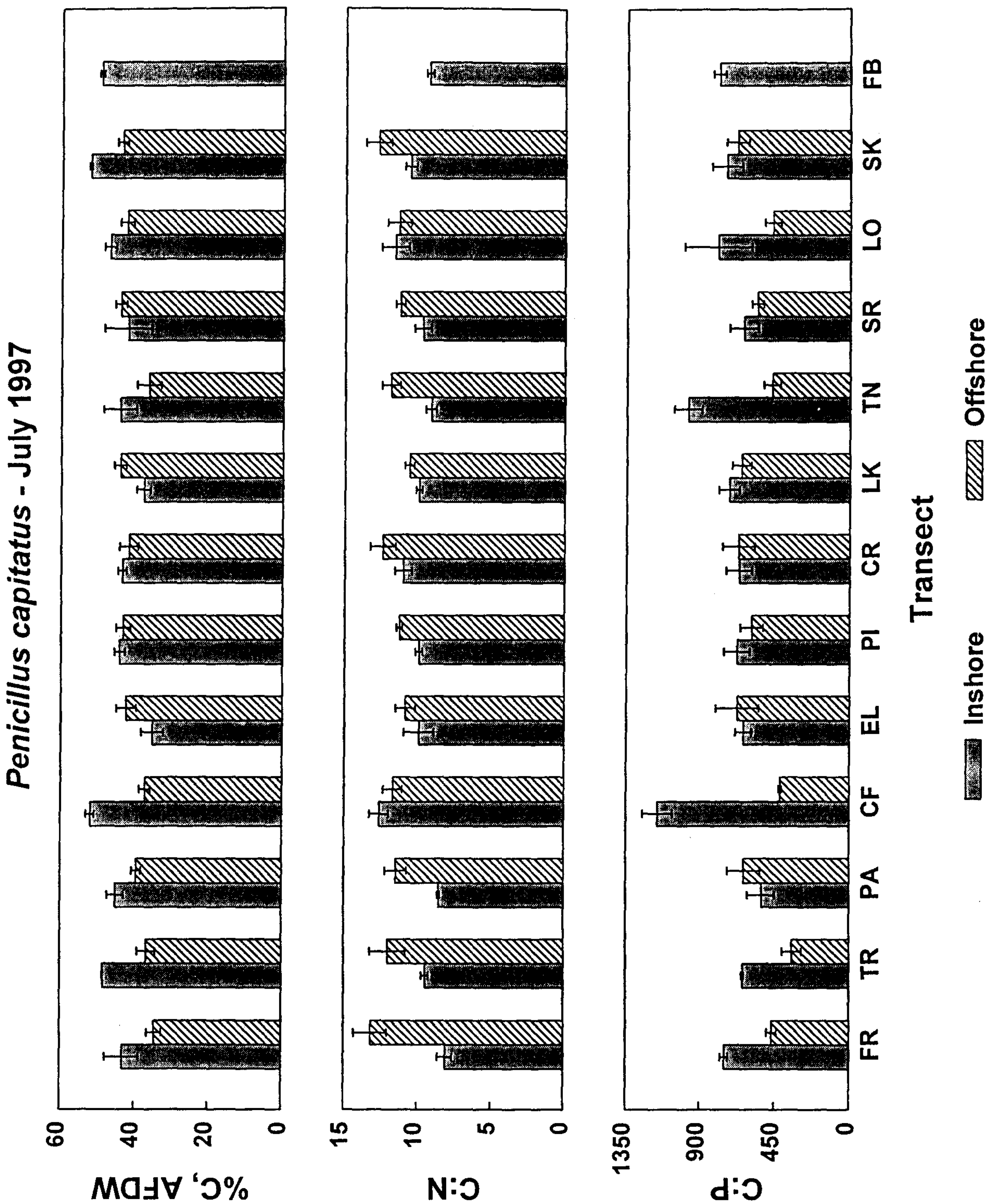

Fig. 73 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus capitatus*, July 1997.

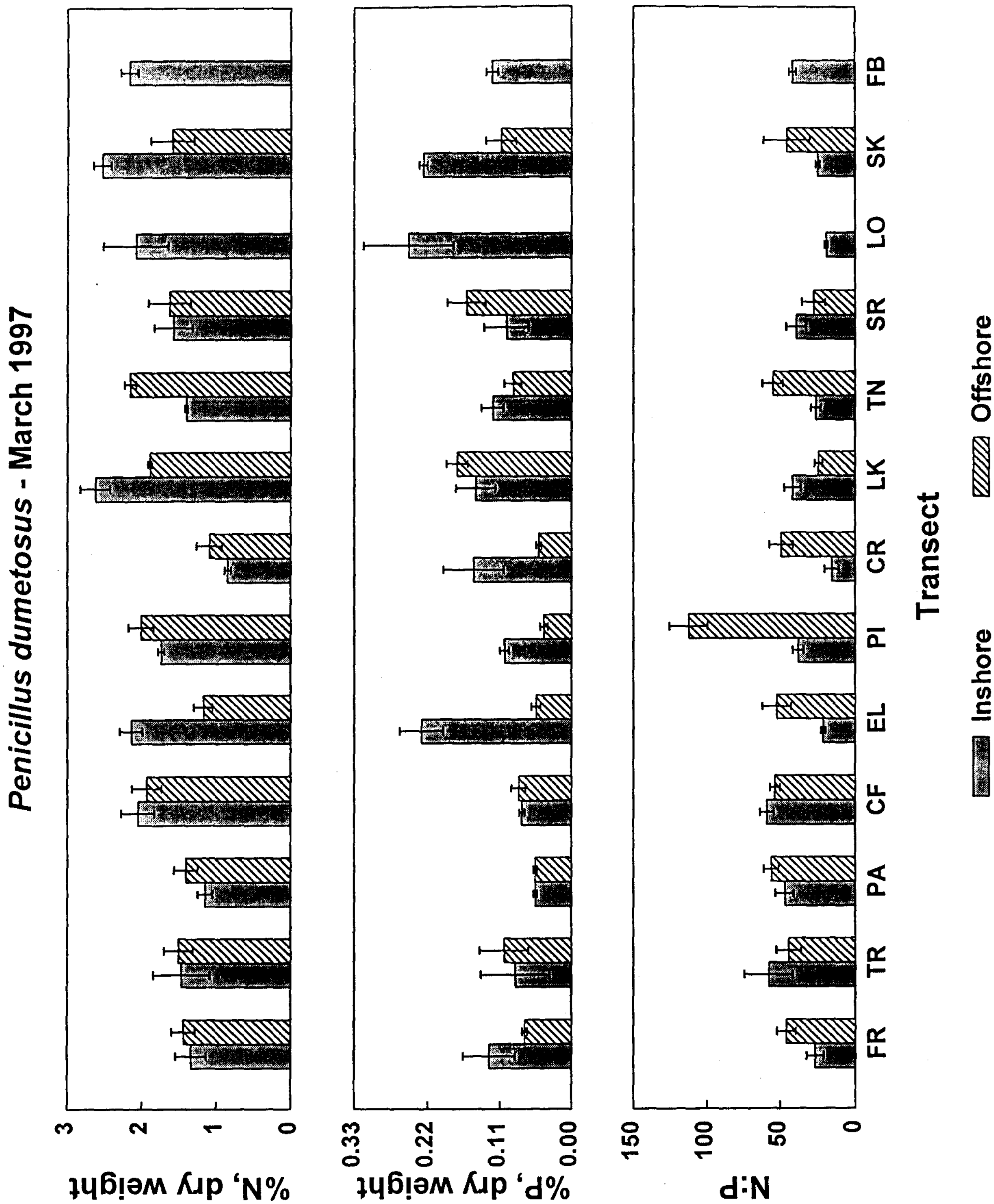

Fig. 74 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Penicillus dumetosus*, March 1997.

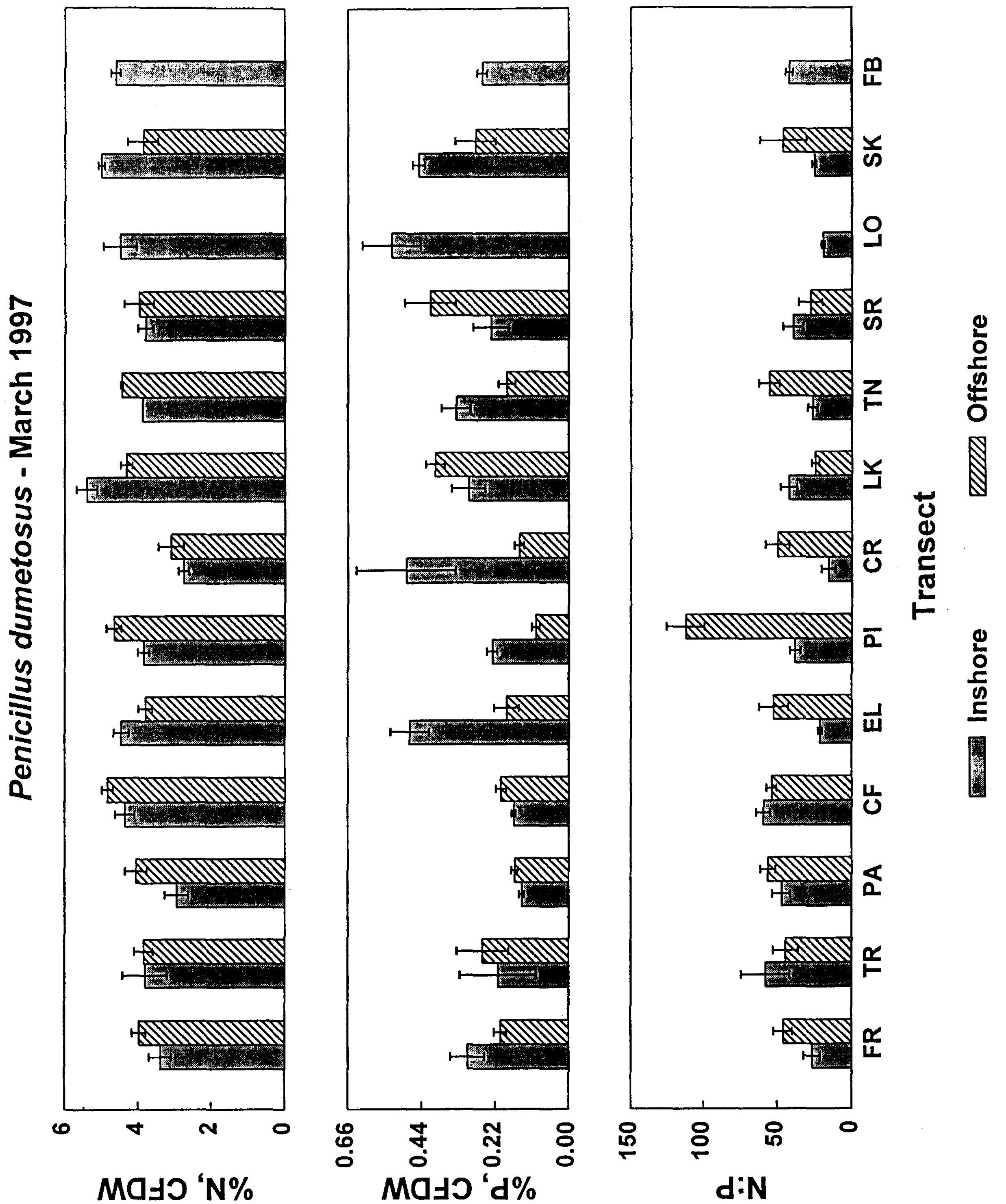

Fig. 75 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus dumetosus*, March 1997.

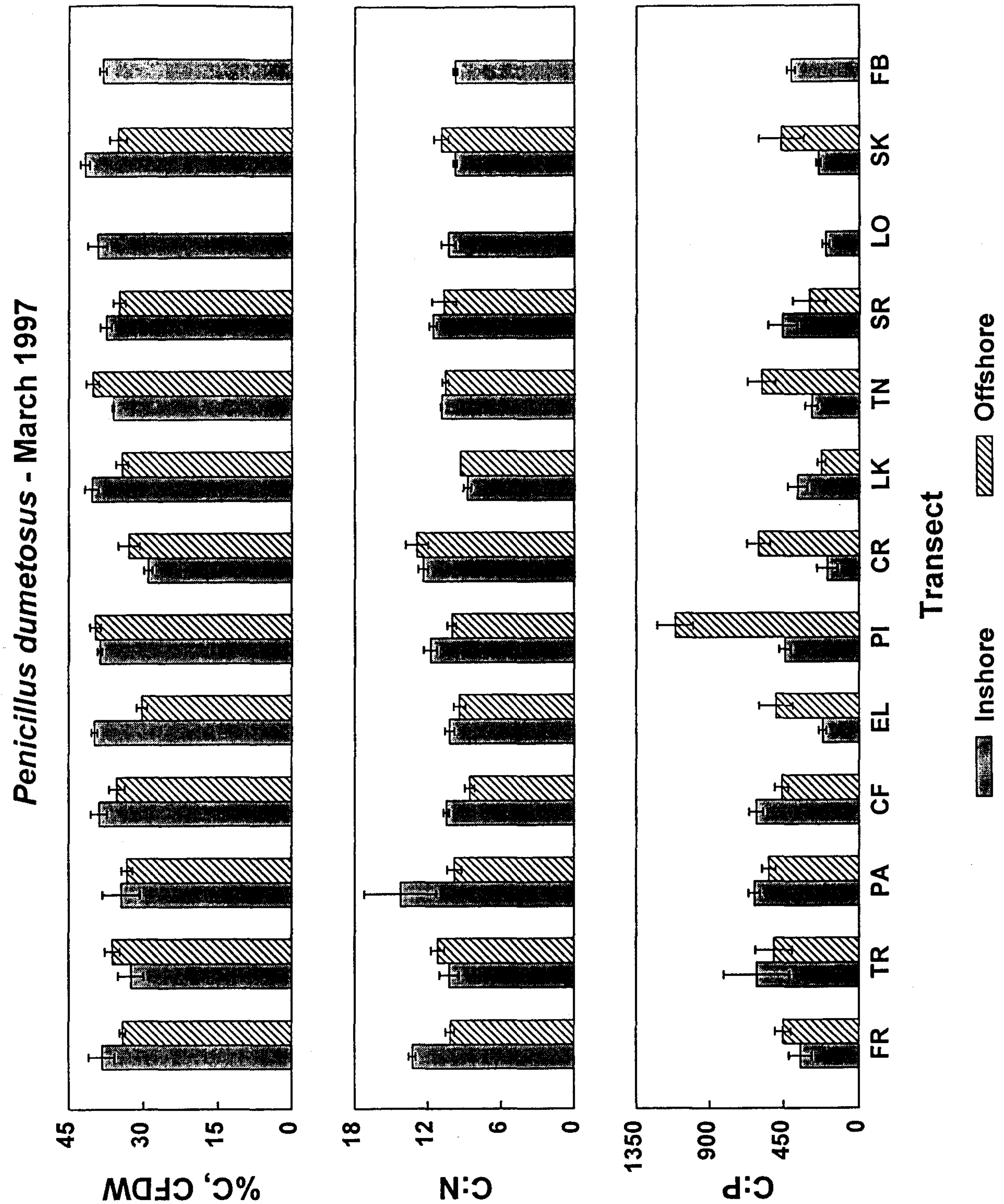

Fig. 76 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus dumetosus*, March 1997.

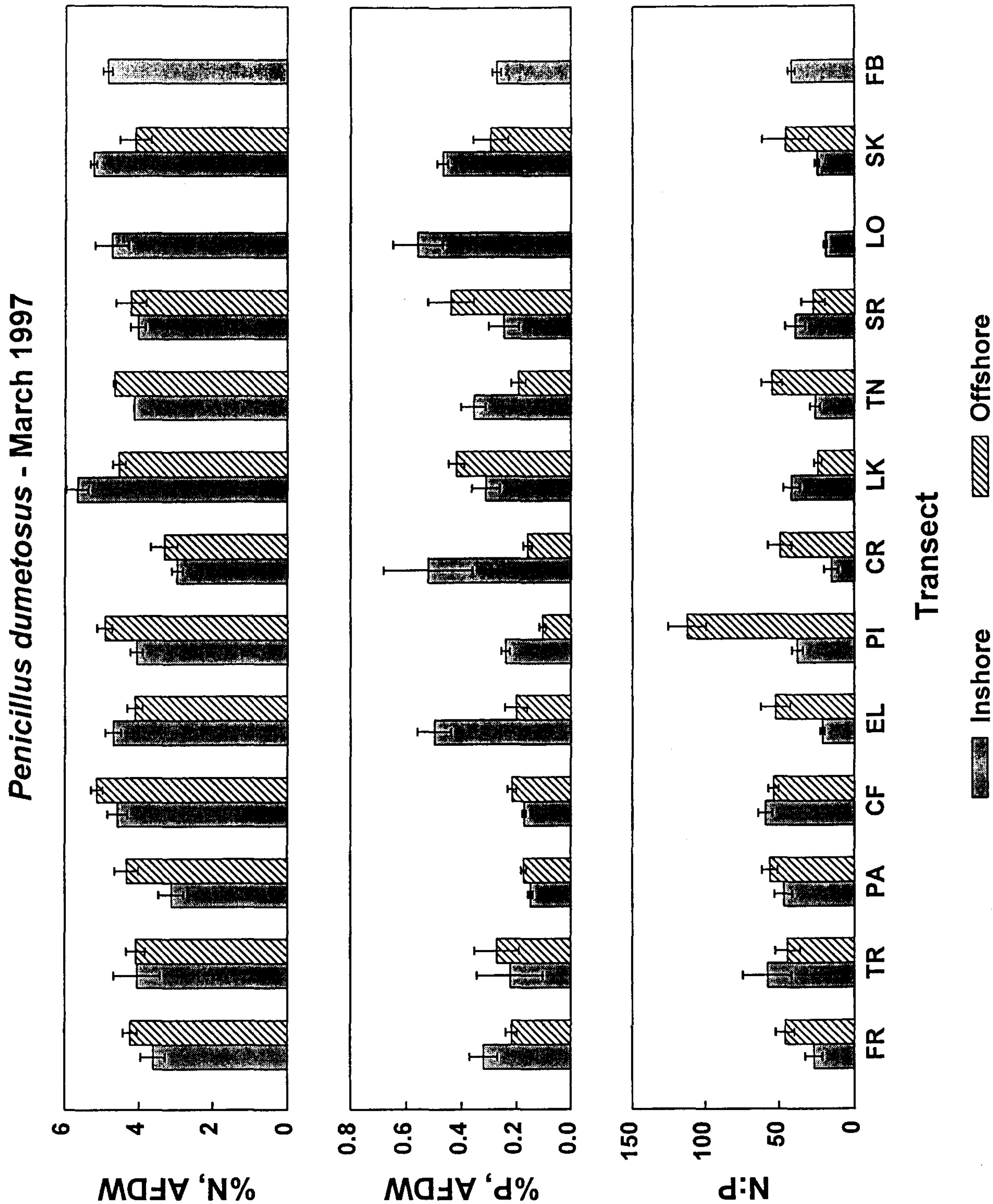

Fig. 77 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus dumetosus*, March 1997.

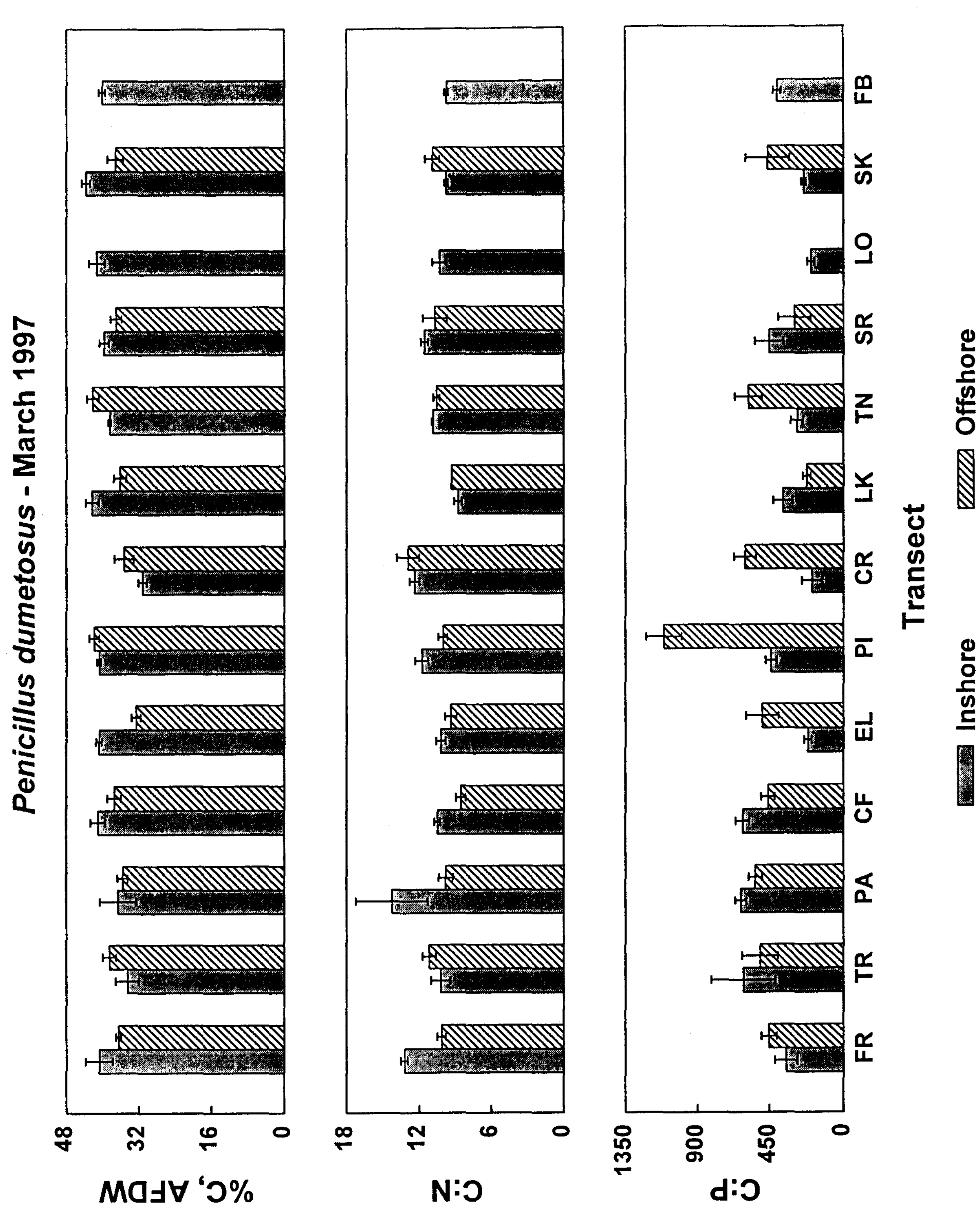

Fig. 78 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus dumetosus*, March 1997.

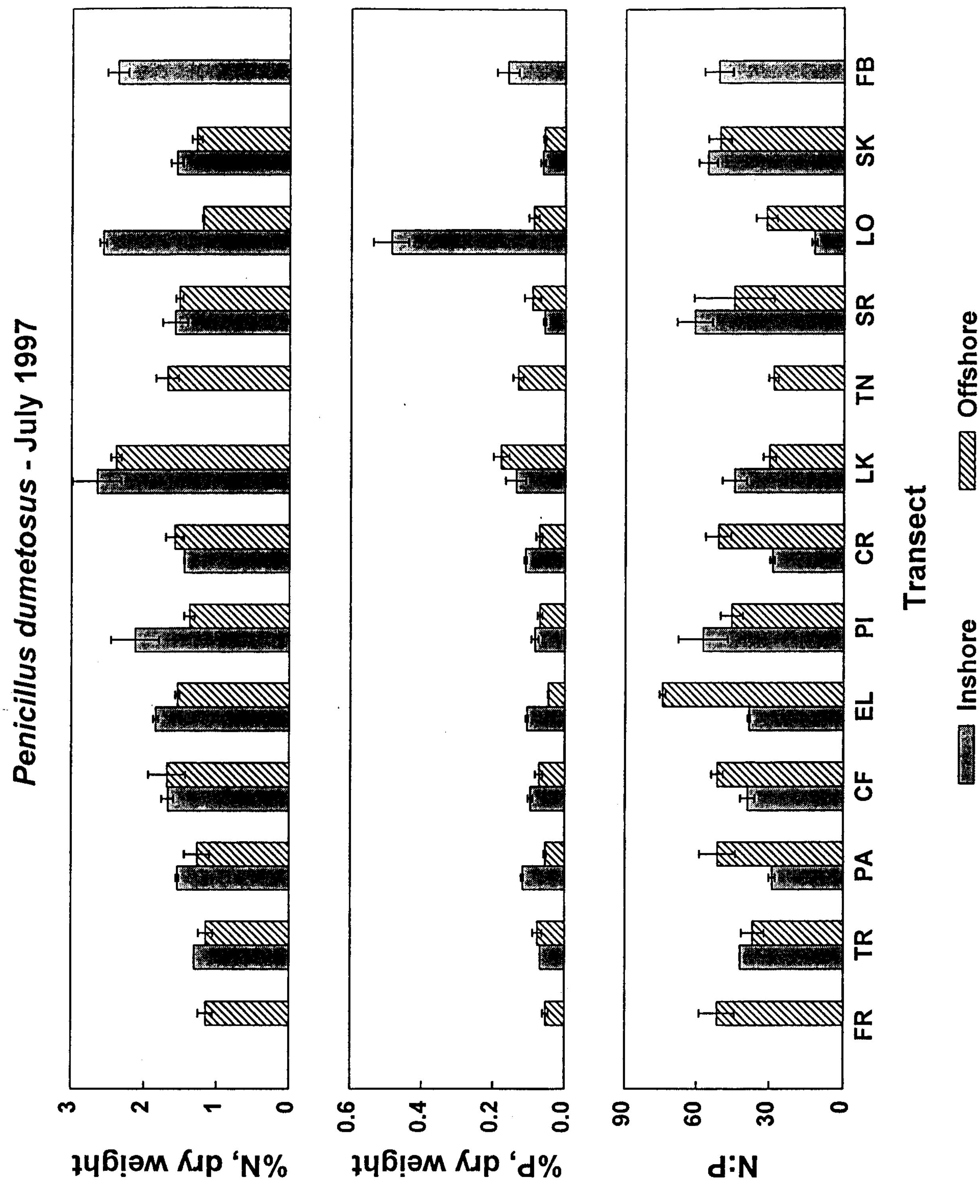

Fig. 79 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Penicillus dumetosus*, July 1997.

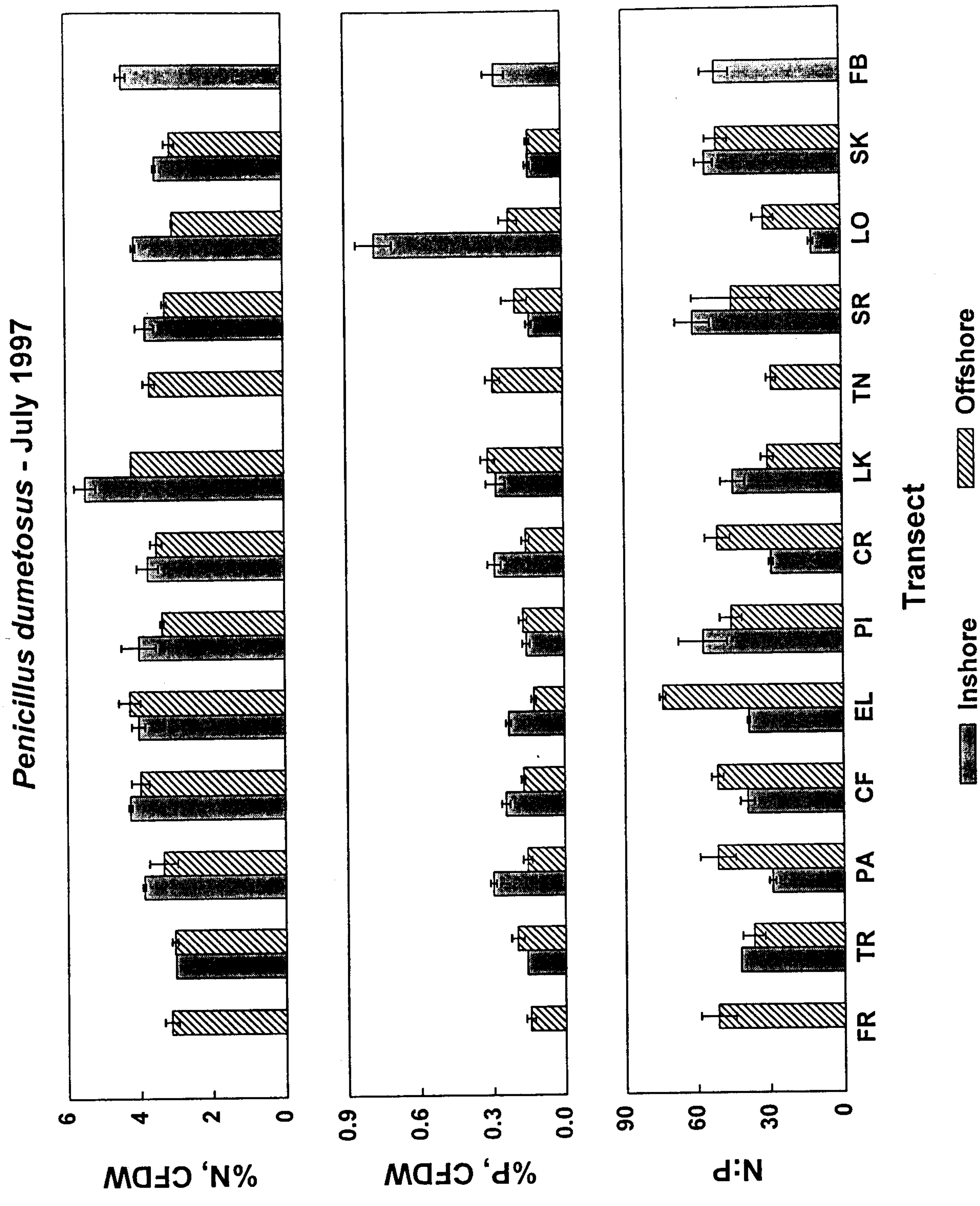

Fig. 80 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus dumetosus*, July 1997.

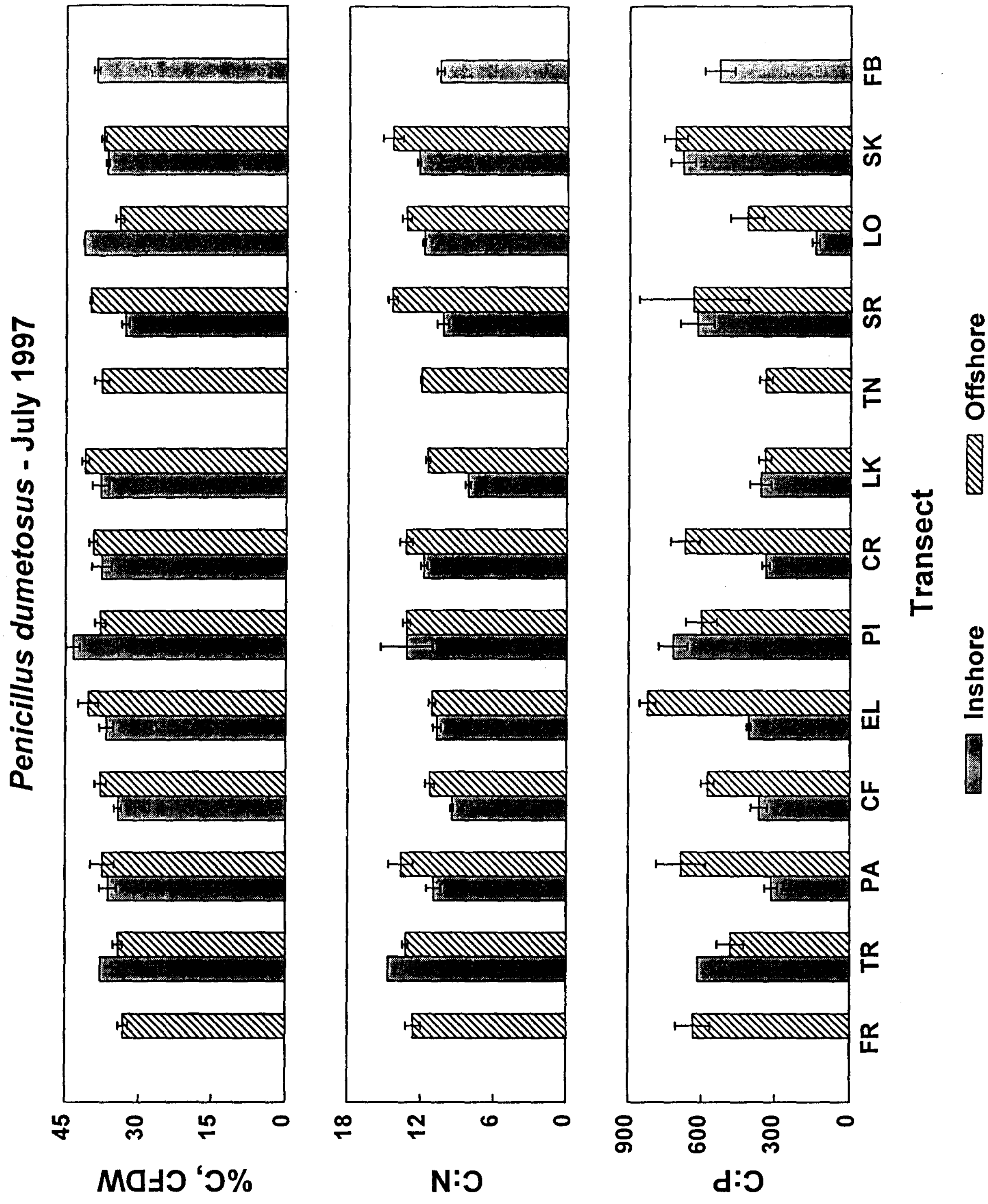

Fig. 81 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus dumetosus*, July 1997.

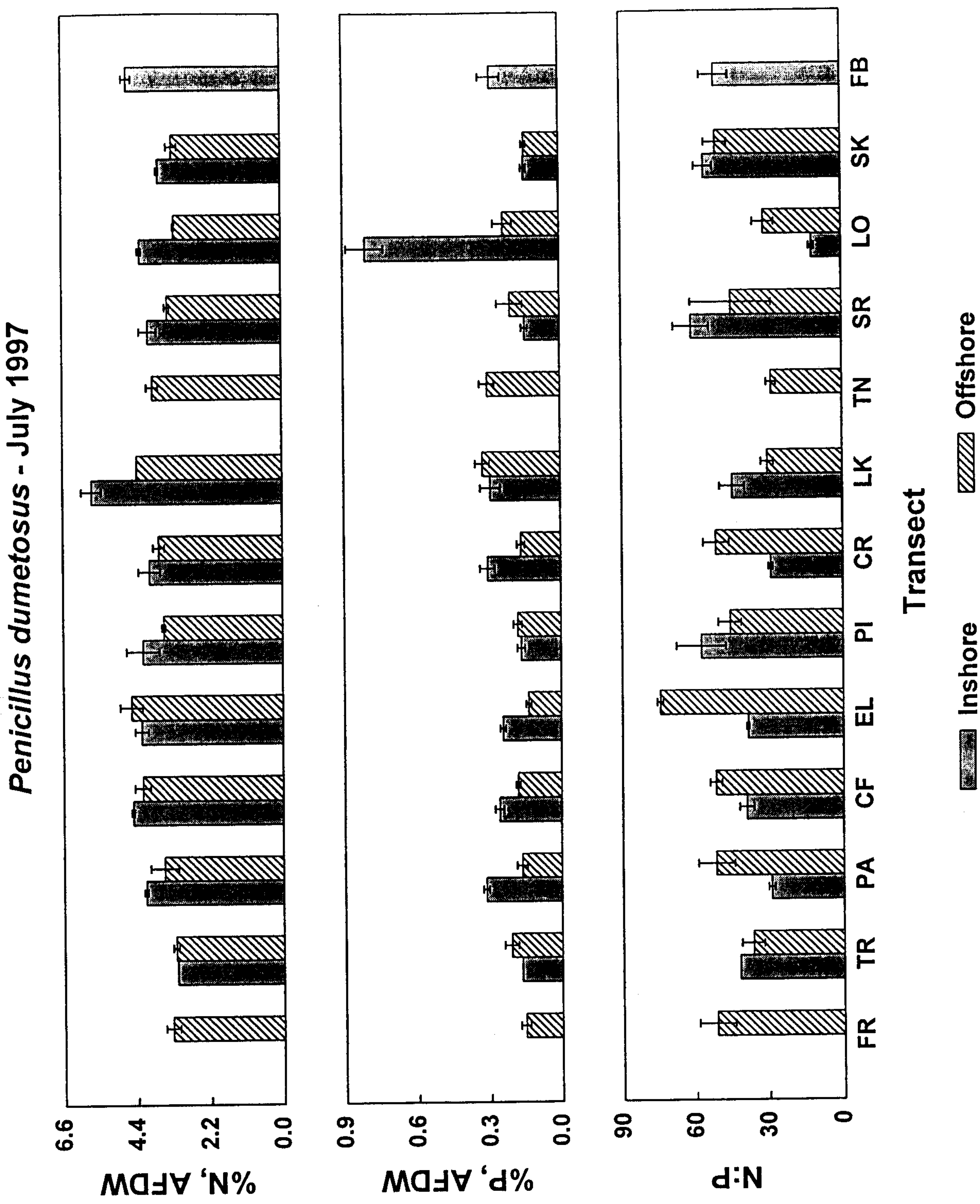

Fig. 82 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus dumetosus*, July 1997.

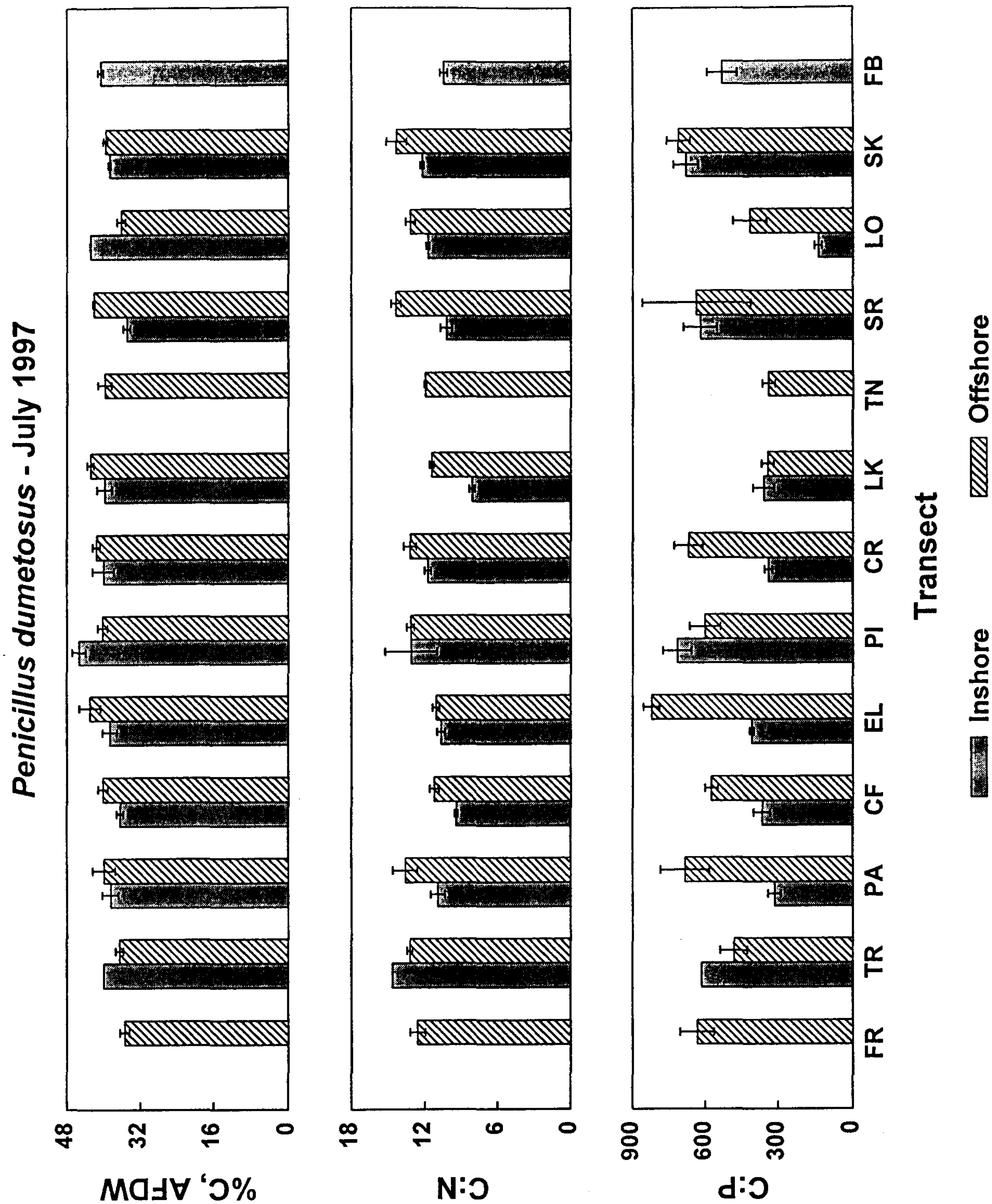

Fig. 83 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus dumetosus*, July 1997.

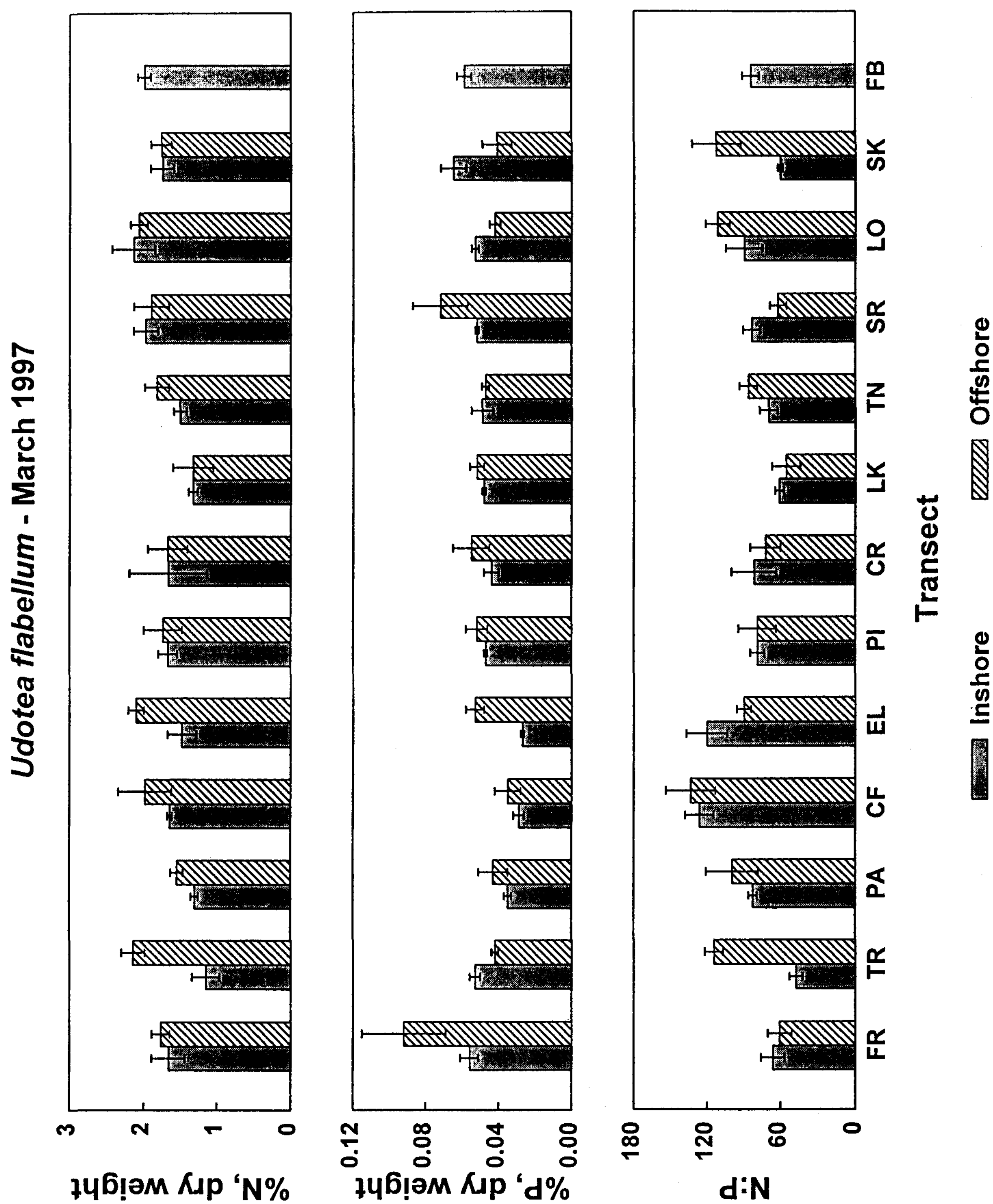

Fig. 84 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Udotea flabellum*, March 1997.

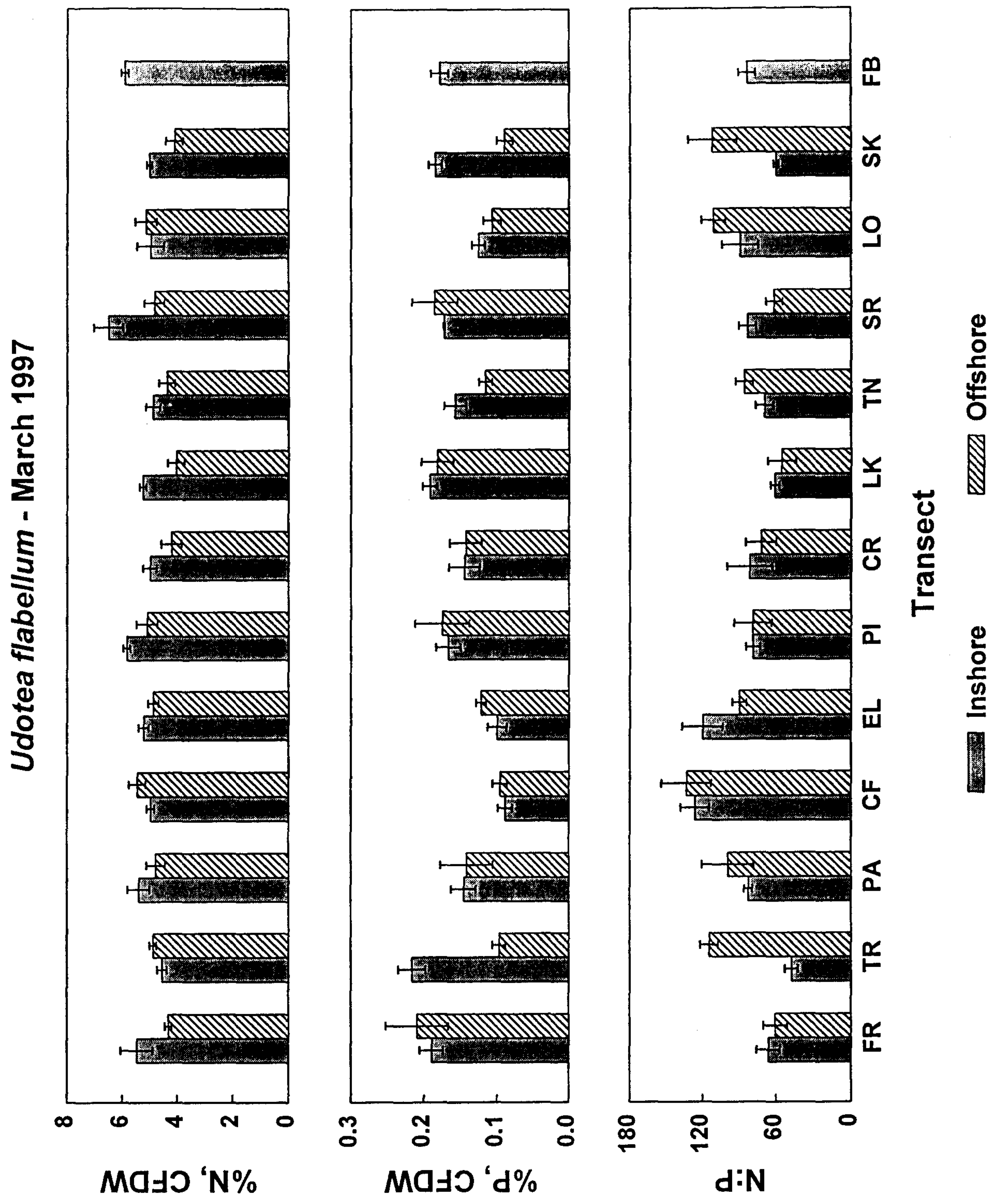

Fig. 85 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Udotea flabellum*, March 1997.

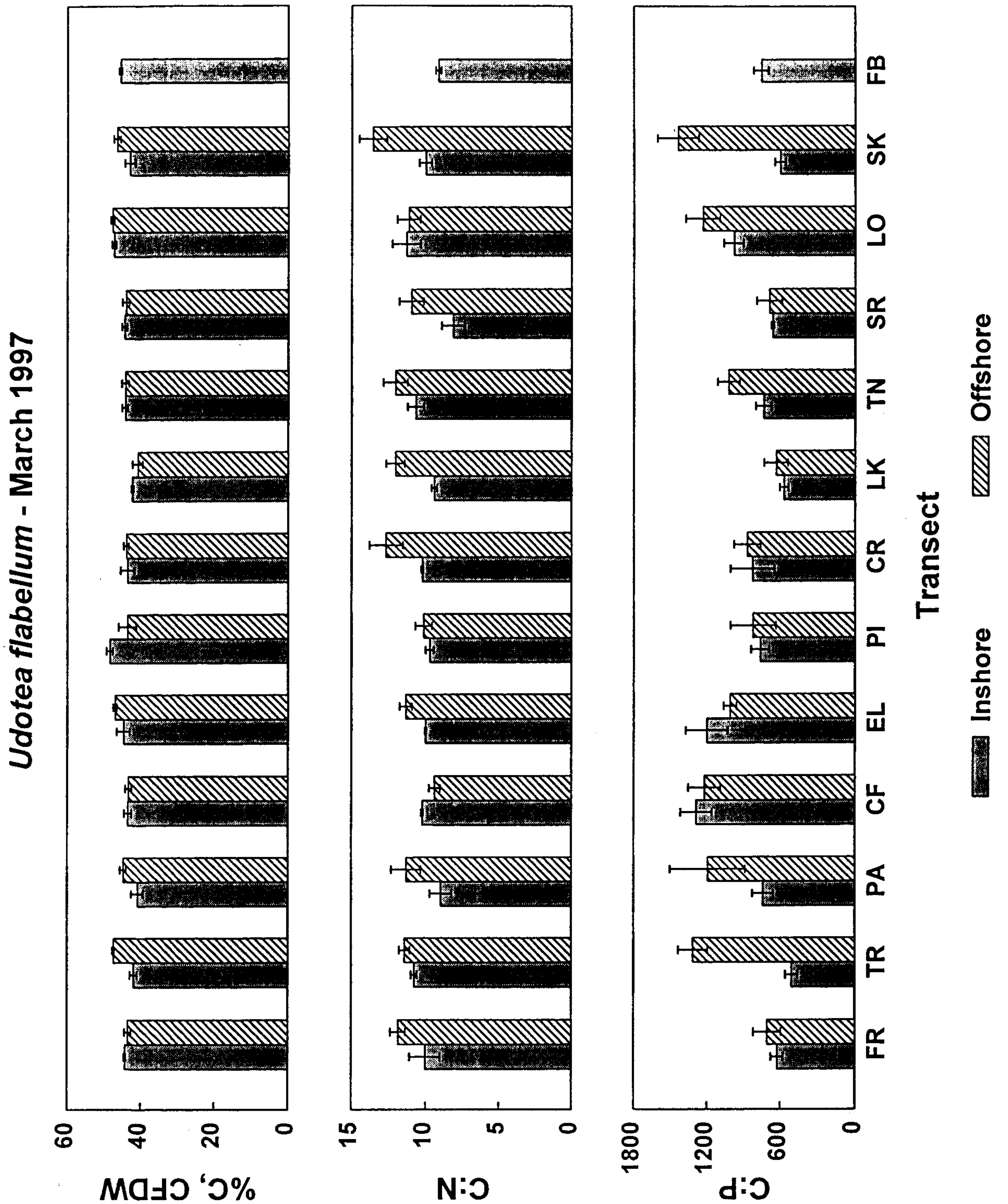

Fig. 86 **Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Udotea flabellum*, March 1997.**

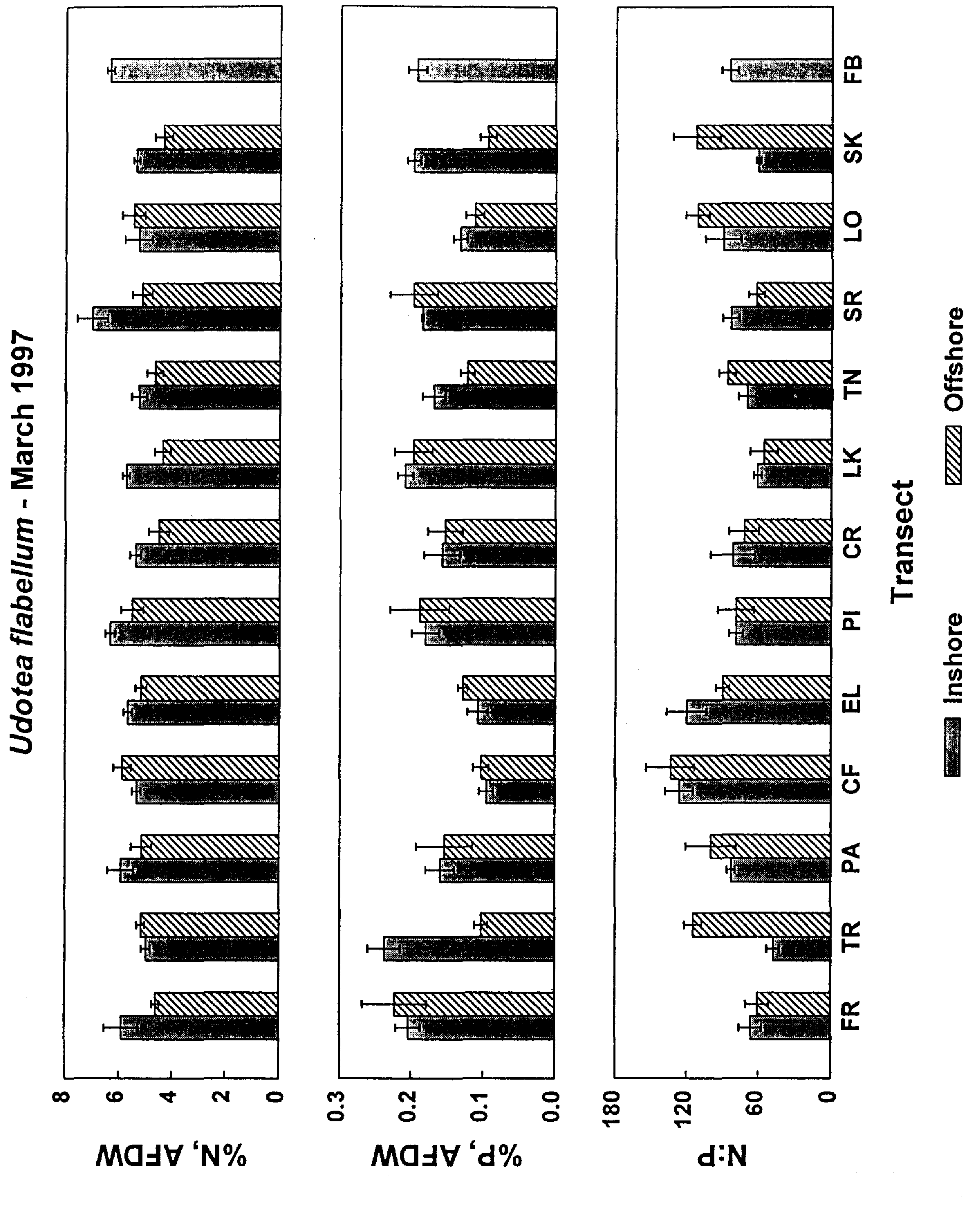

Fig. 87 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Udotea flabellum*, March 1997.

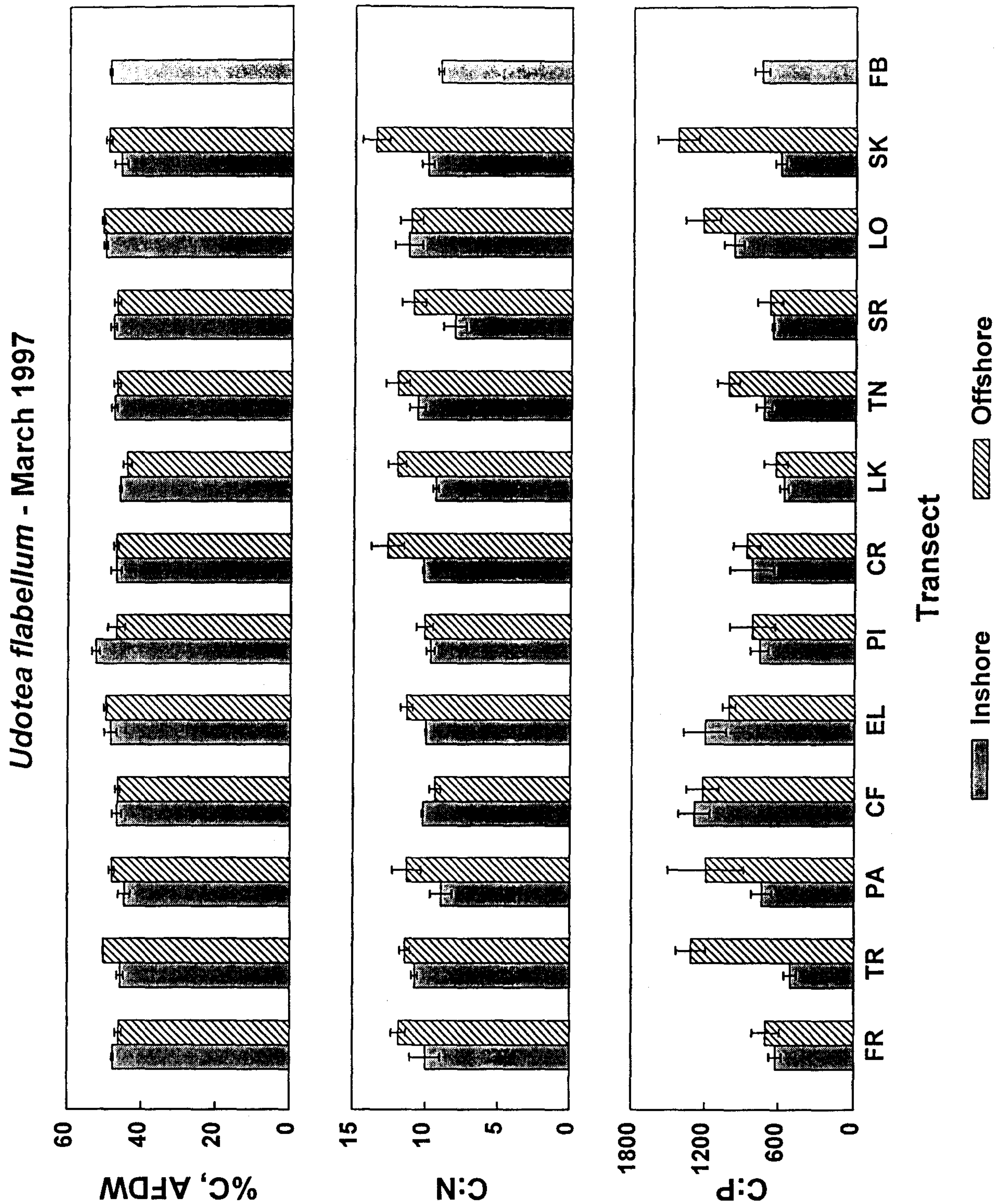

Fig. 88 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Udotea flabellum*, March 1997.

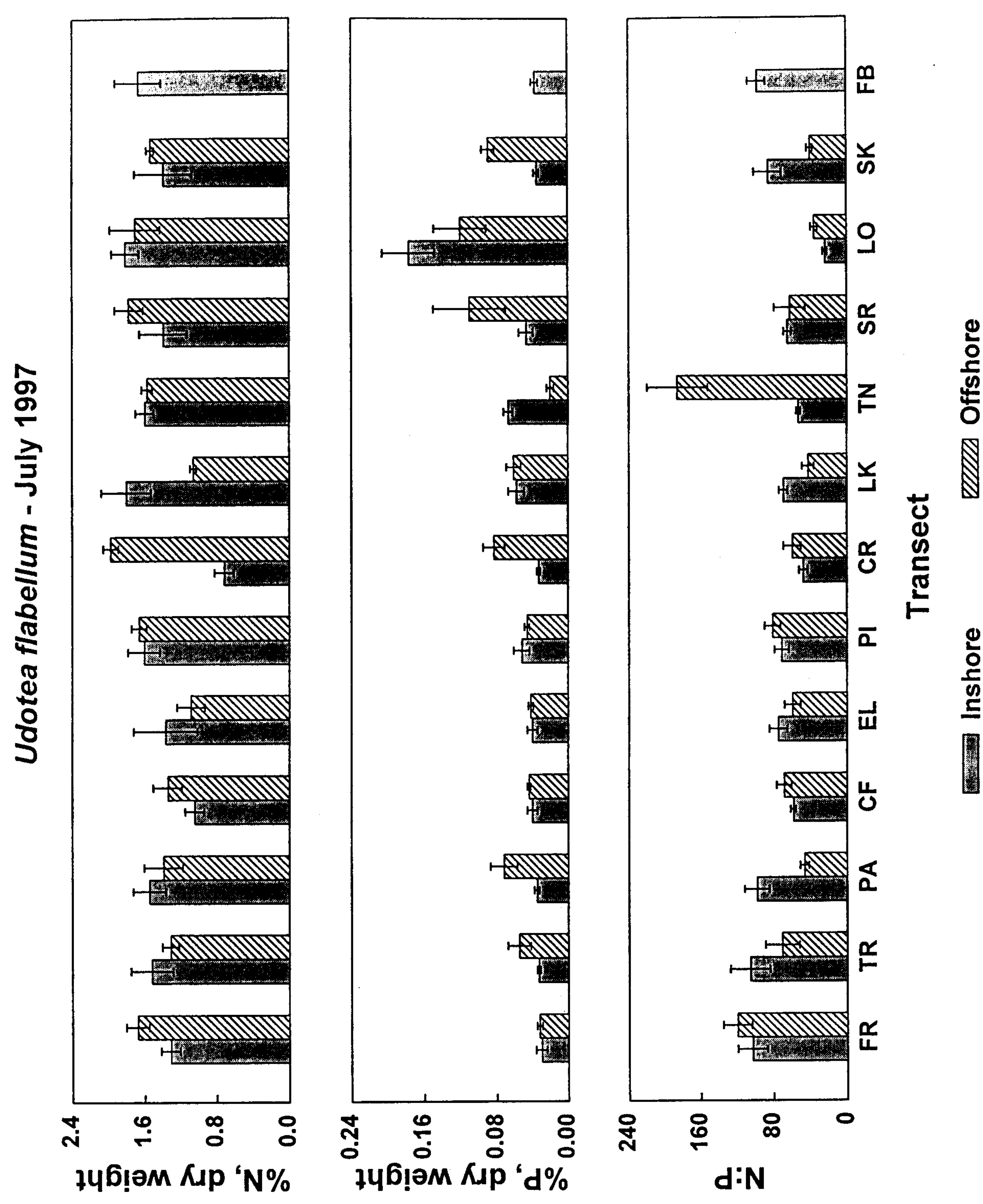

Fig. 89 Transect means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Udotea flabellum*, July 1997.

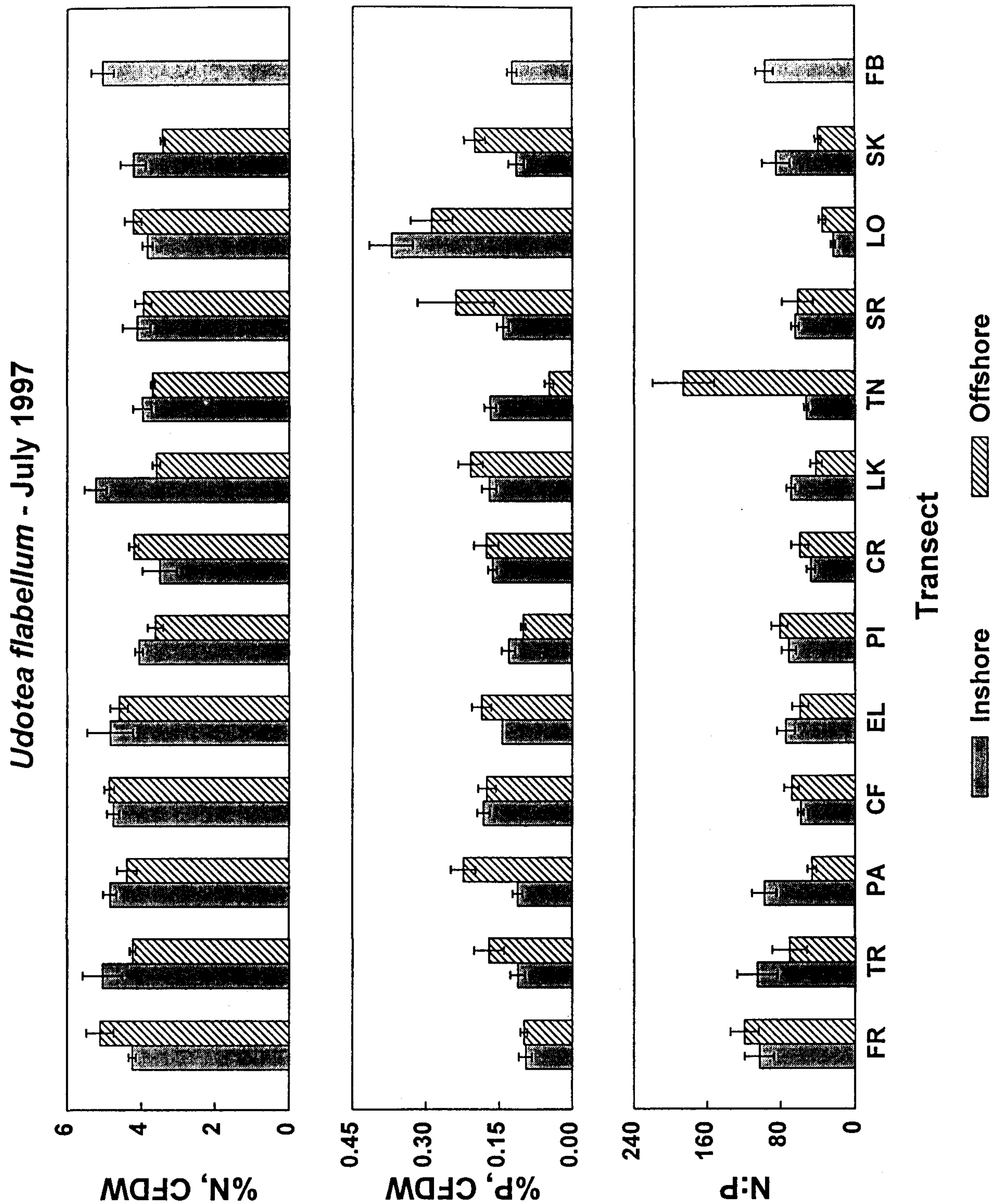

Fig. 90 Transect means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Udotea flabellum*, July 1997.

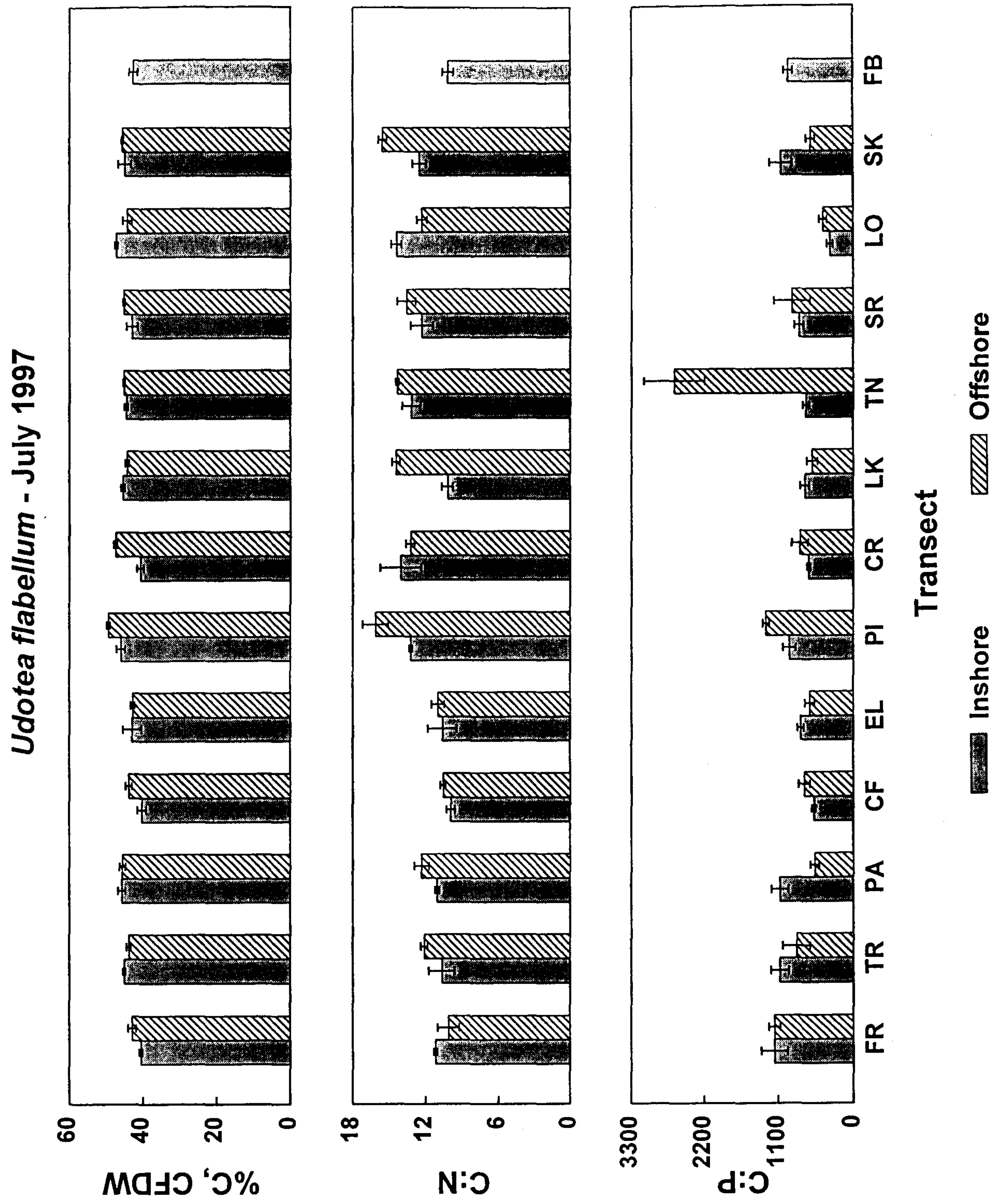

Fig. 91 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Udotea flabellum*, July 1997.

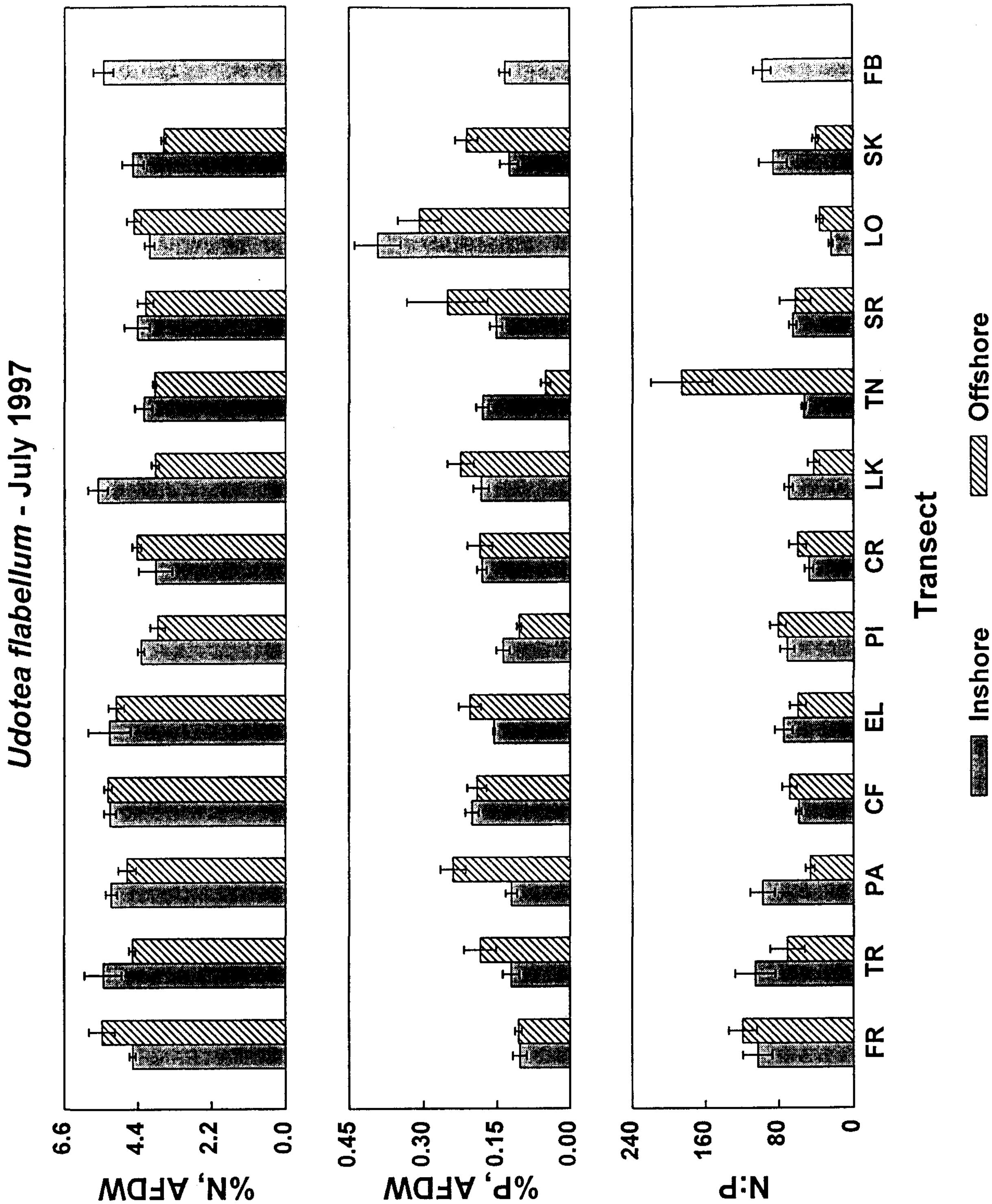

Fig. 92 Transect means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Udotea flabellum*, July 1997.

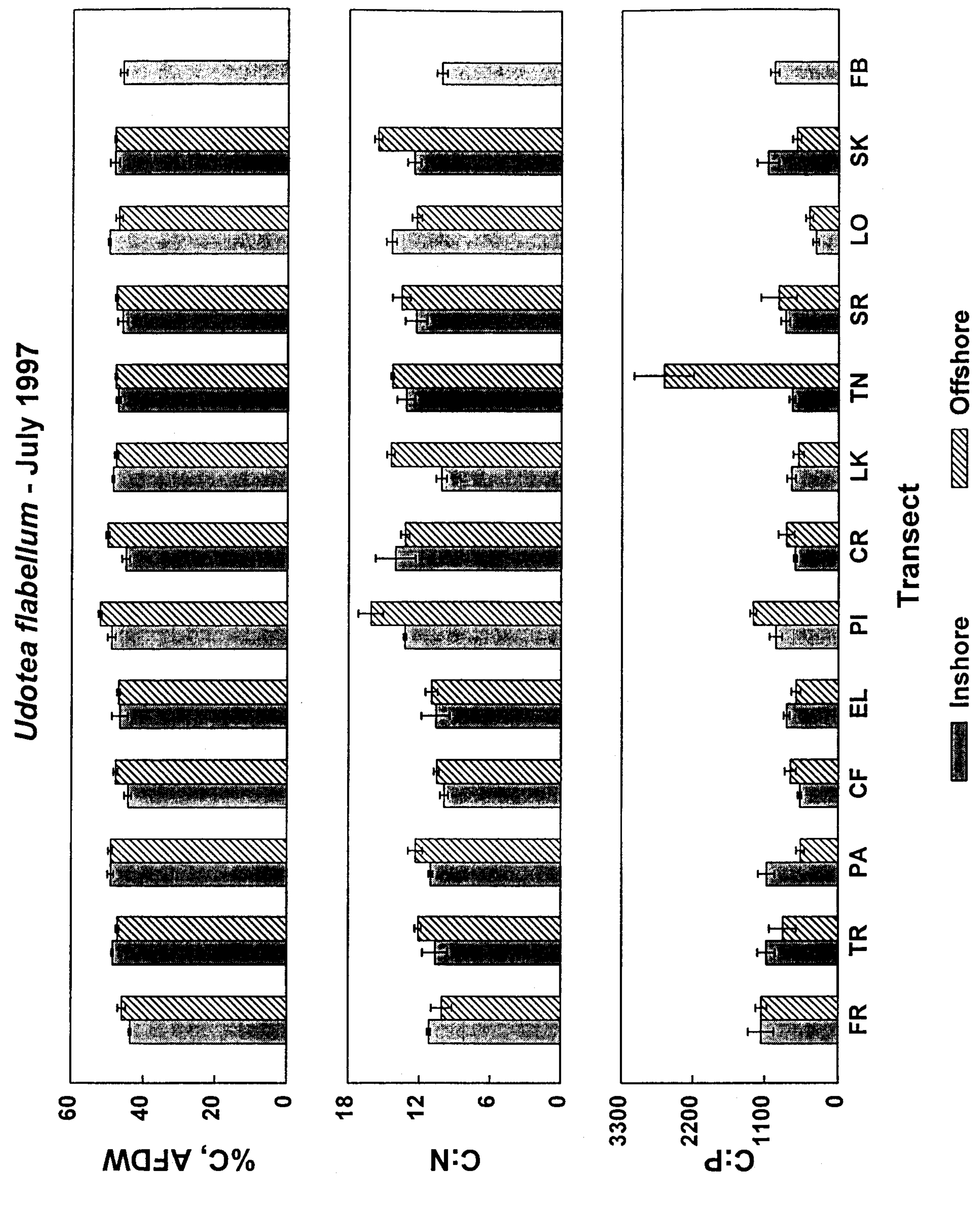

Fig. 93 Transect means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Udotea flabellum*, July 1997.

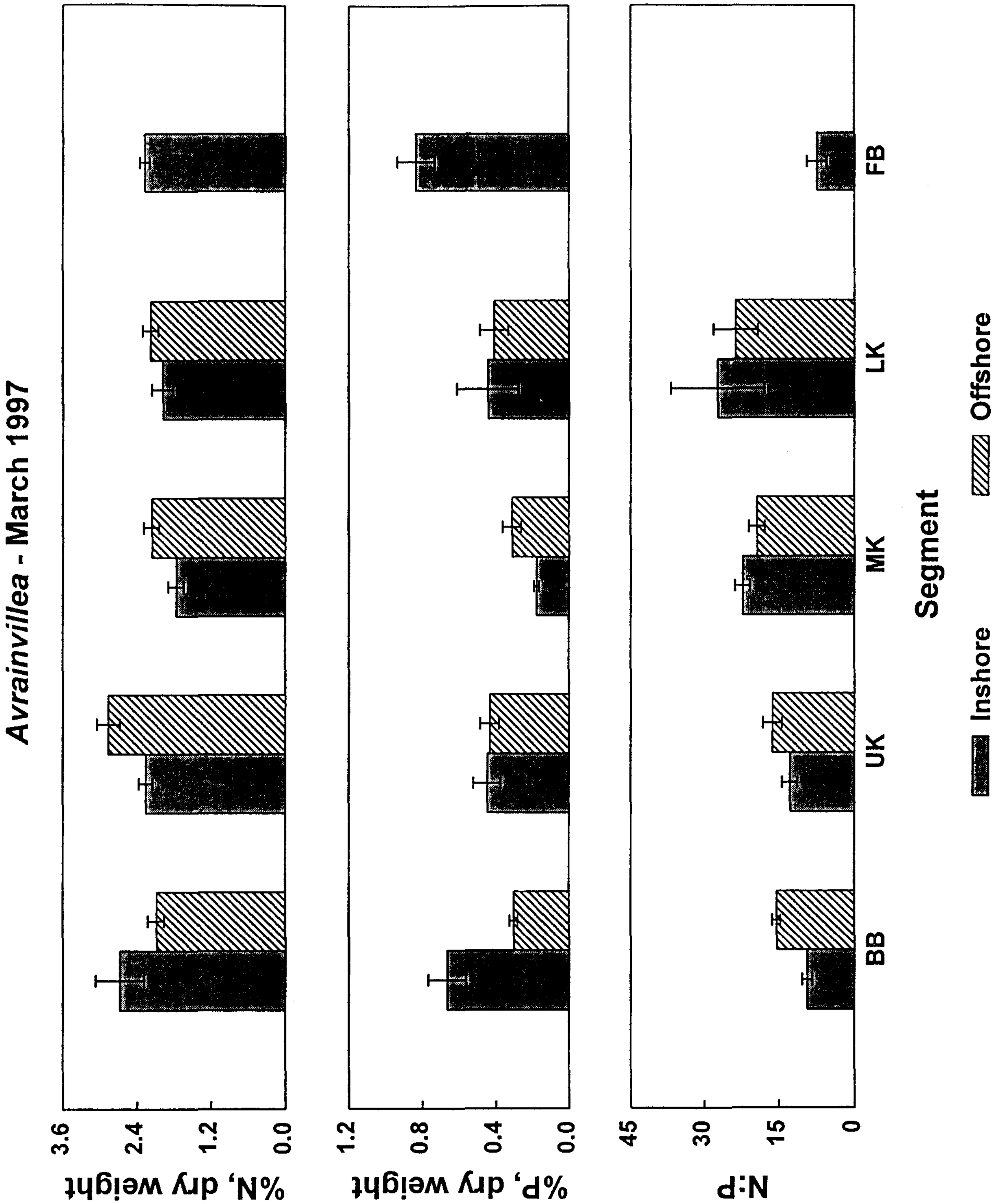

Fig. 94 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Avrainvillea* sp., March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

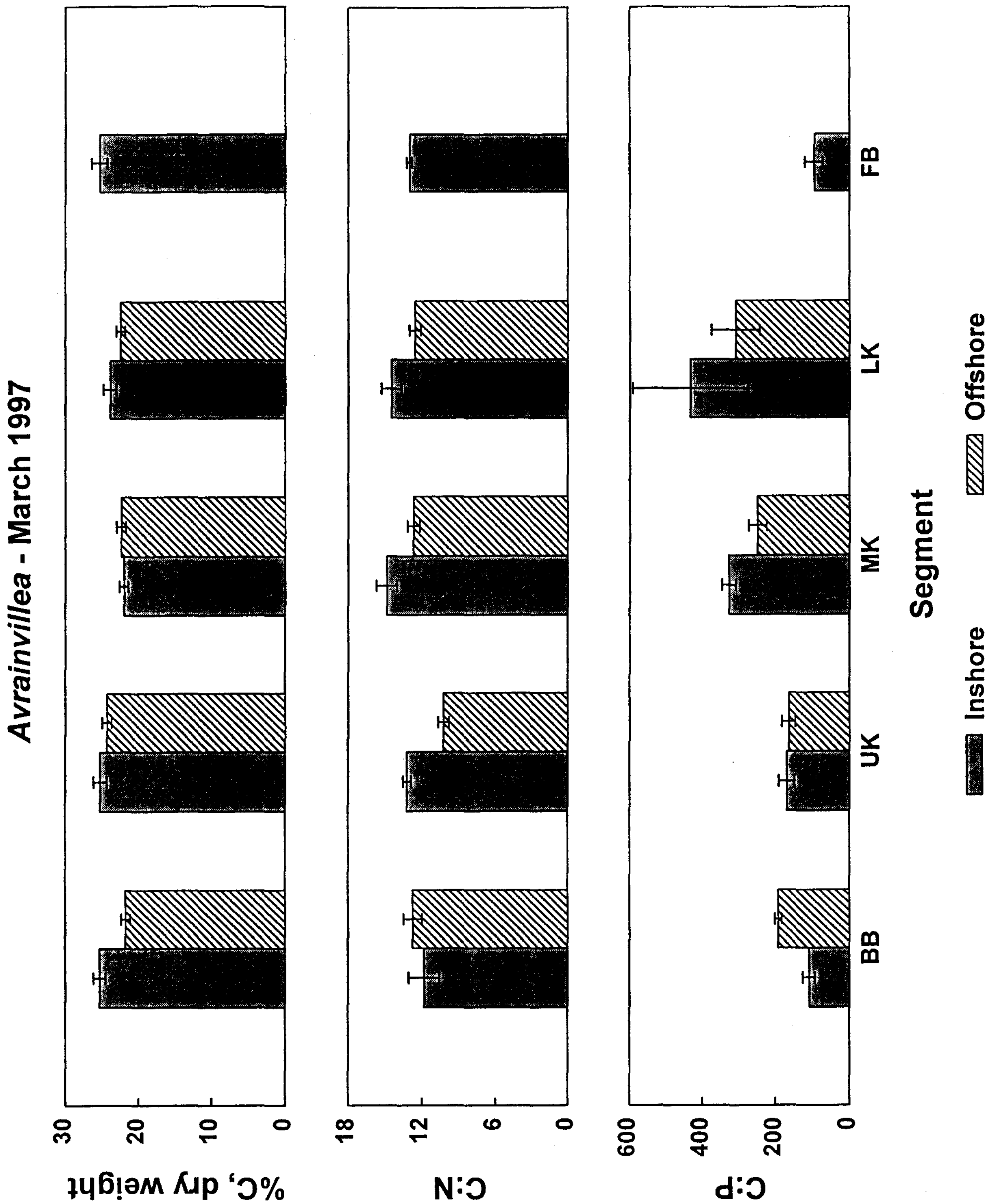

Fig. 95 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Avrainvillea* sp., March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

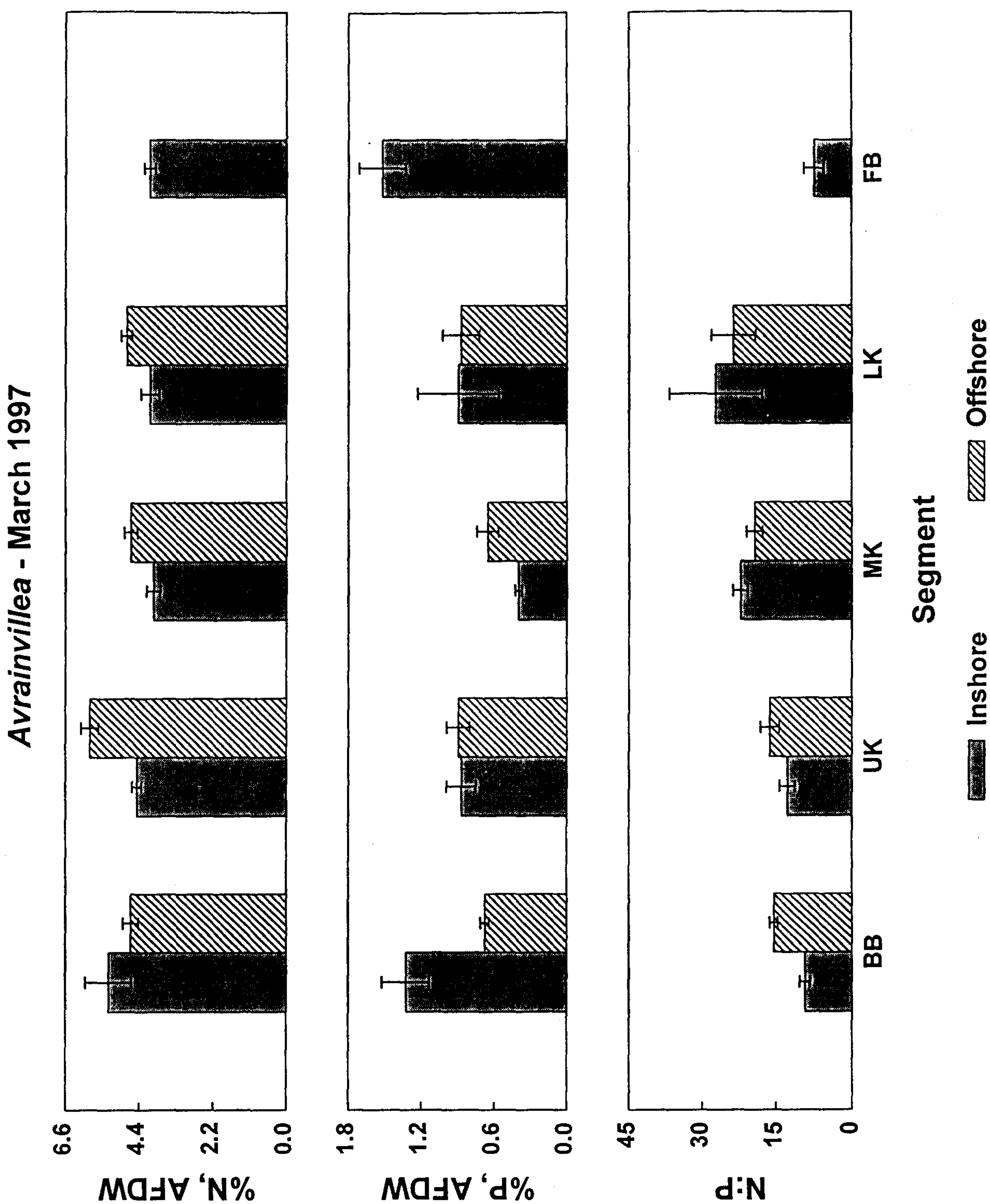

Fig. 96 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Avrainvillea* sp., March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

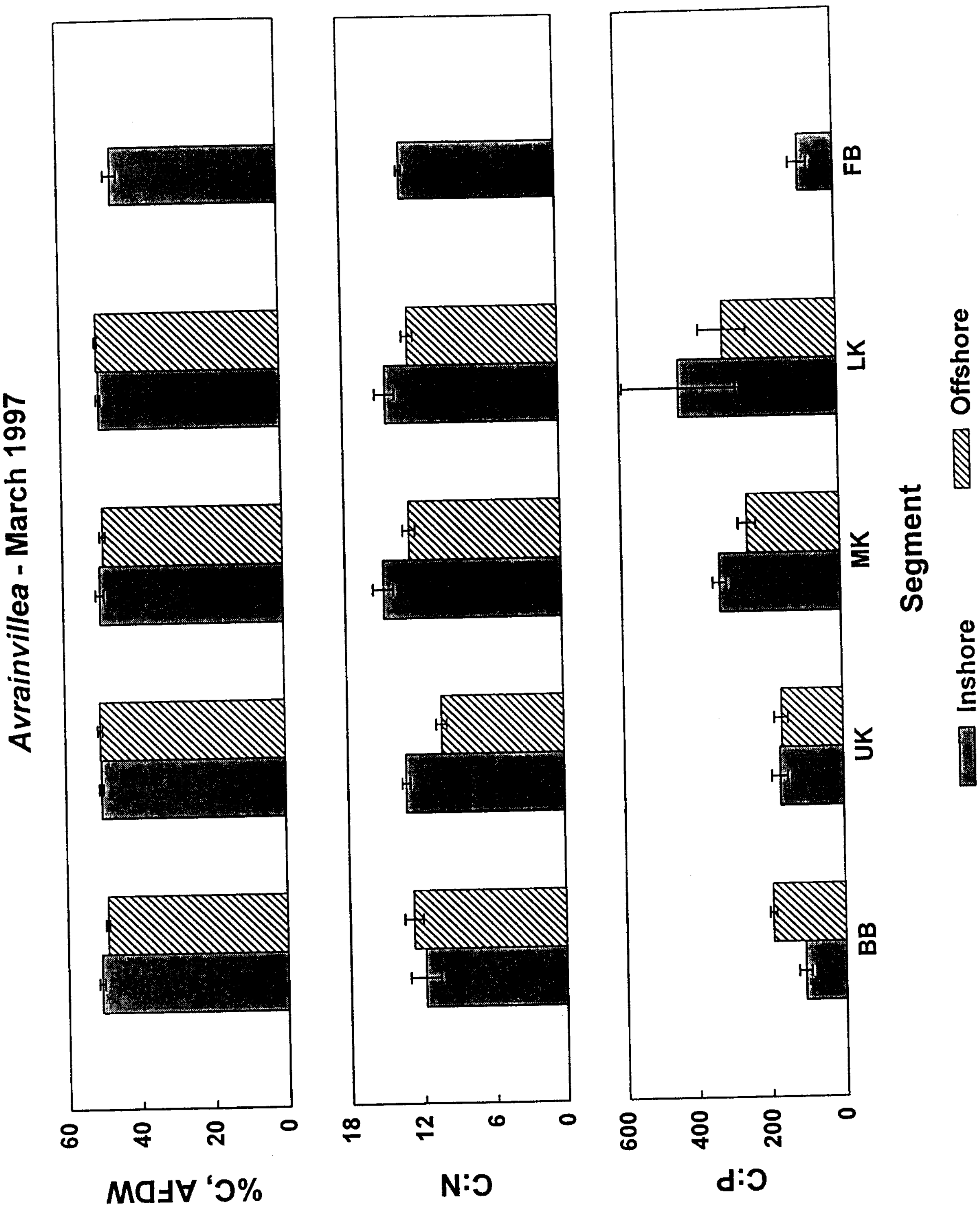

Fig. 97 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Avrainvillea* sp., March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

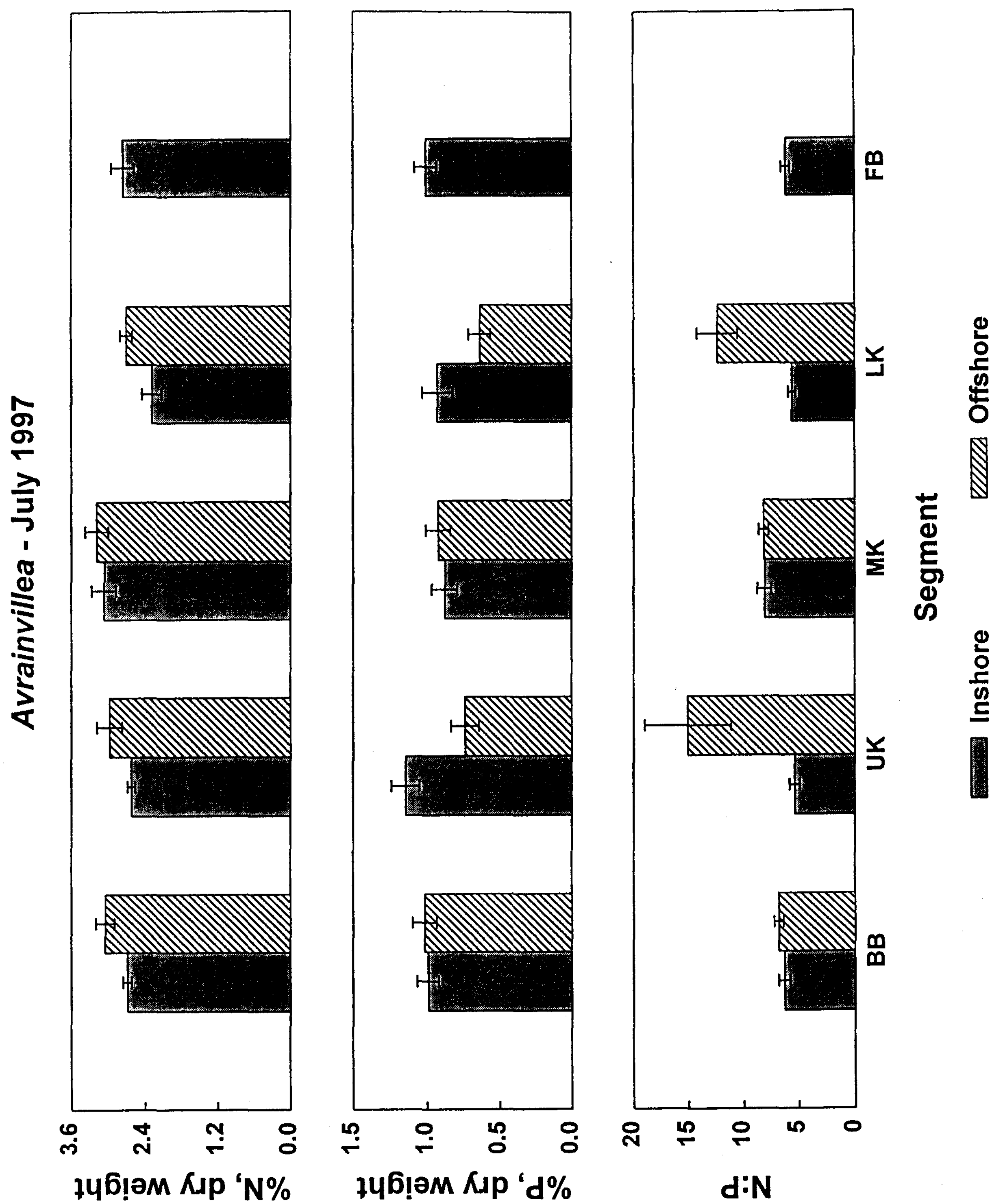

Fig. 98 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Avrainvillea* sp., July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

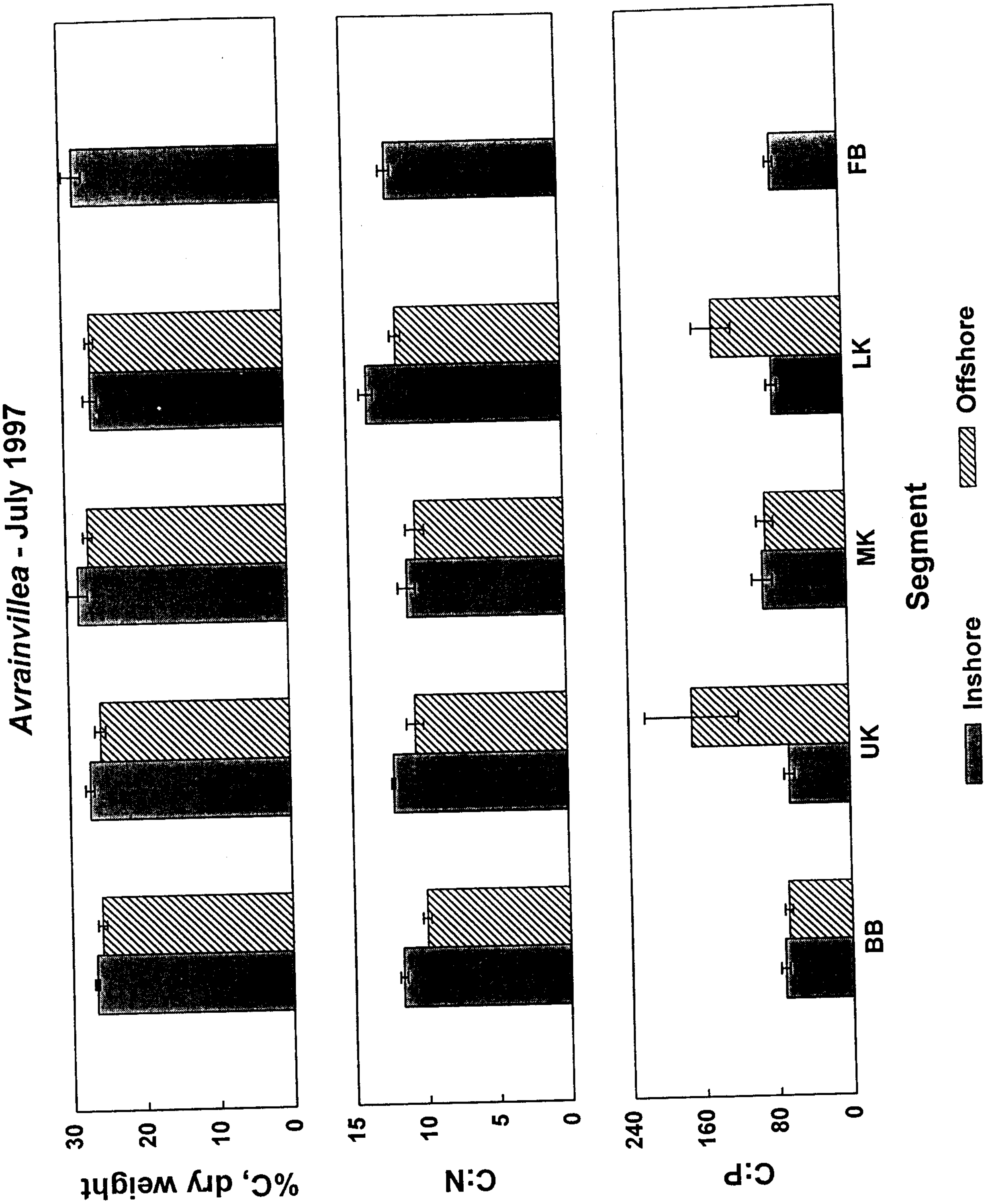

Fig. 99 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Avrainvillea* sp., July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

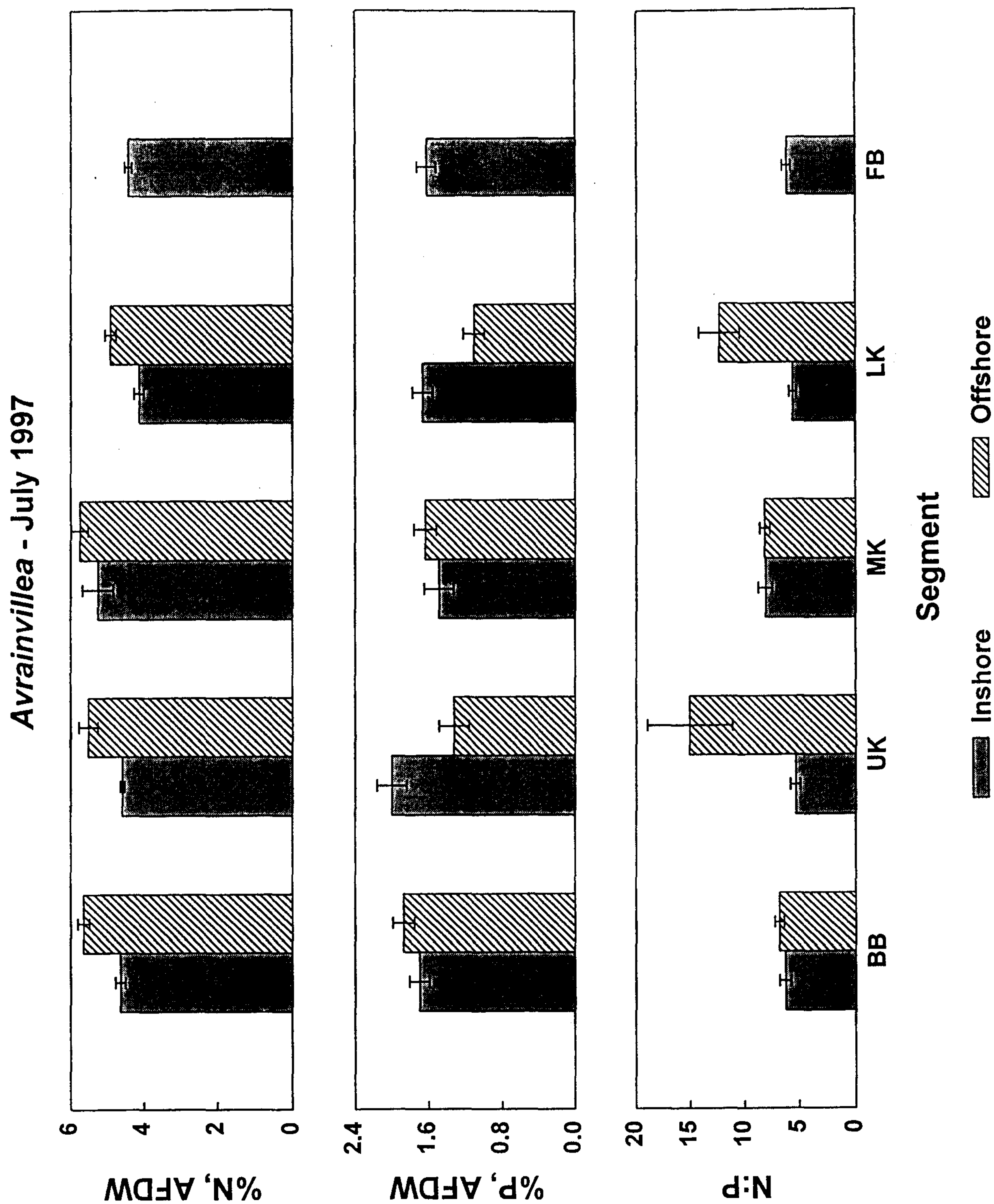

Fig. 100 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Avrainvillea* sp., July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

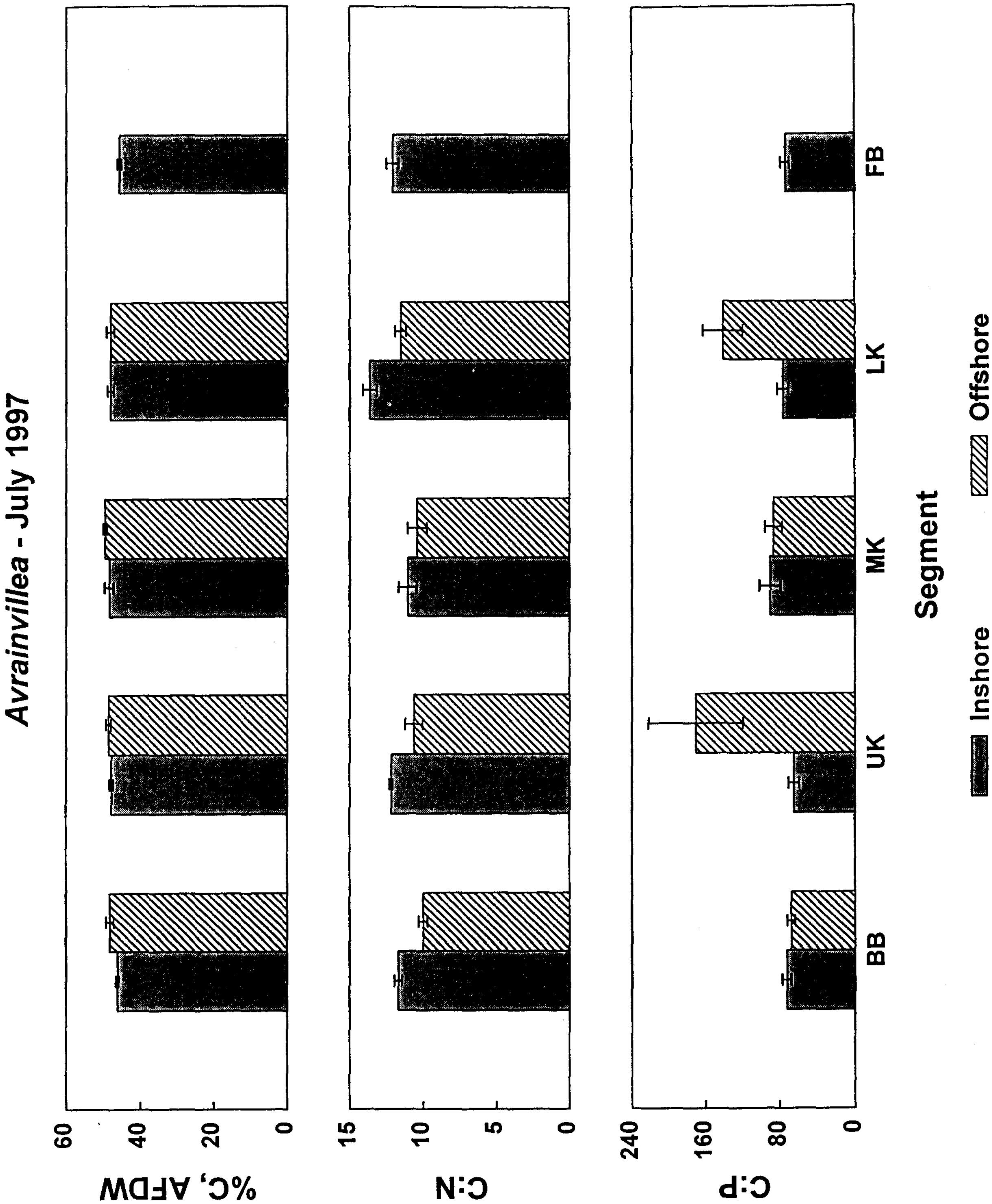

Fig. 101 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Avrainvillea* sp., July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

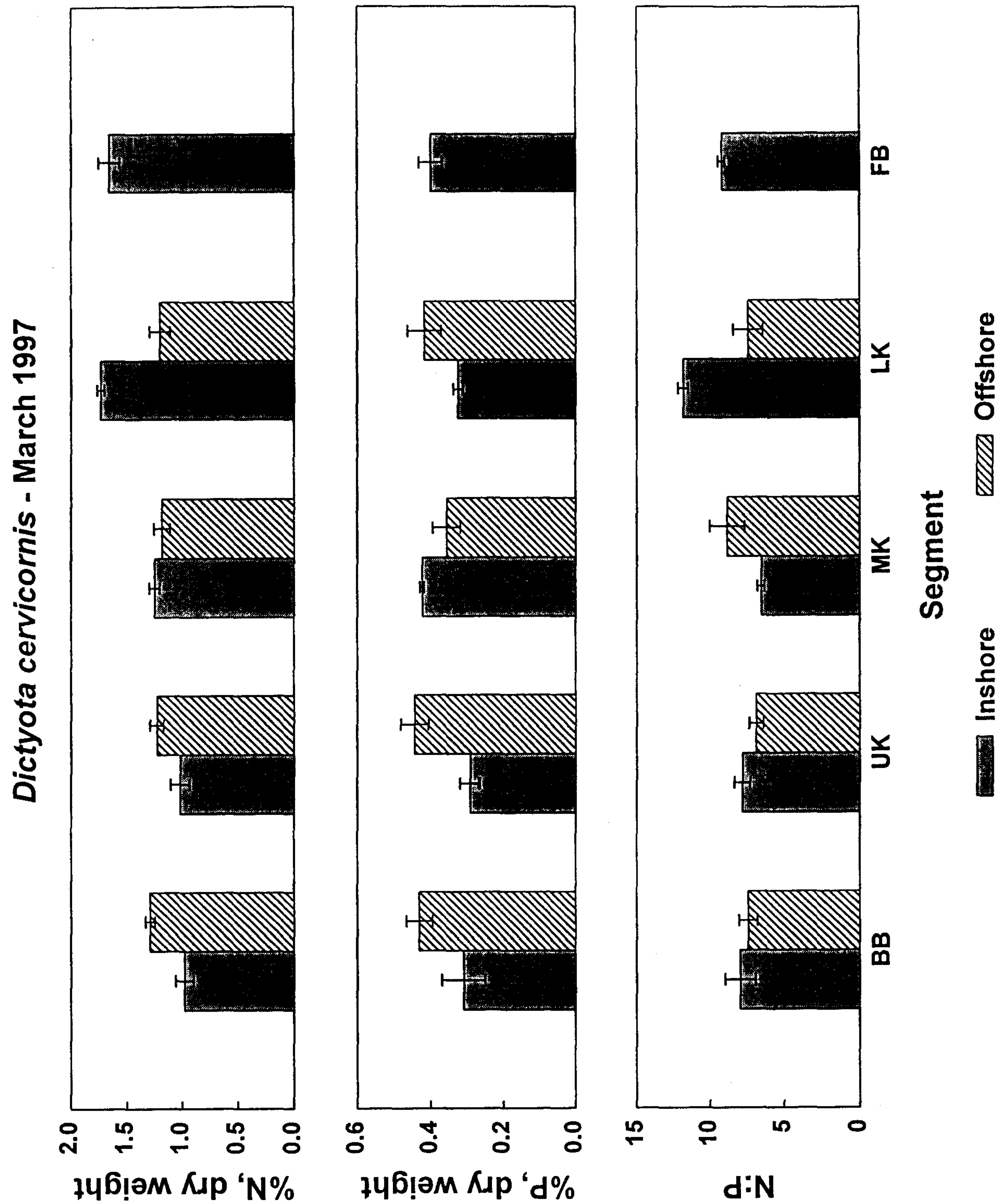

Fig. 102 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Dictyota cervicornis*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

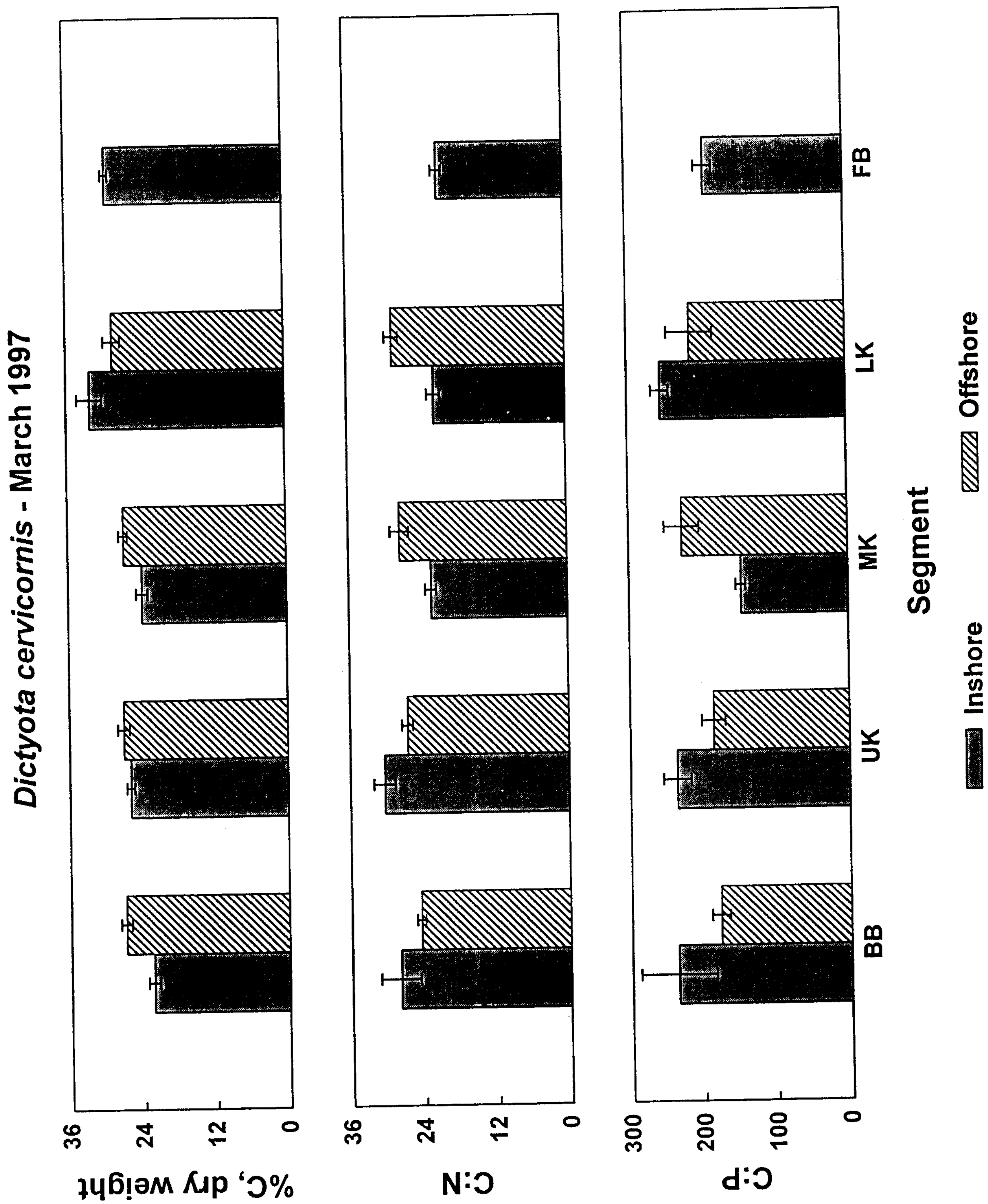

Fig. 103 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Dictyota cervicornis*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

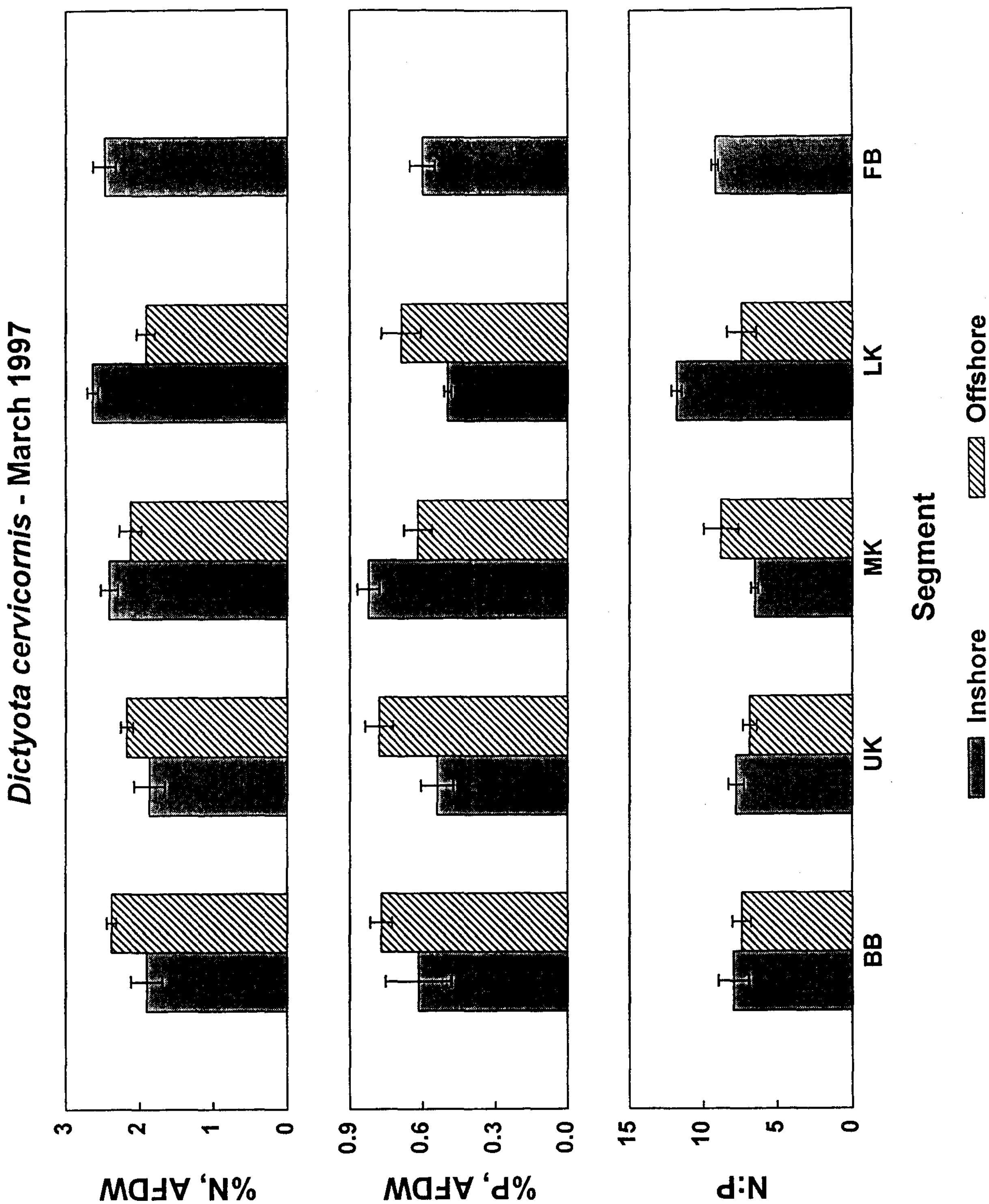

Fig. 104 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Dictyota cervicornis*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

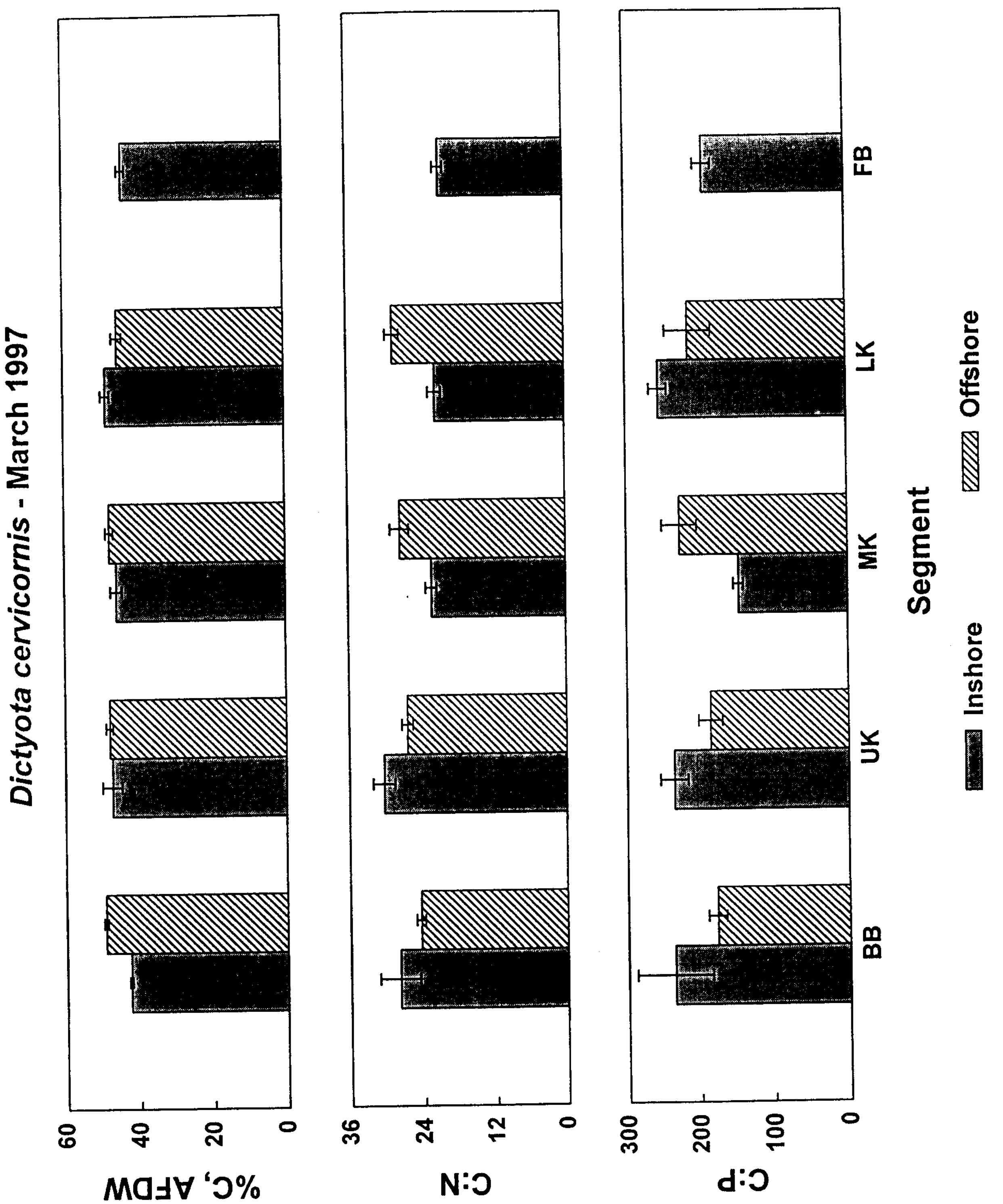

Fig. 105 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Dictyota cervicornis*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

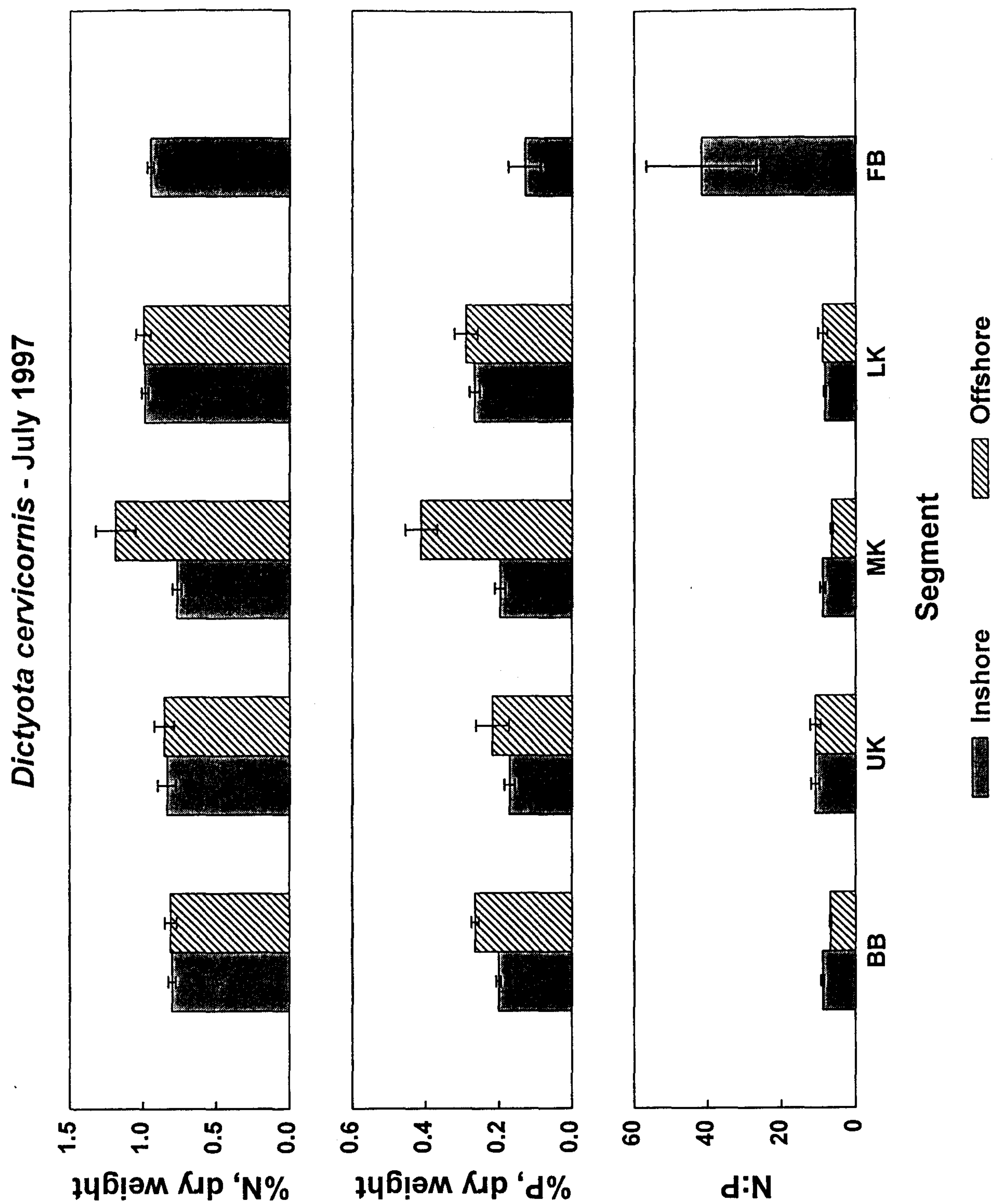

Fig. 106 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Dictyota cervicornis*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

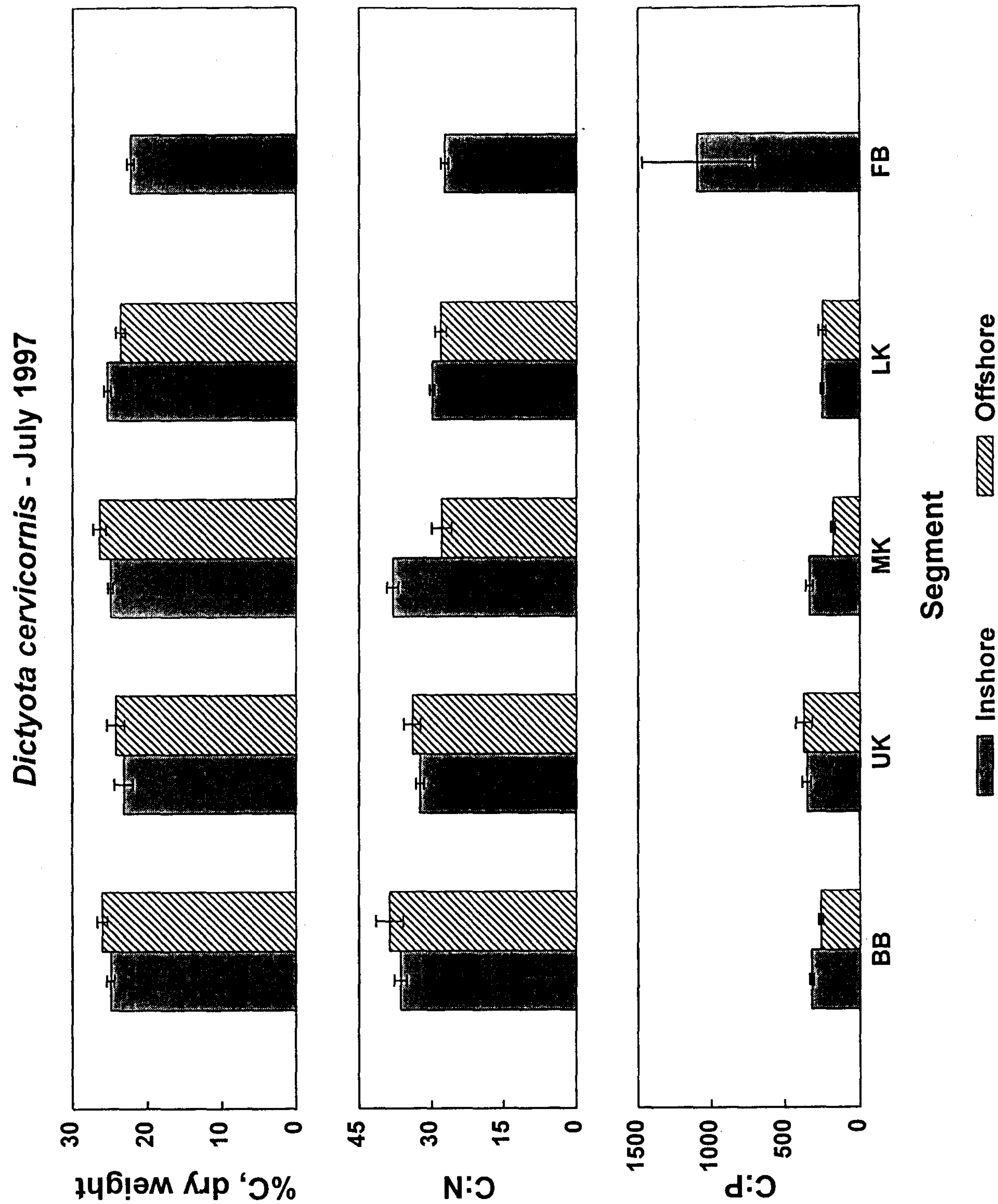

Fig. 107 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Dictyota cervicornis*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

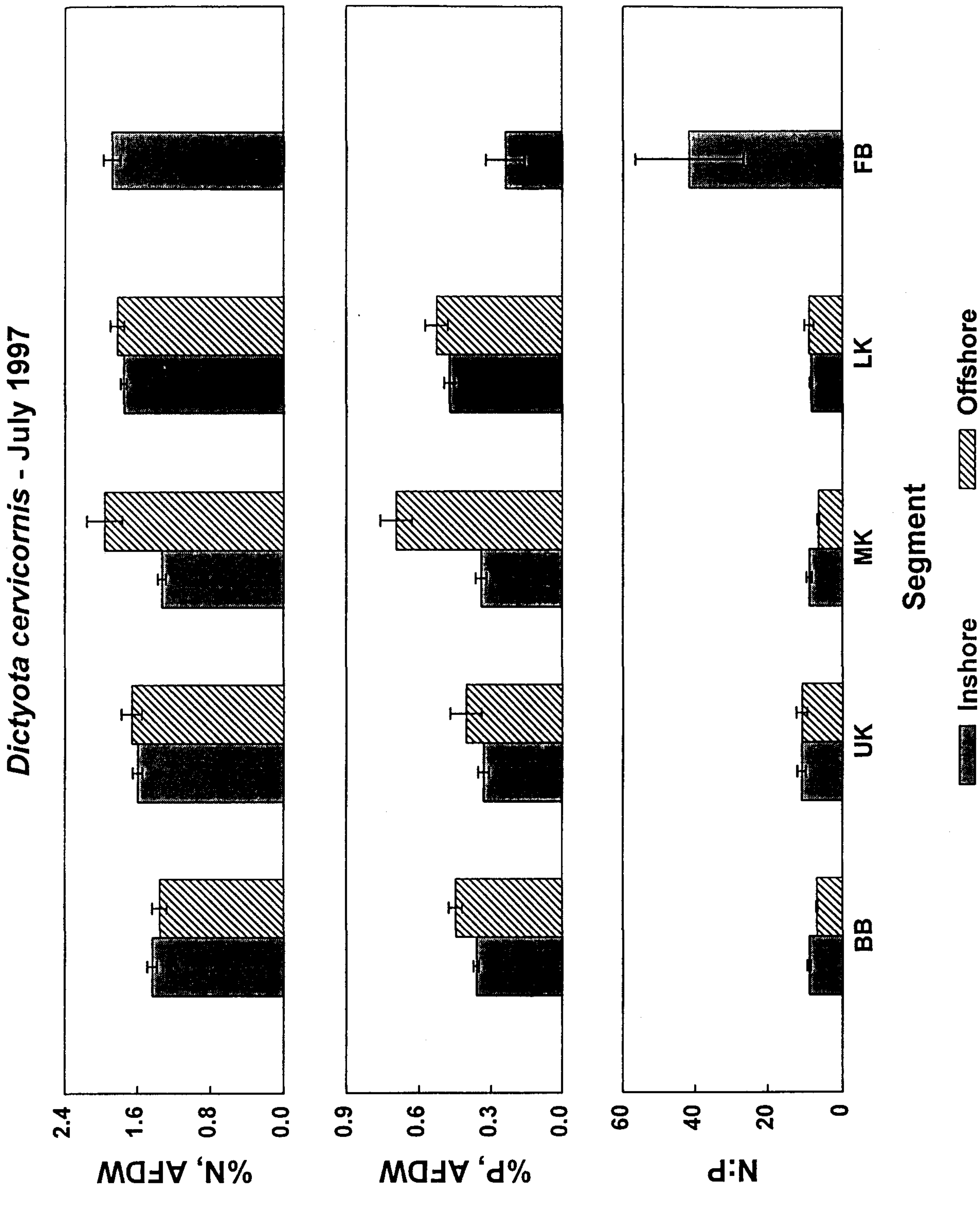

Fig. 108 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Dictyota cervicornis*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

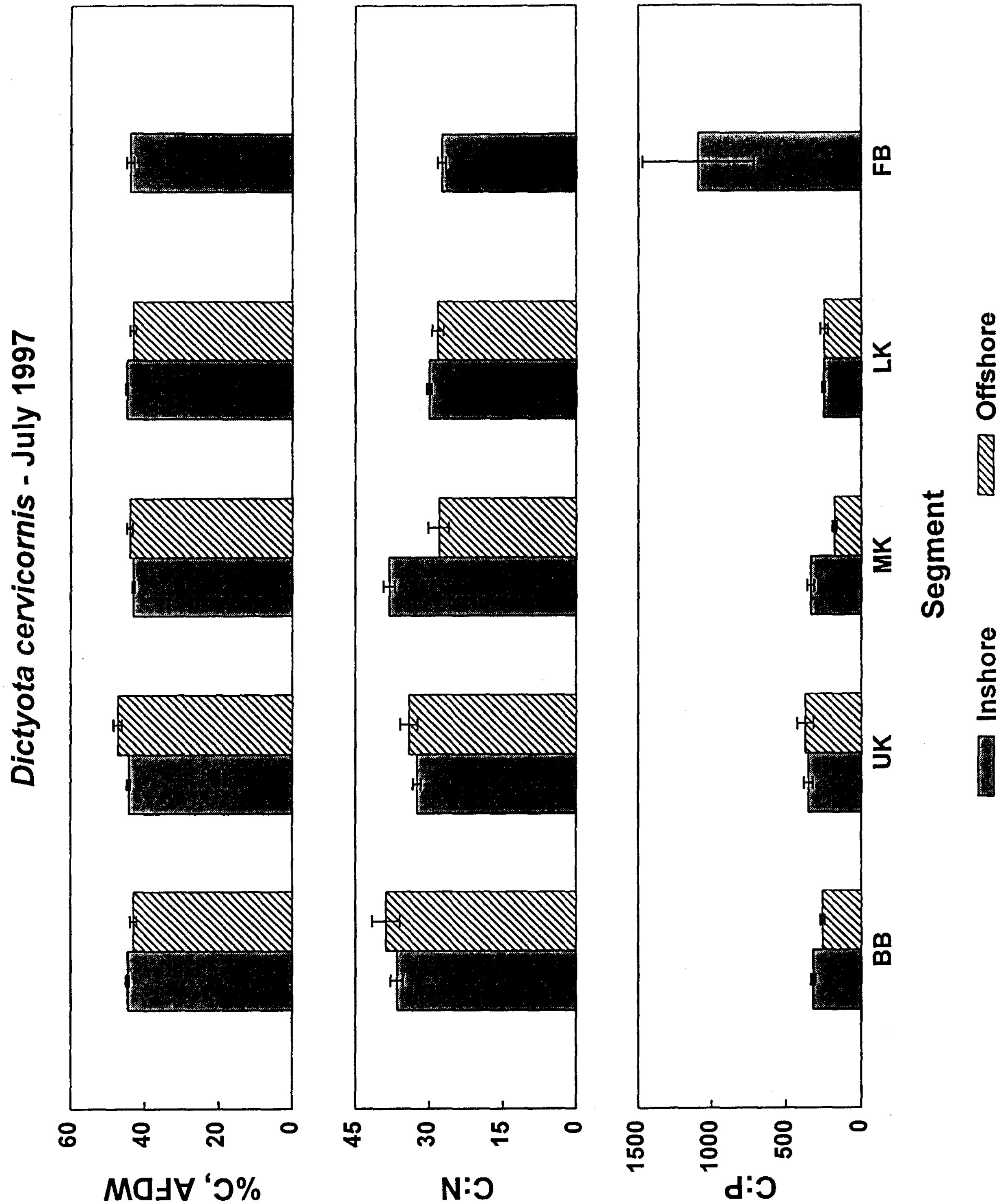

Fig. 109 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Dictyota cervicornis*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

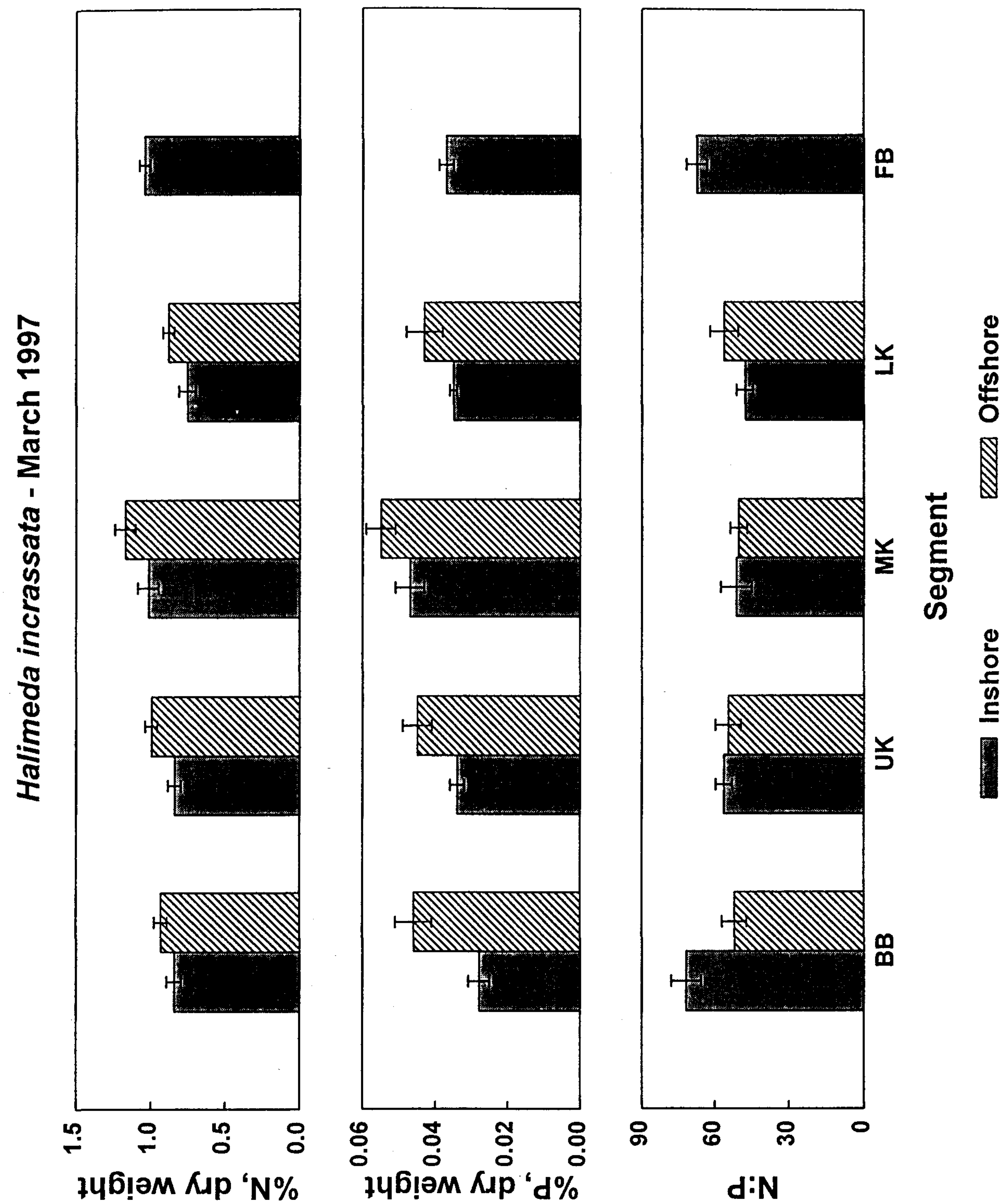

Fig. 110 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda incrassata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

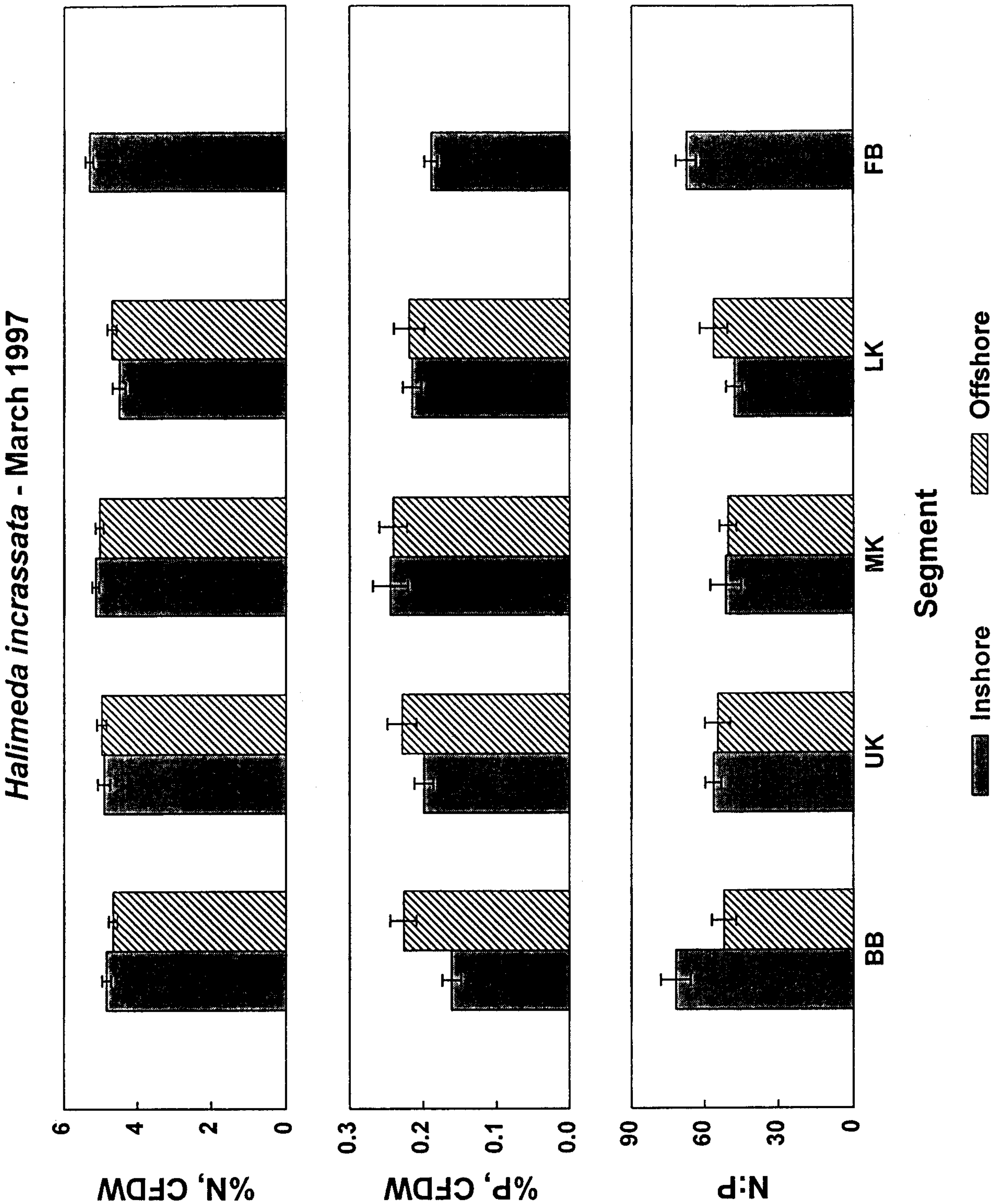

Fig. 111 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda incrassata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

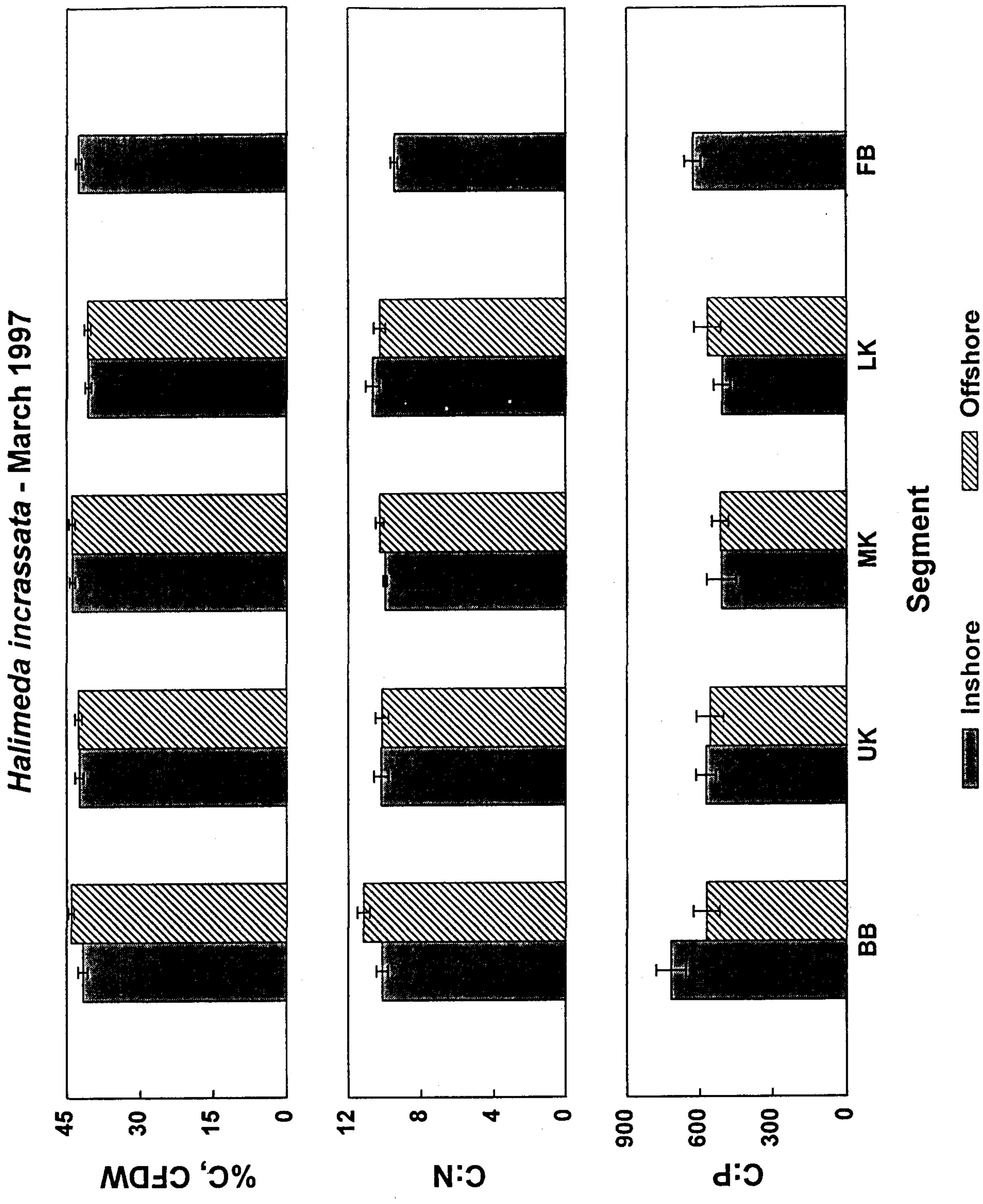

Fig. 112 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda incrassata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

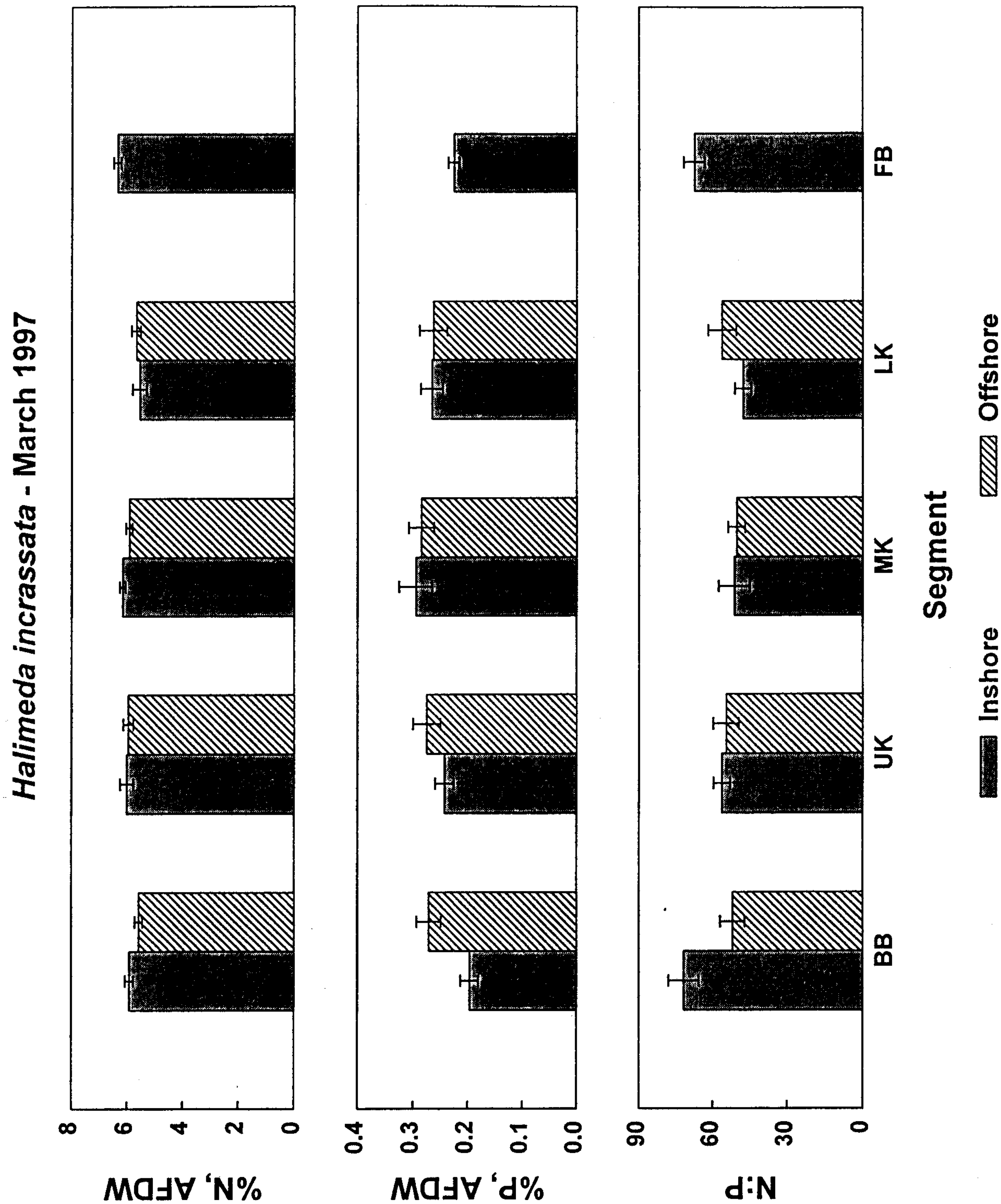

Fig. 113 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda incrassata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

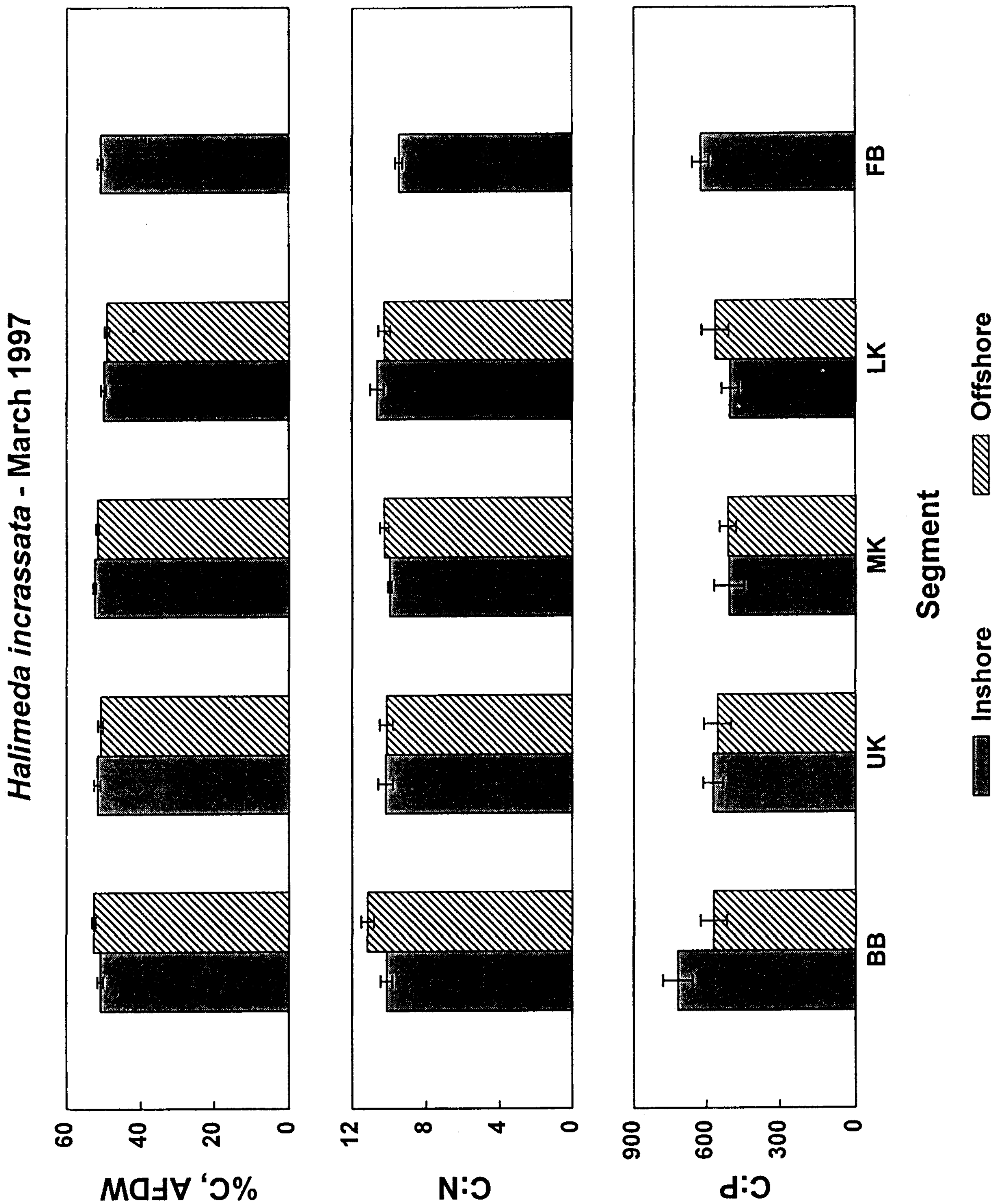

Fig. 114 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda incrassata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

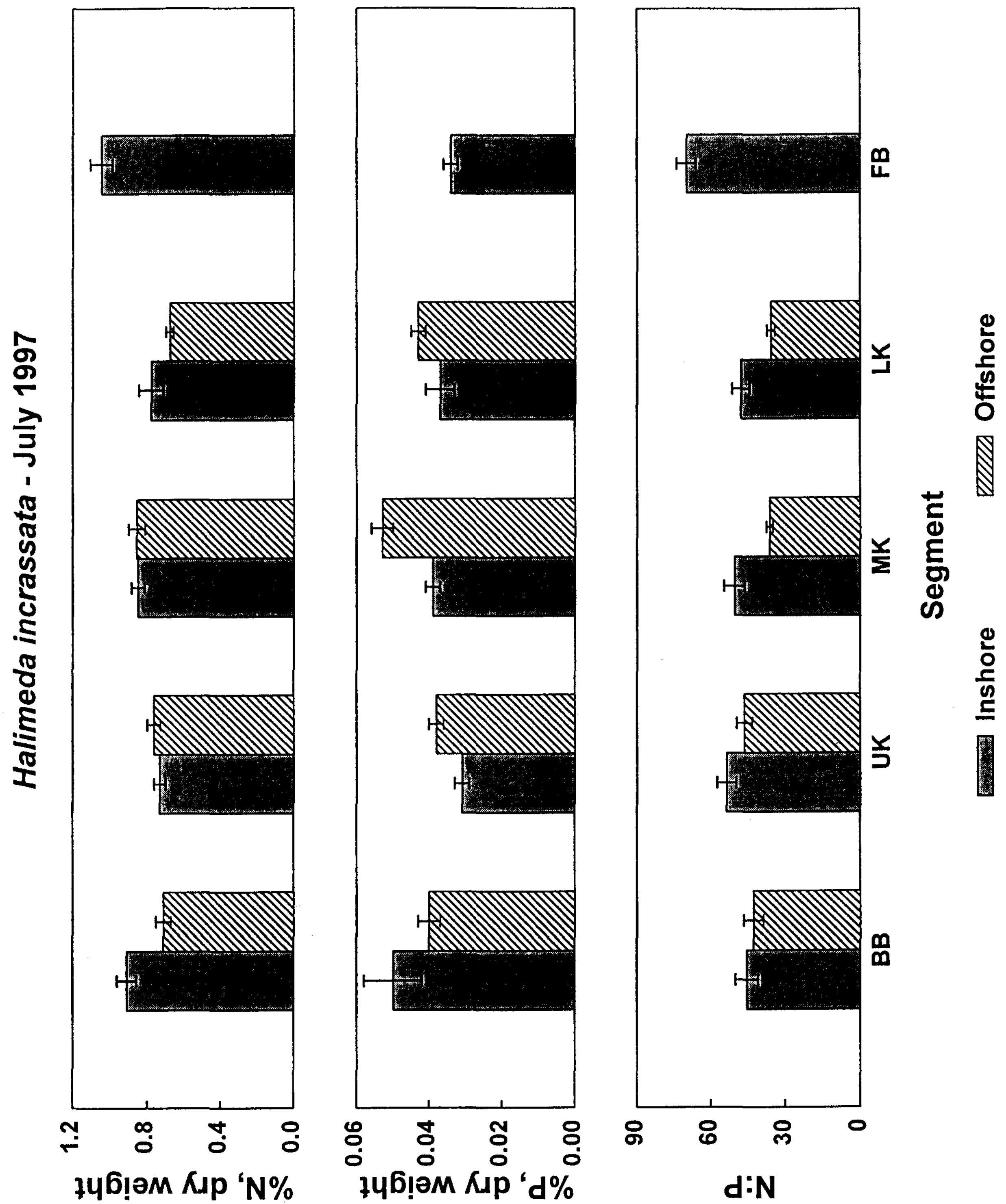

Fig. 115 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda incrassata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

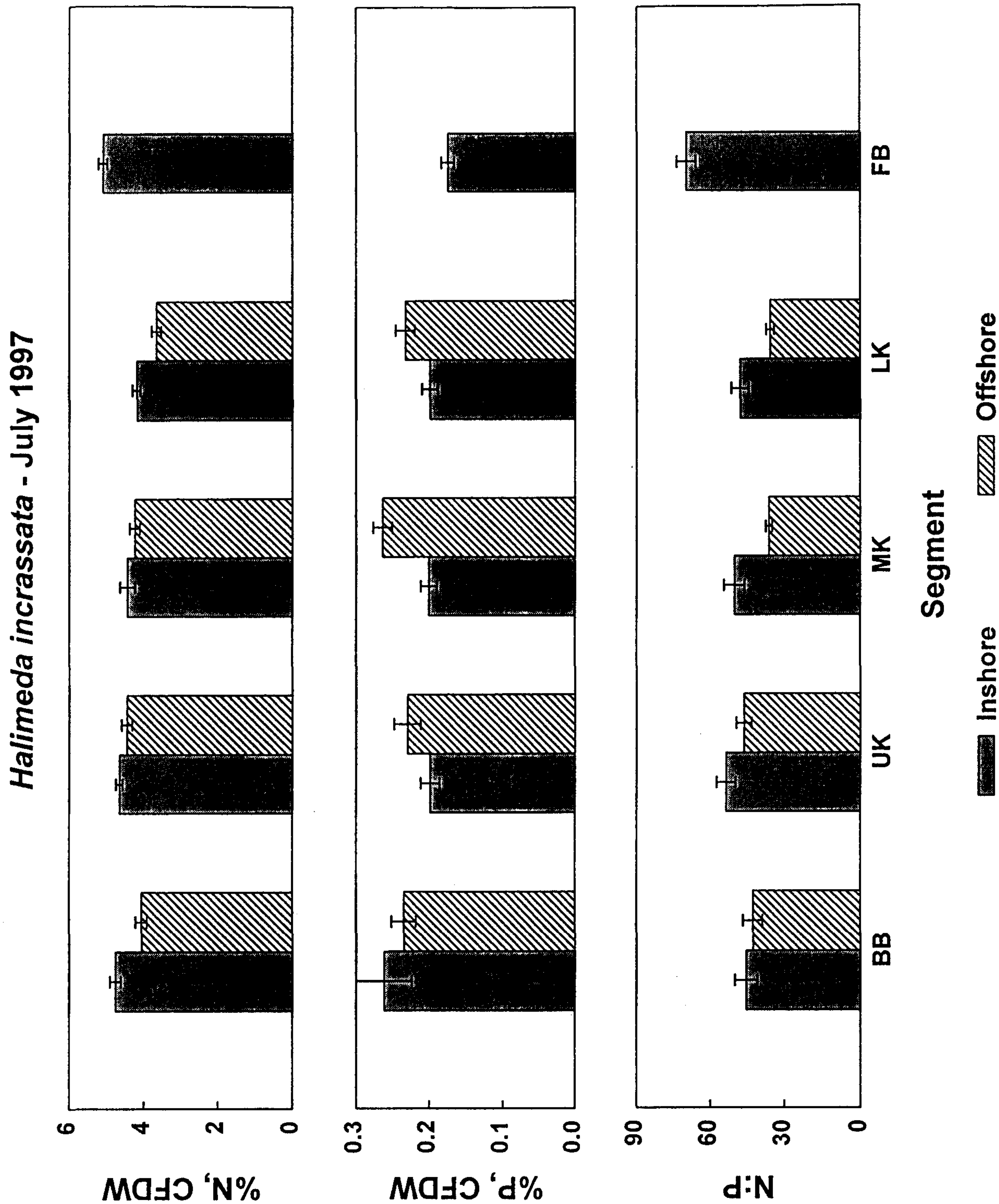

Fig. 116 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda incrassata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

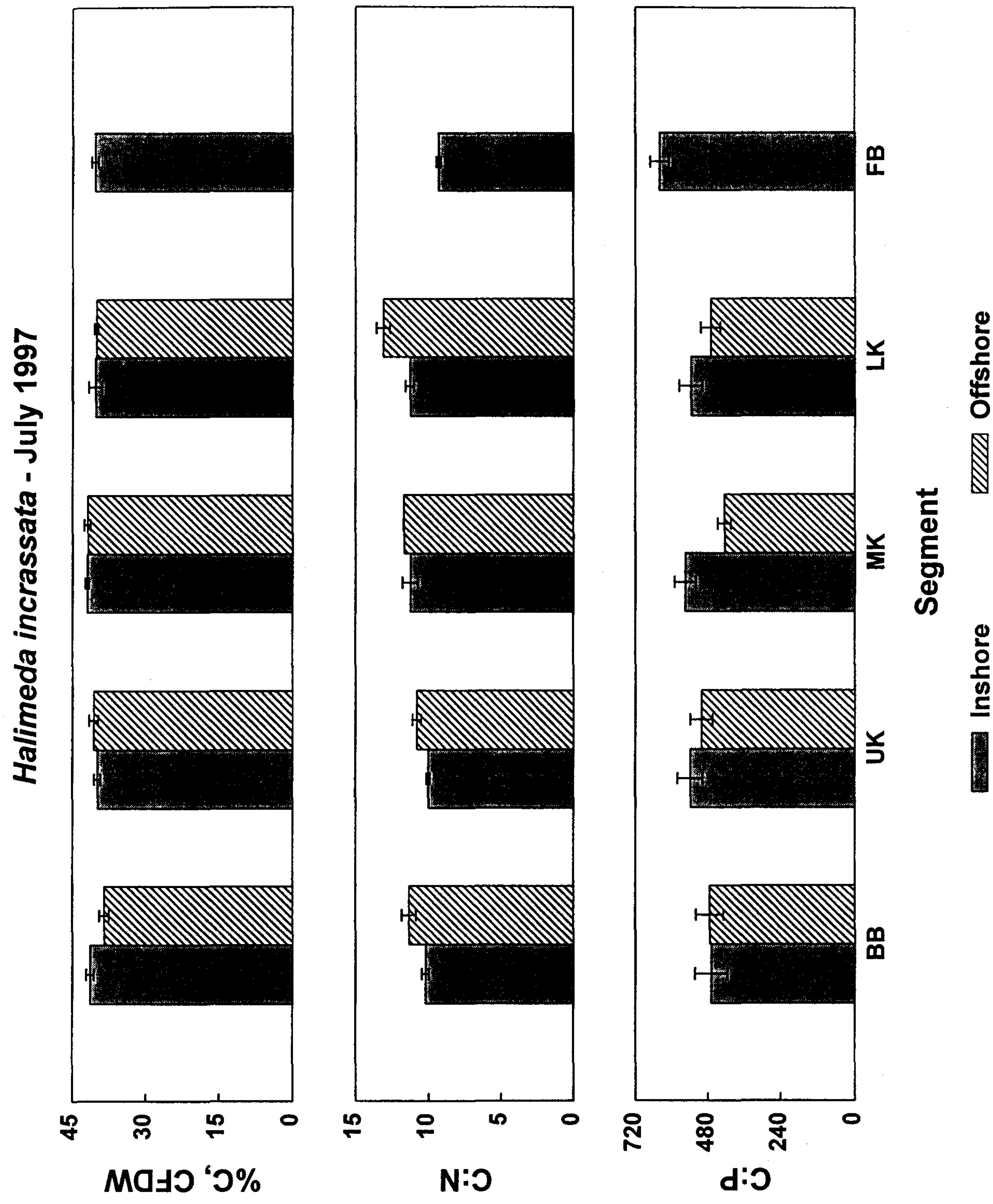

Fig. 117 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda incrassata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

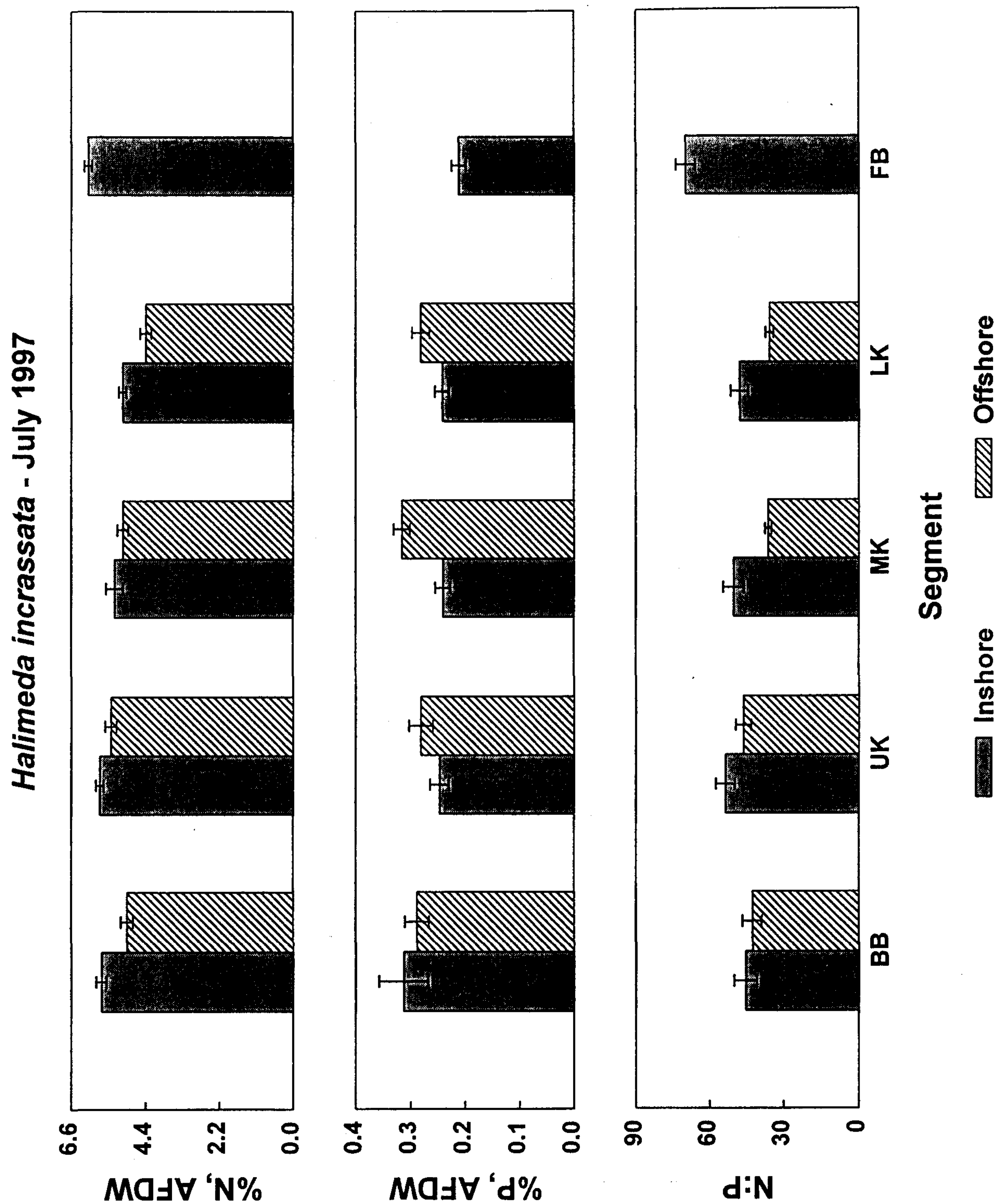

Fig. 118 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda incrassata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

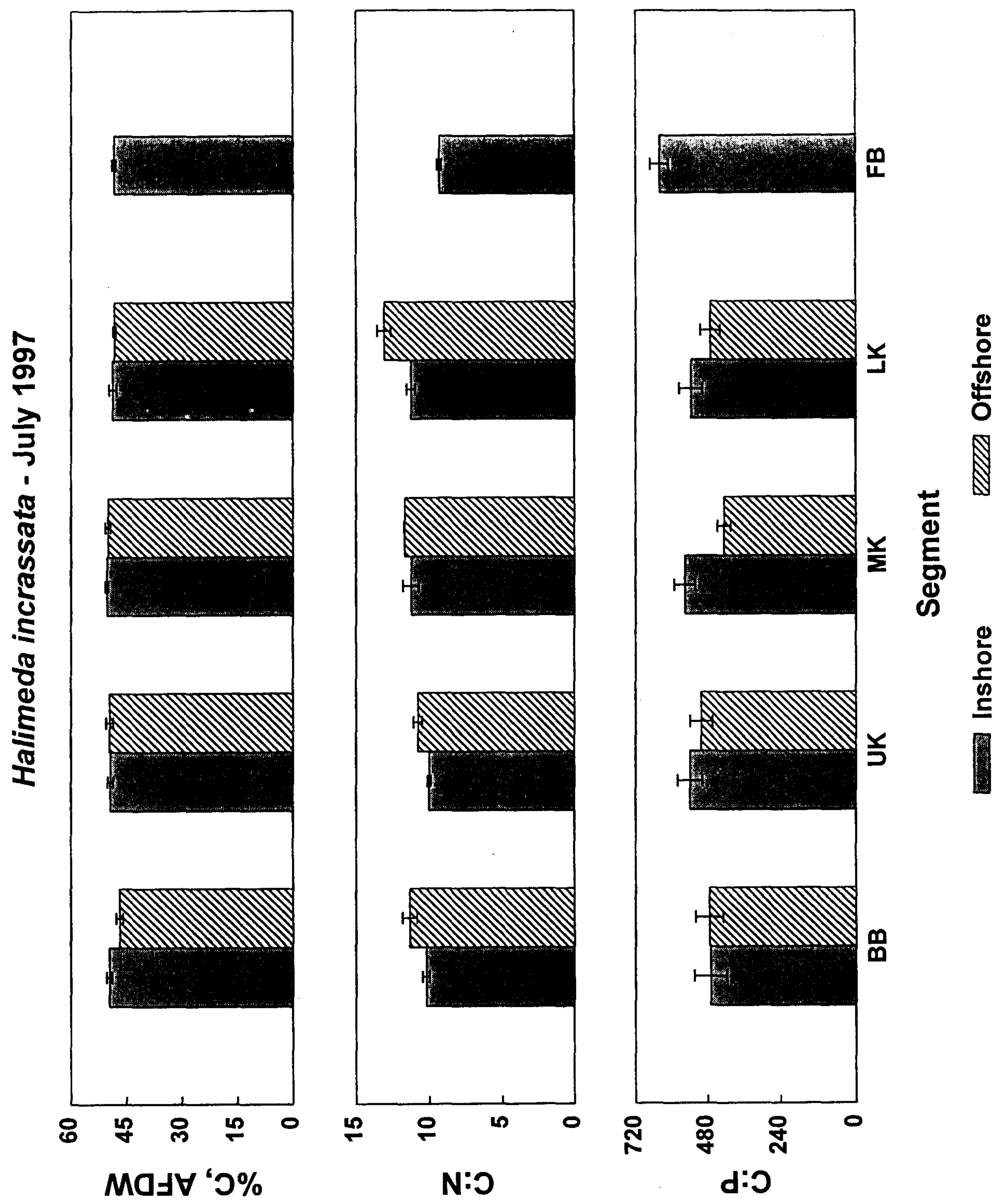

Fig. 119 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda incrassata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

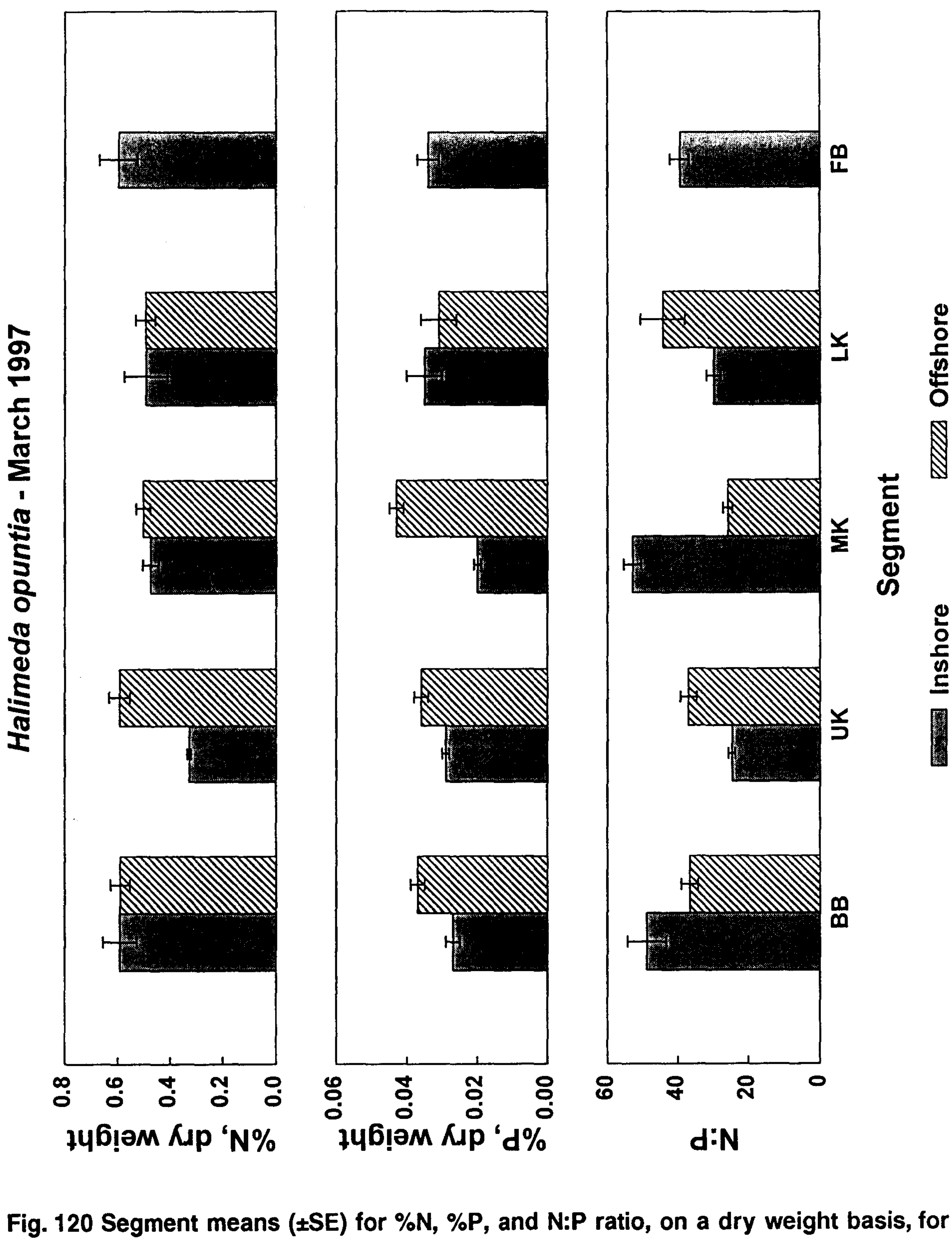

Fig. 120 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda opuntia*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

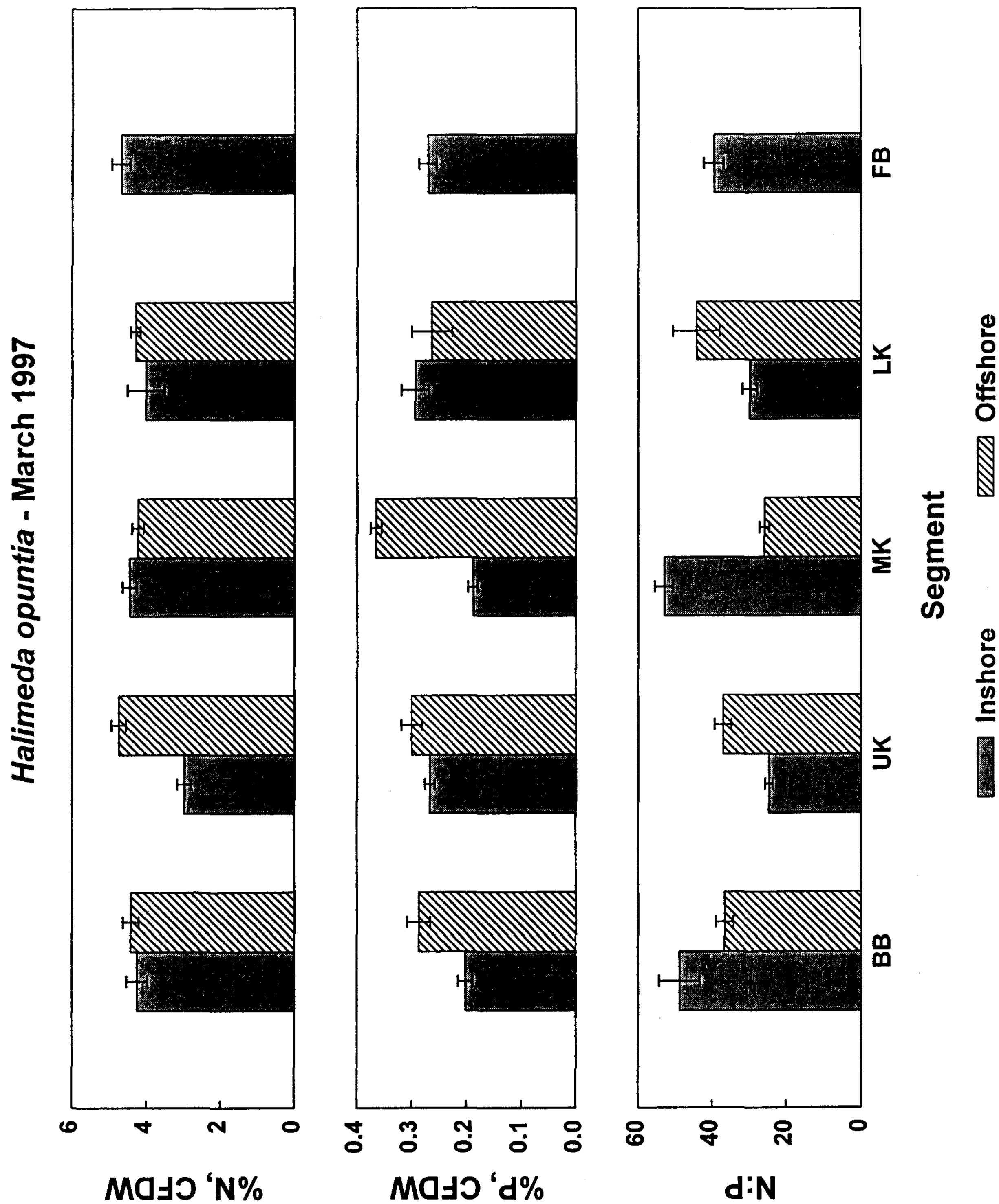

Fig. 121 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda opuntia*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

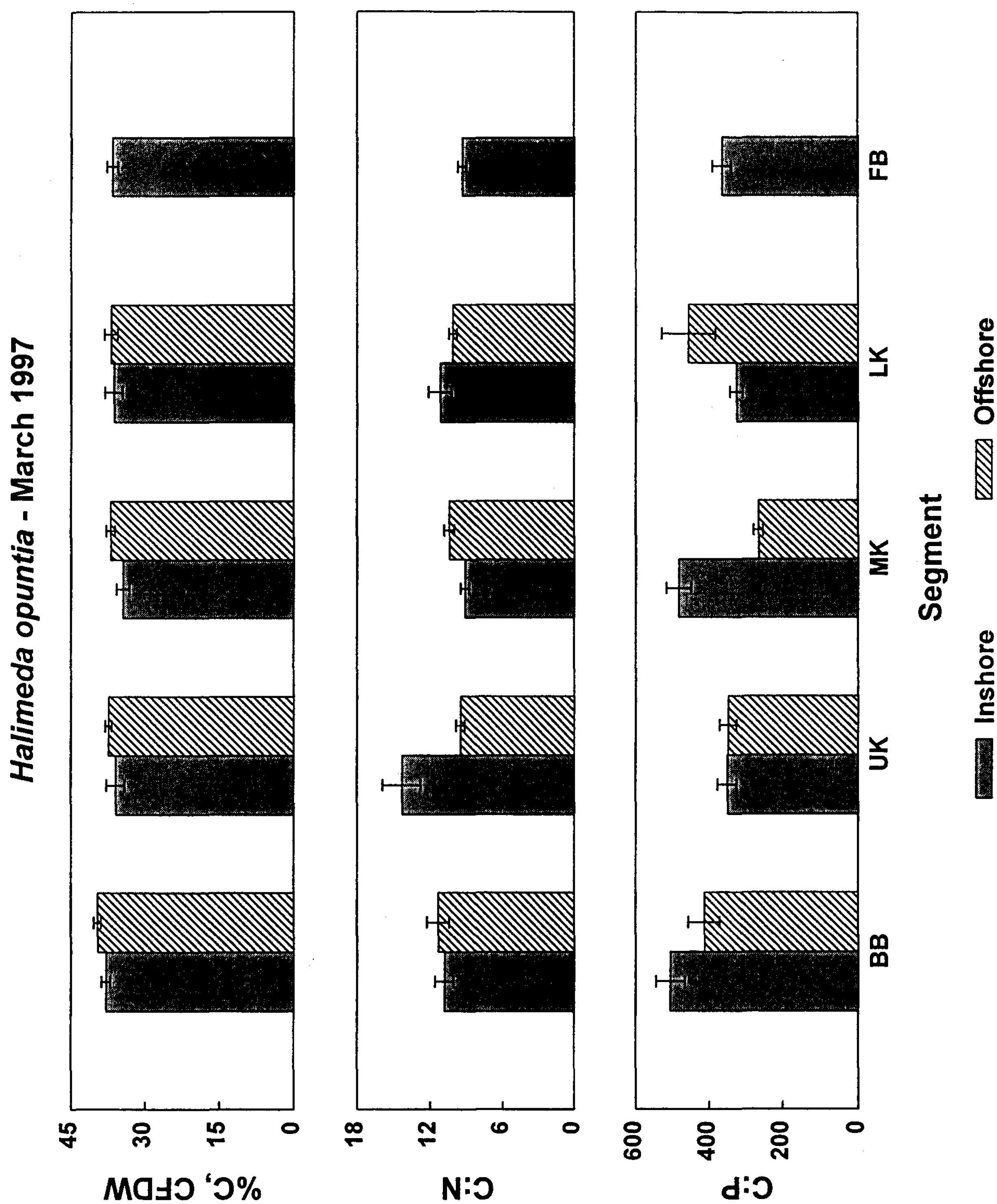

Fig. 122 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda opuntia*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

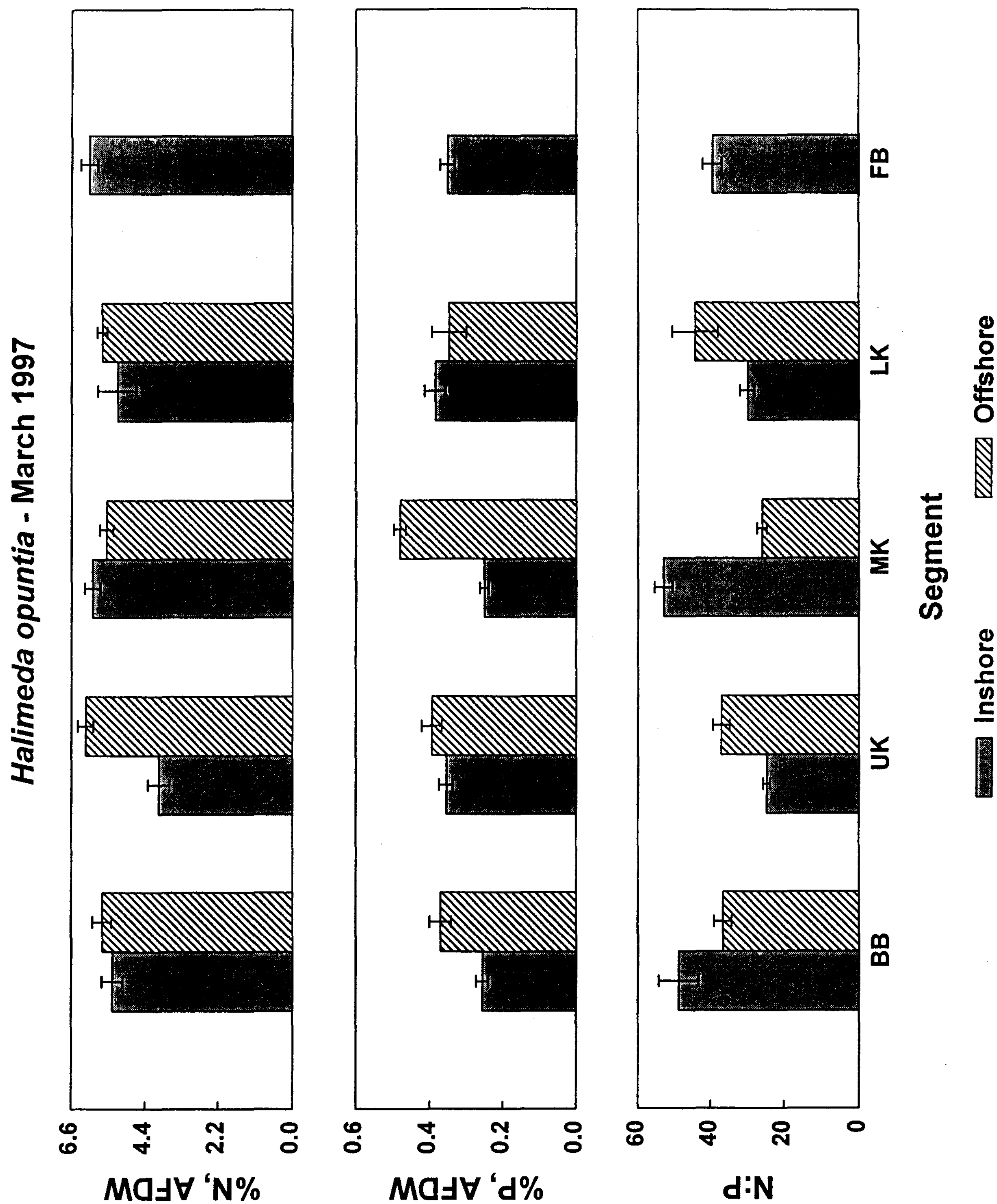

Fig. 123 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda opuntia*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

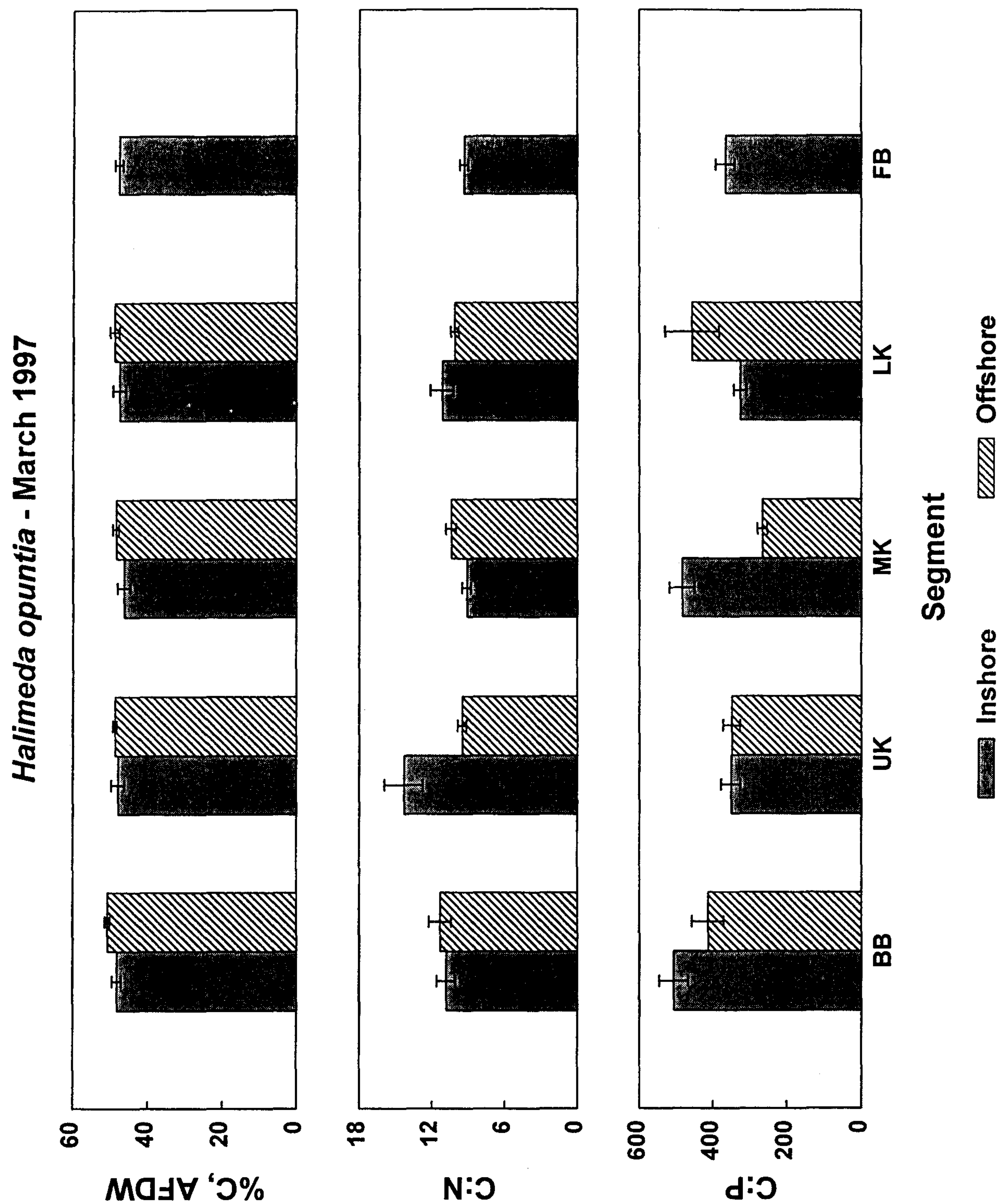

Fig. 124 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda opuntia*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

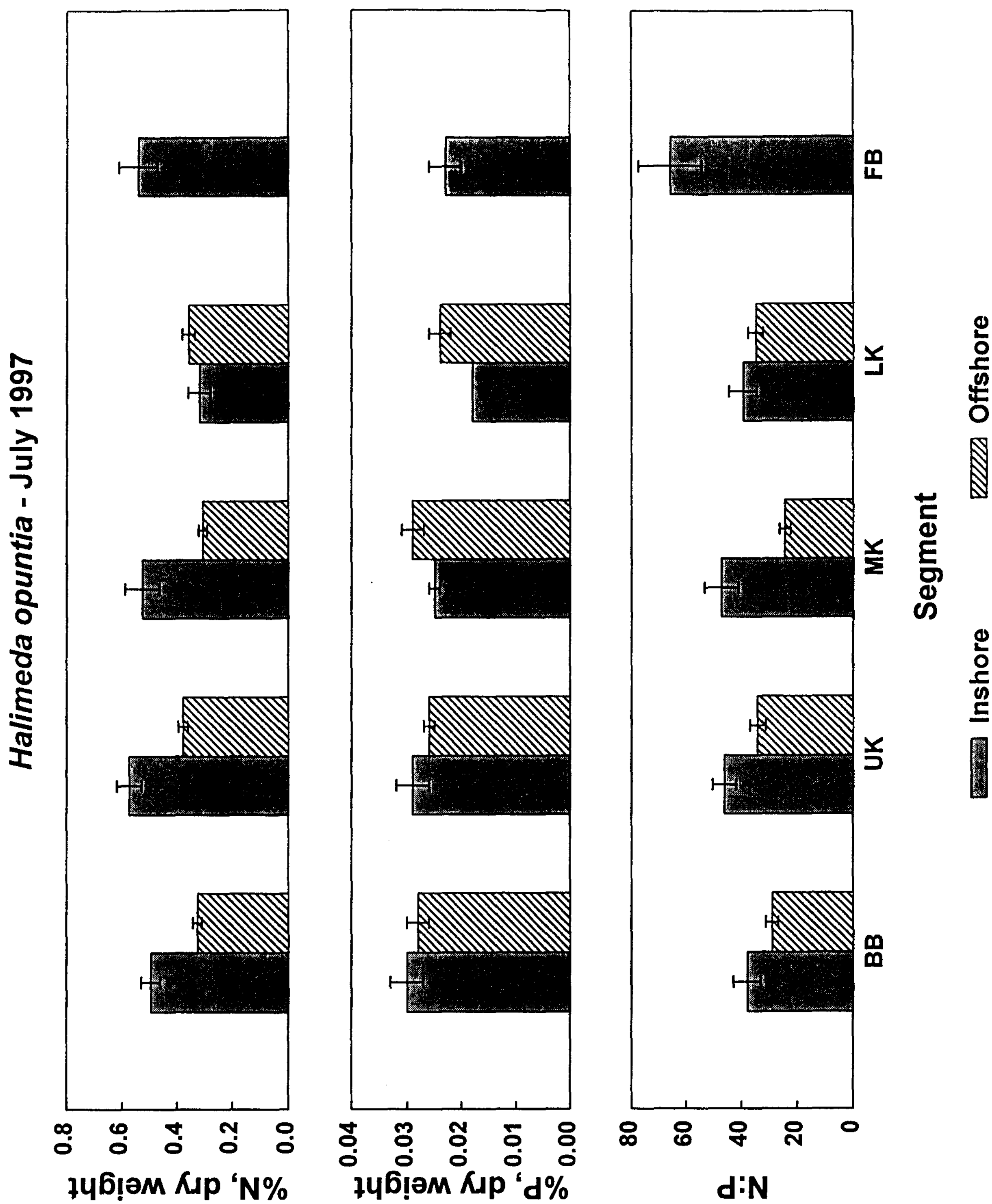

Fig. 125 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda opuntia*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

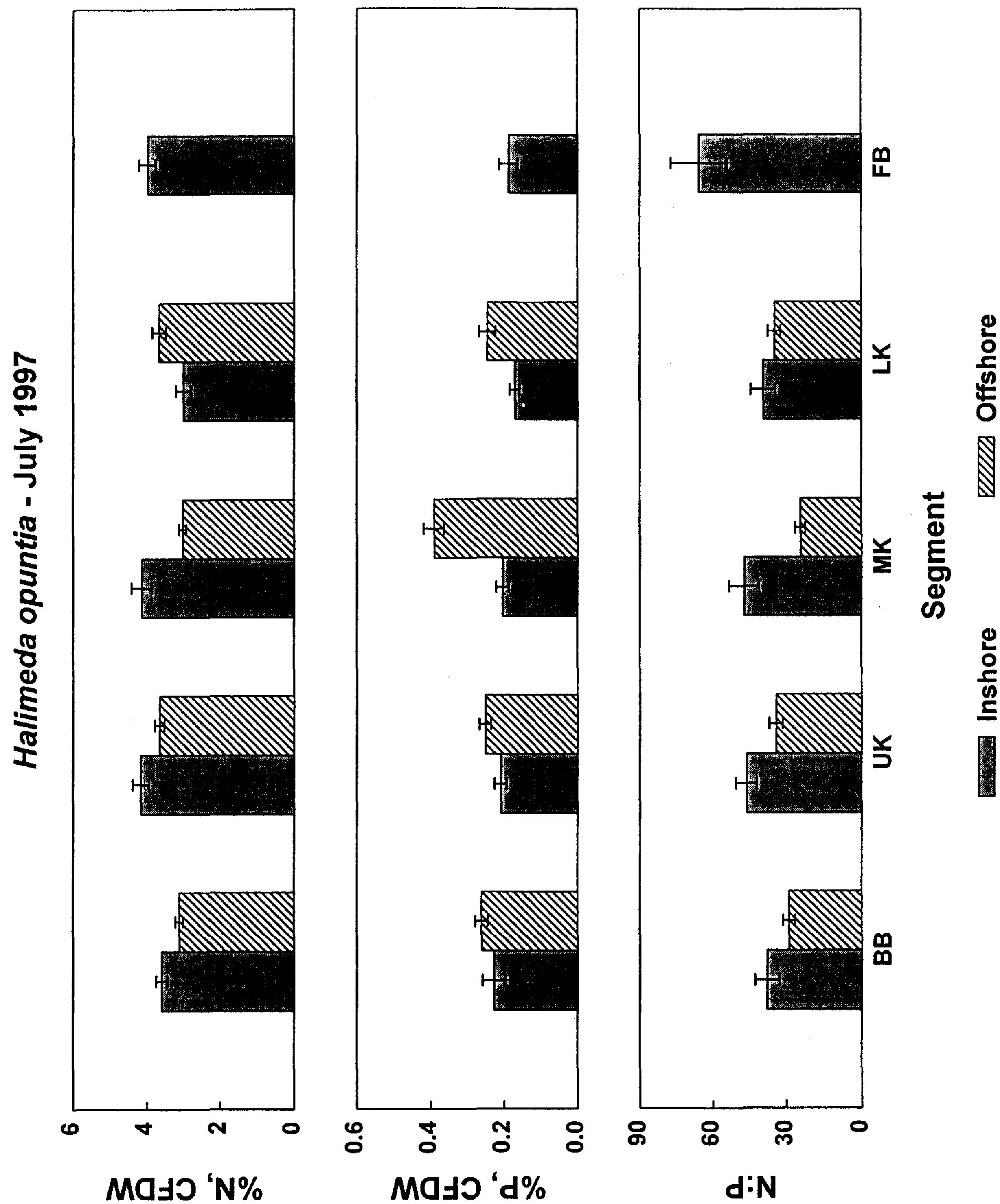

Fig. 126 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda opuntia*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

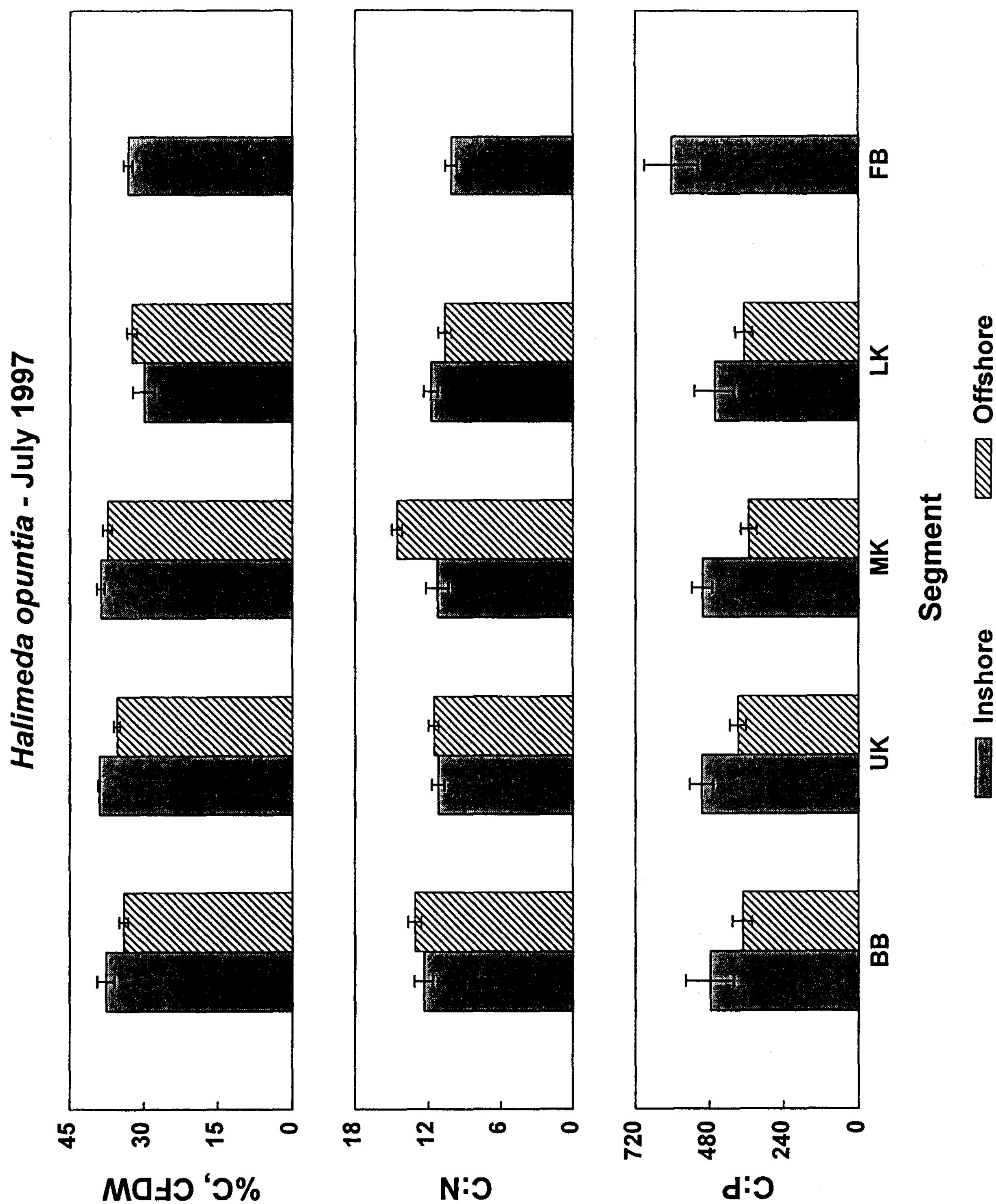

Fig. 127 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda opuntia*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

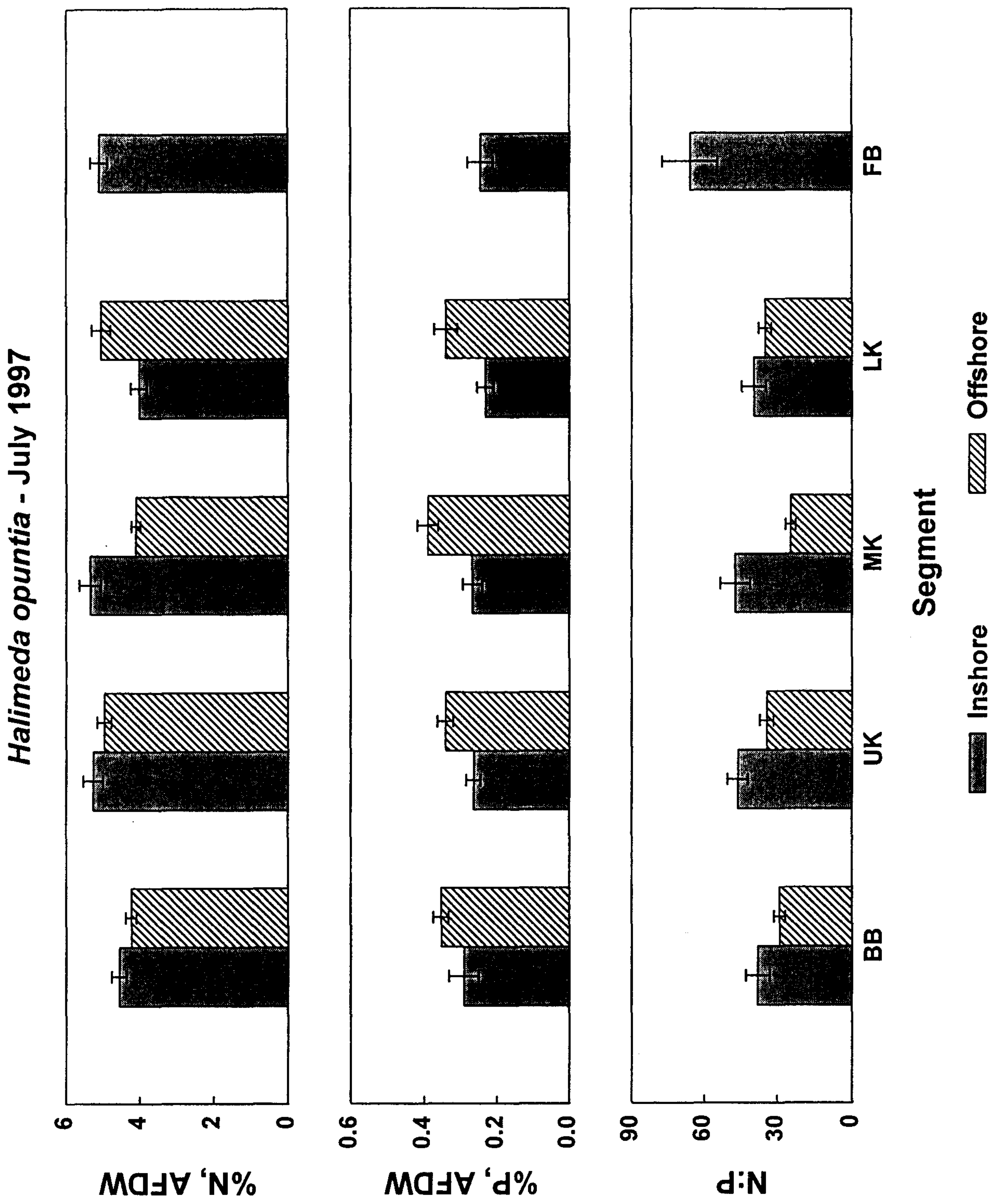

Fig. 128 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda opuntia*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

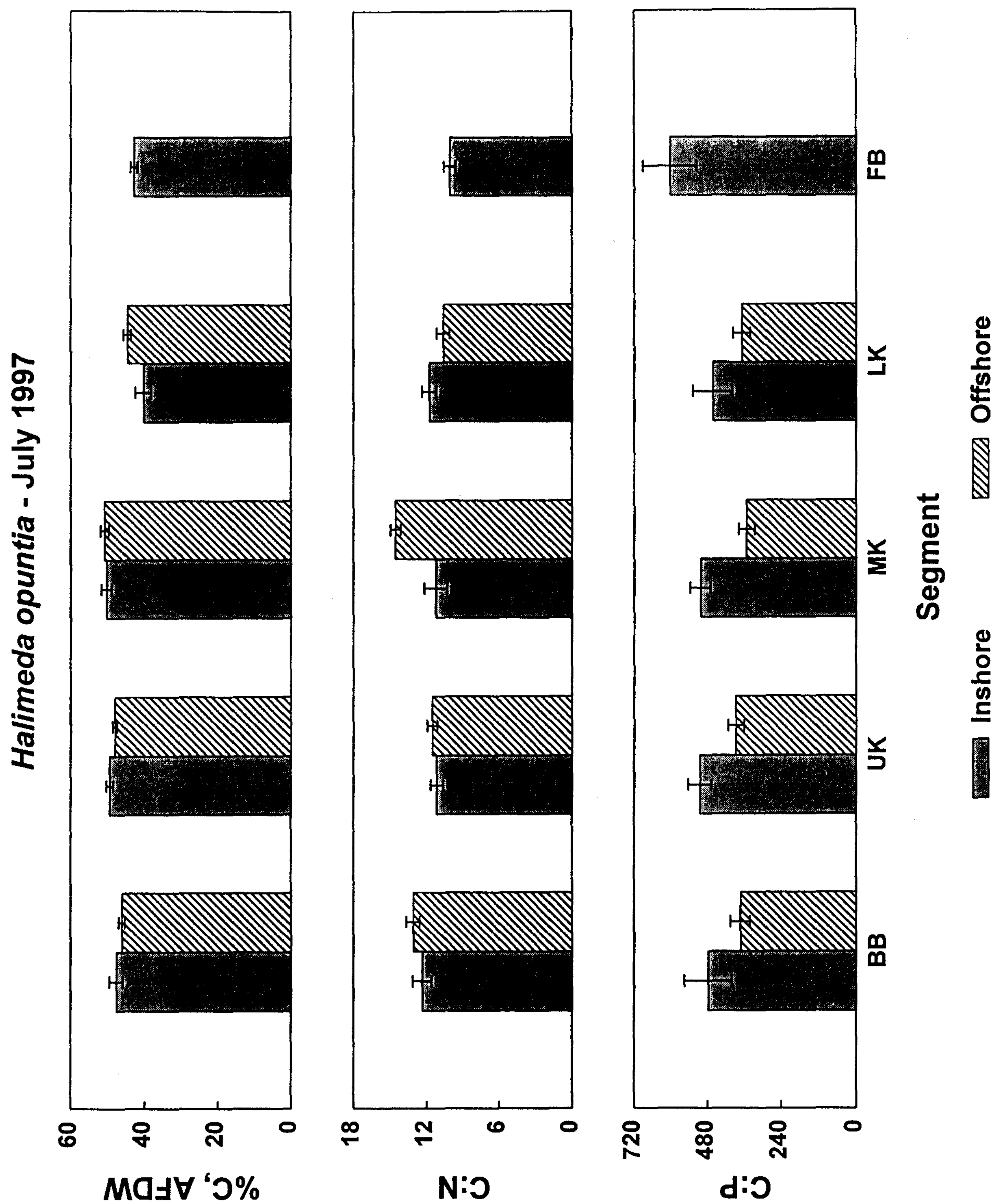

Fig. 129 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda opuntia*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

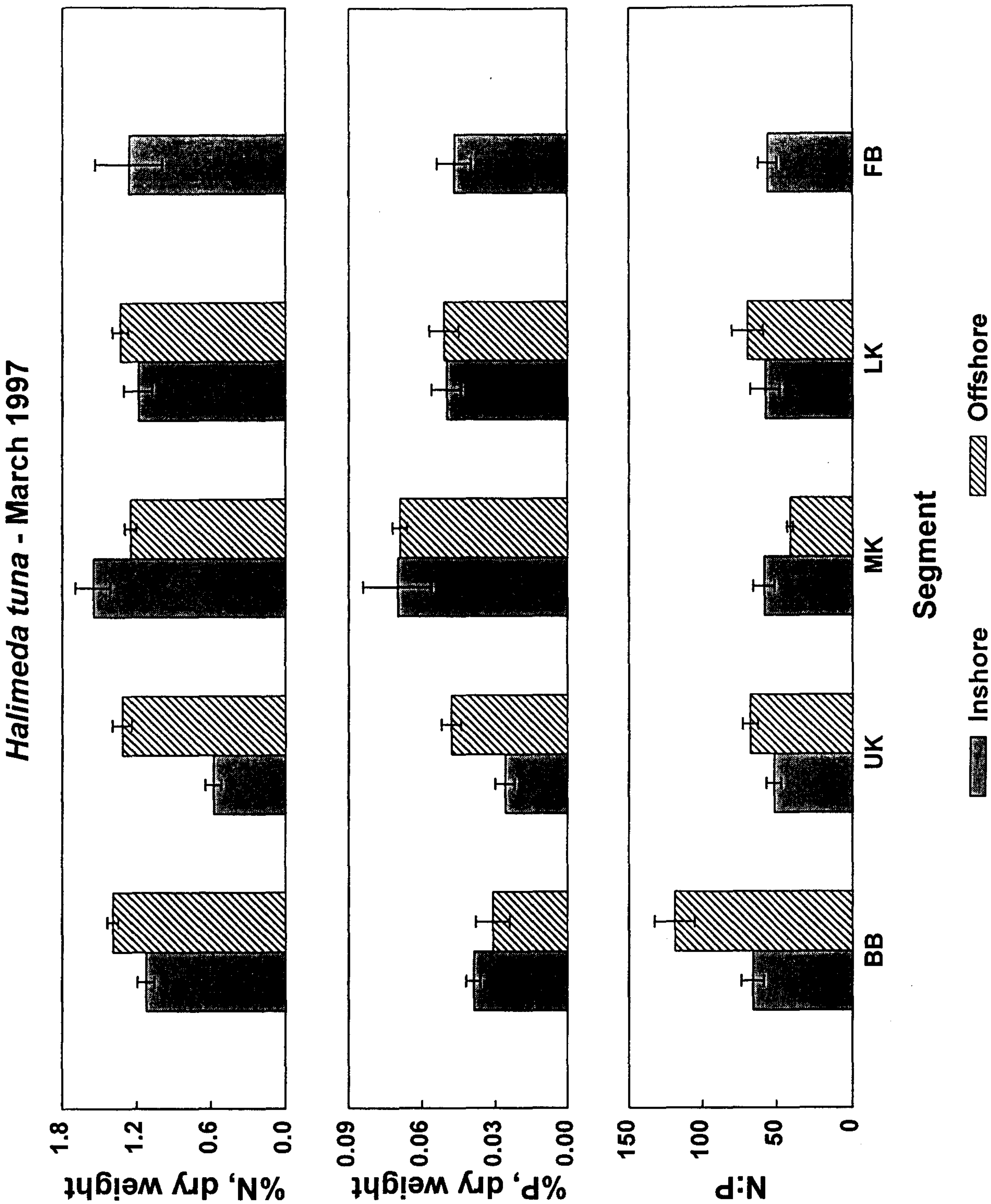

Fig. 130 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda tuna*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

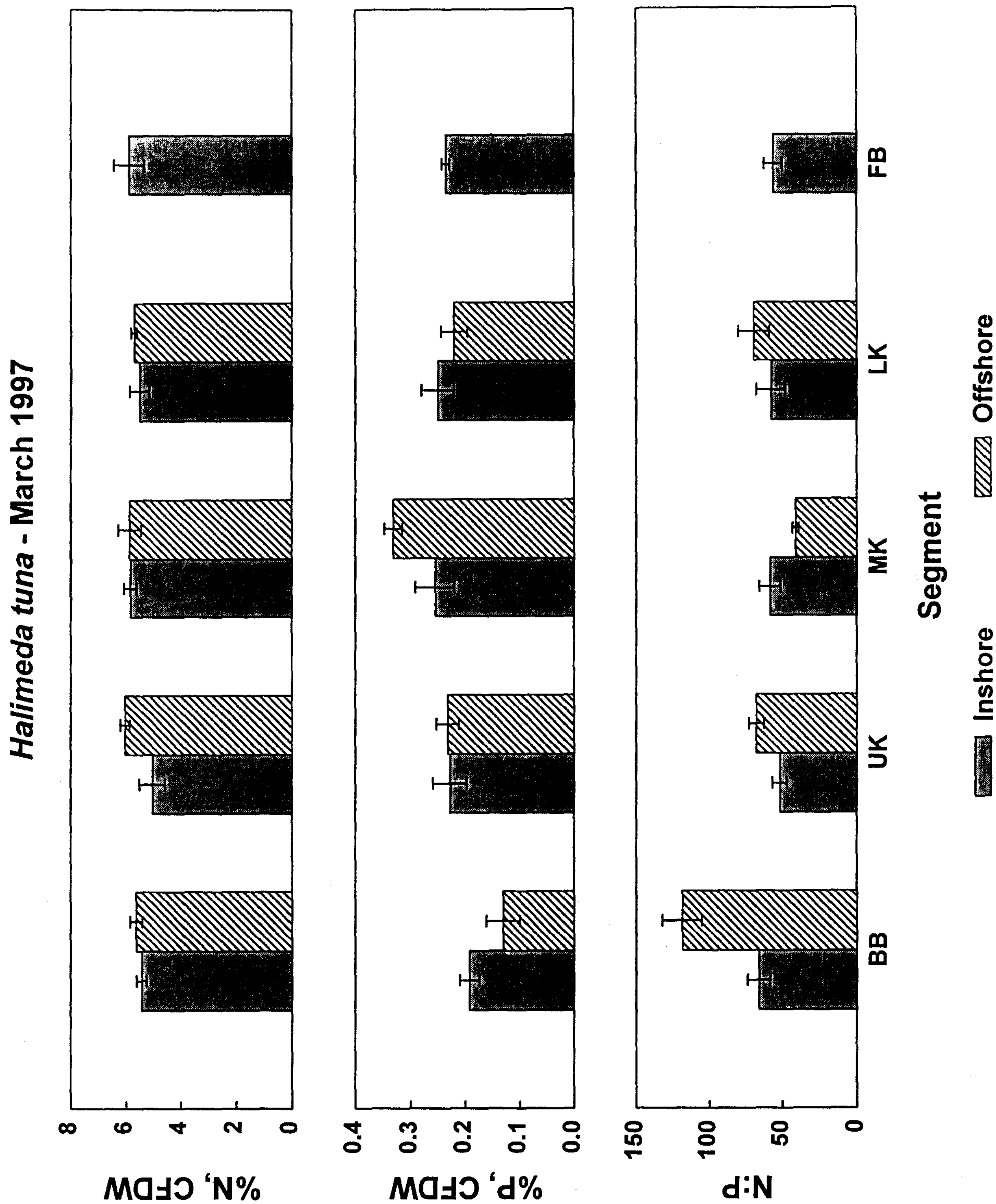

Fig. 131 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda tuna*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

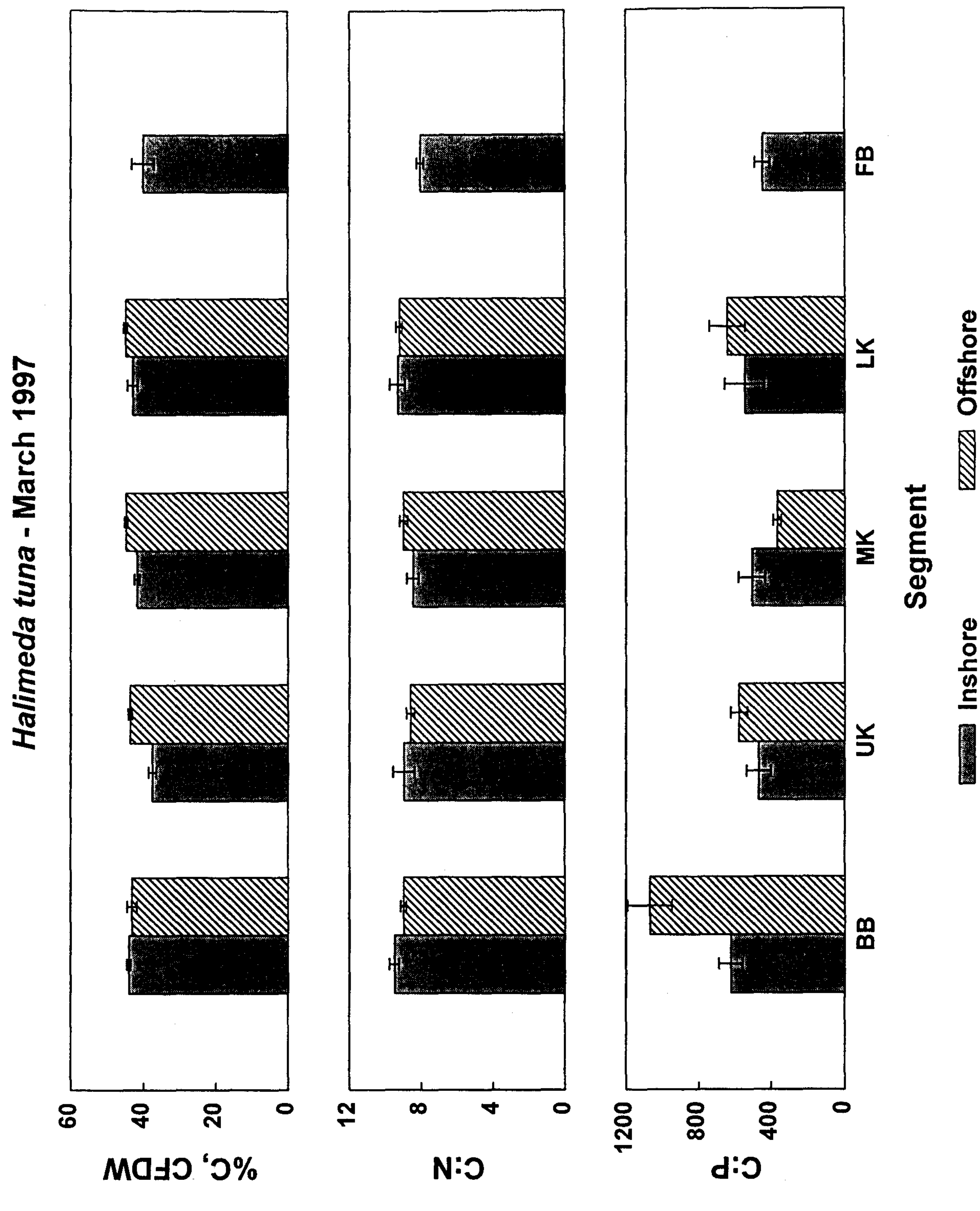

Fig. 132 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda tuna*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

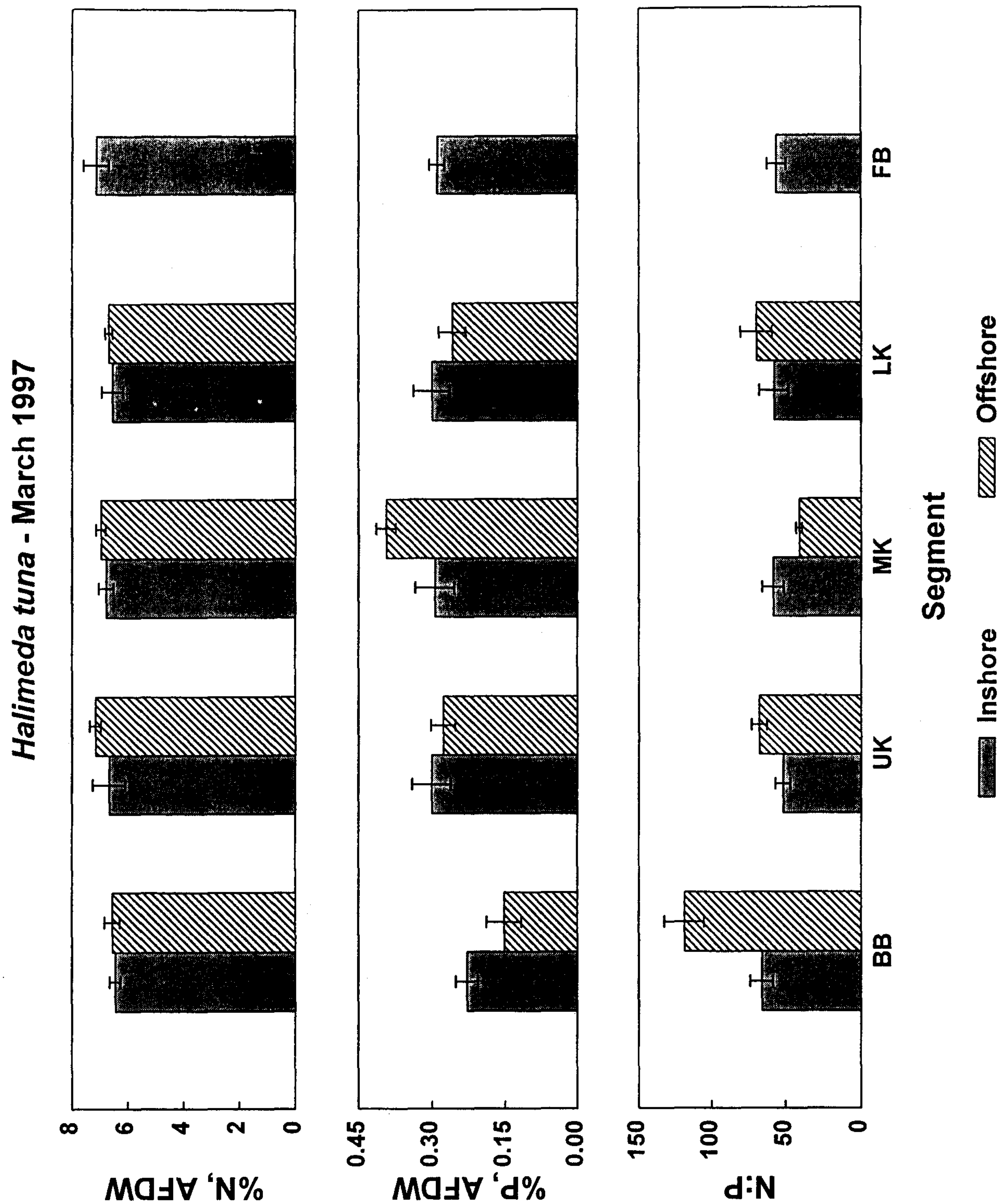

Fig. 133 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda tuna*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

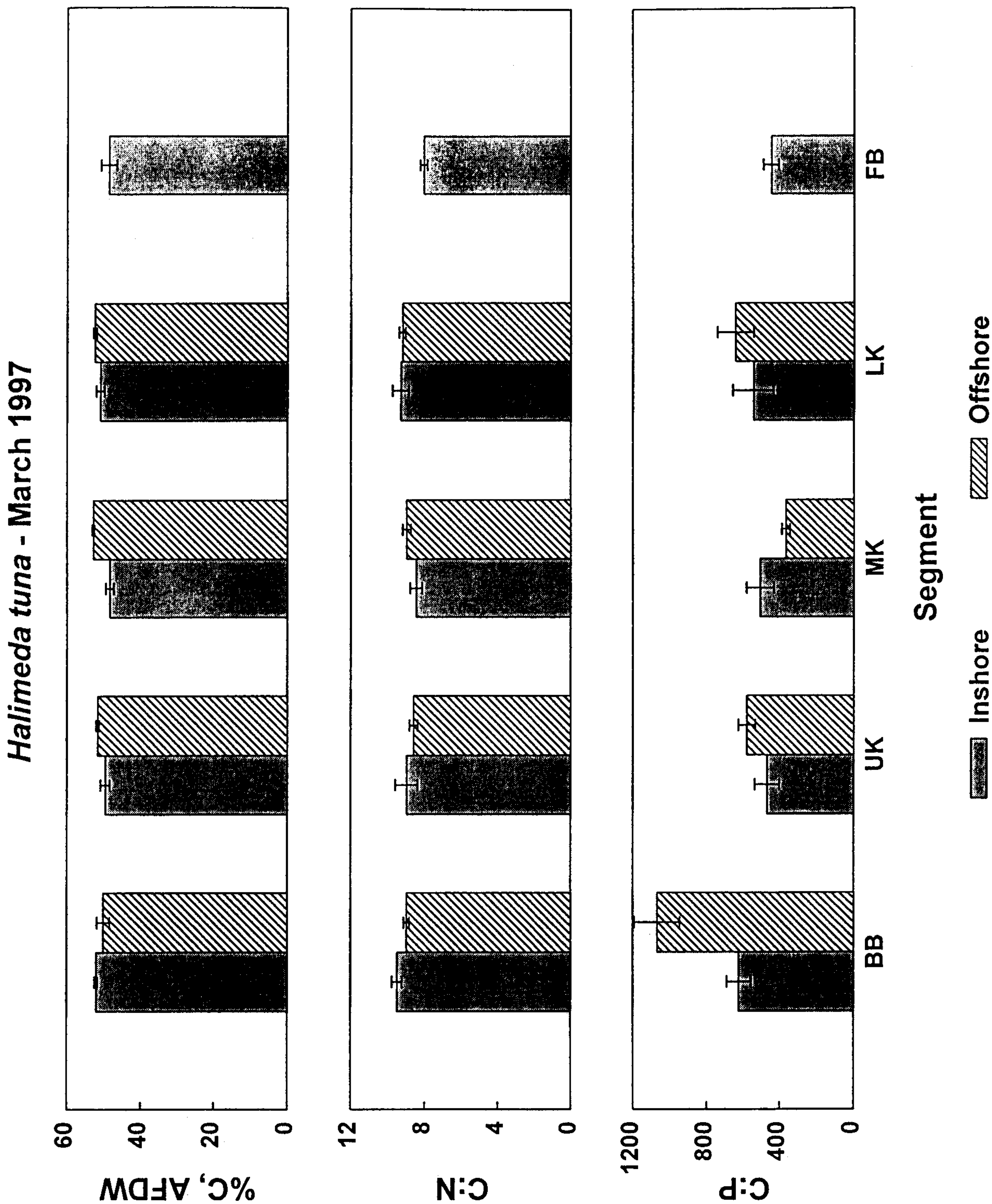

Fig. 134 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda tuna*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

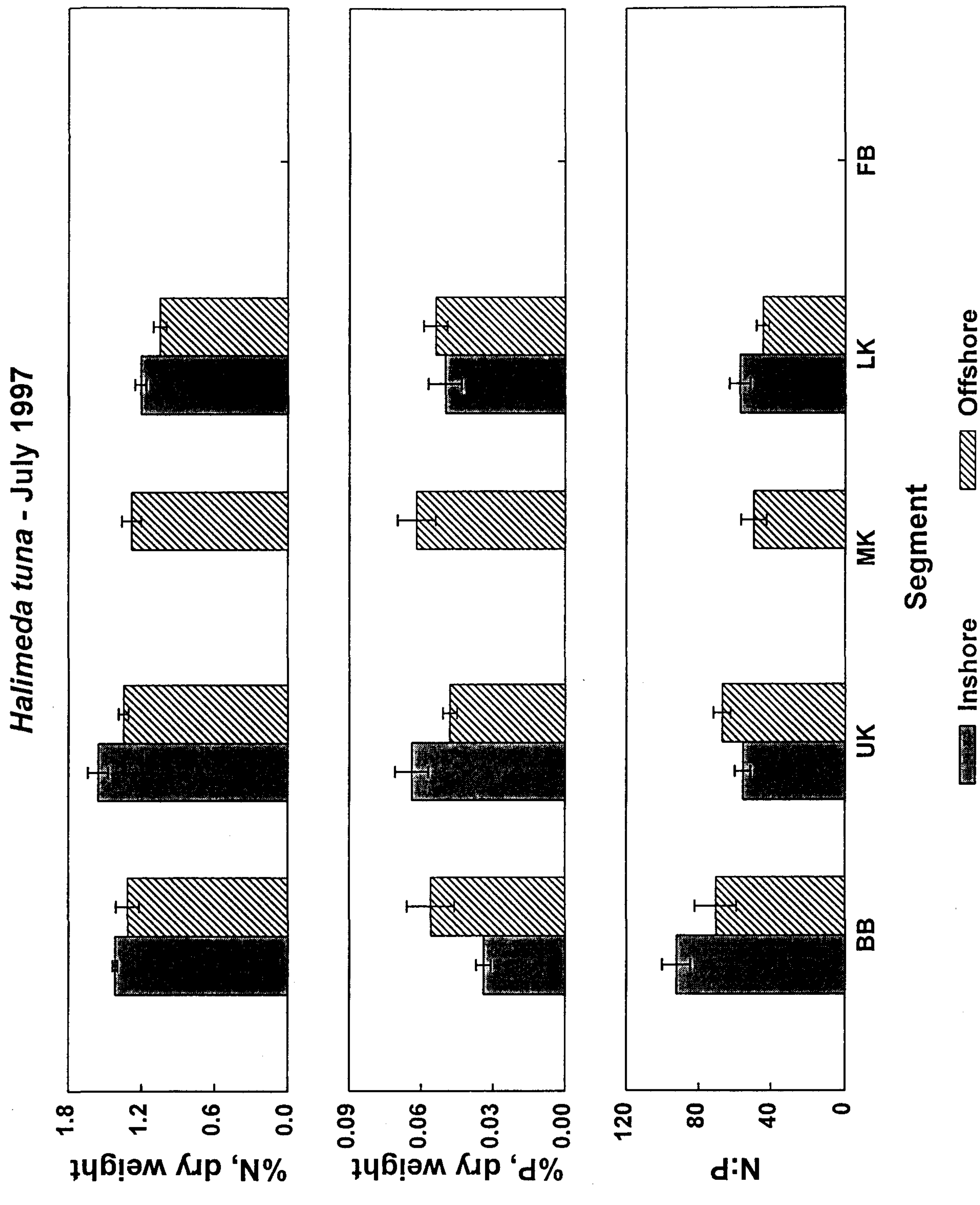

Fig. 135 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Halimeda tuna*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

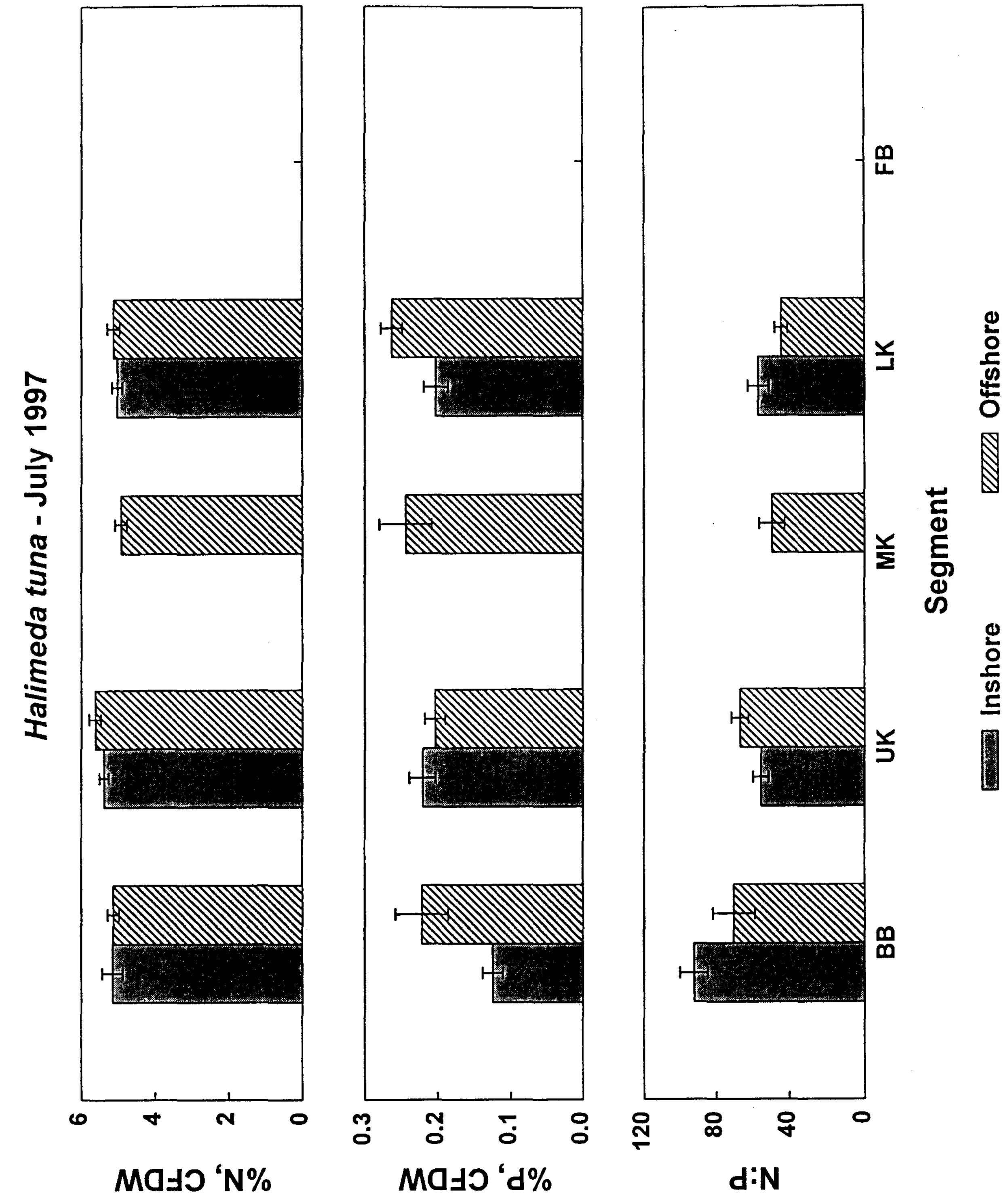

Fig. 136 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda tuna*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

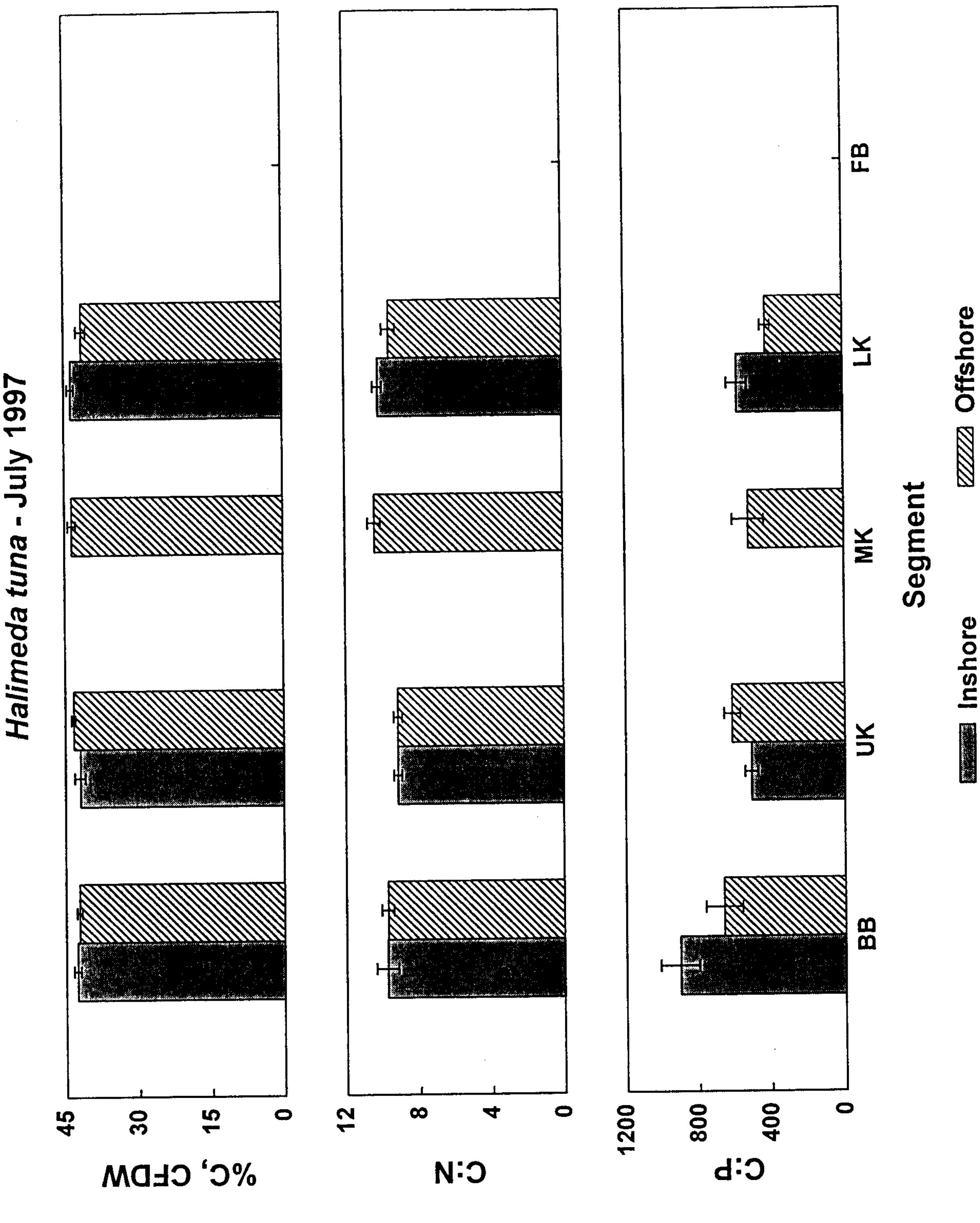

Fig. 137 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Halimeda tuna*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

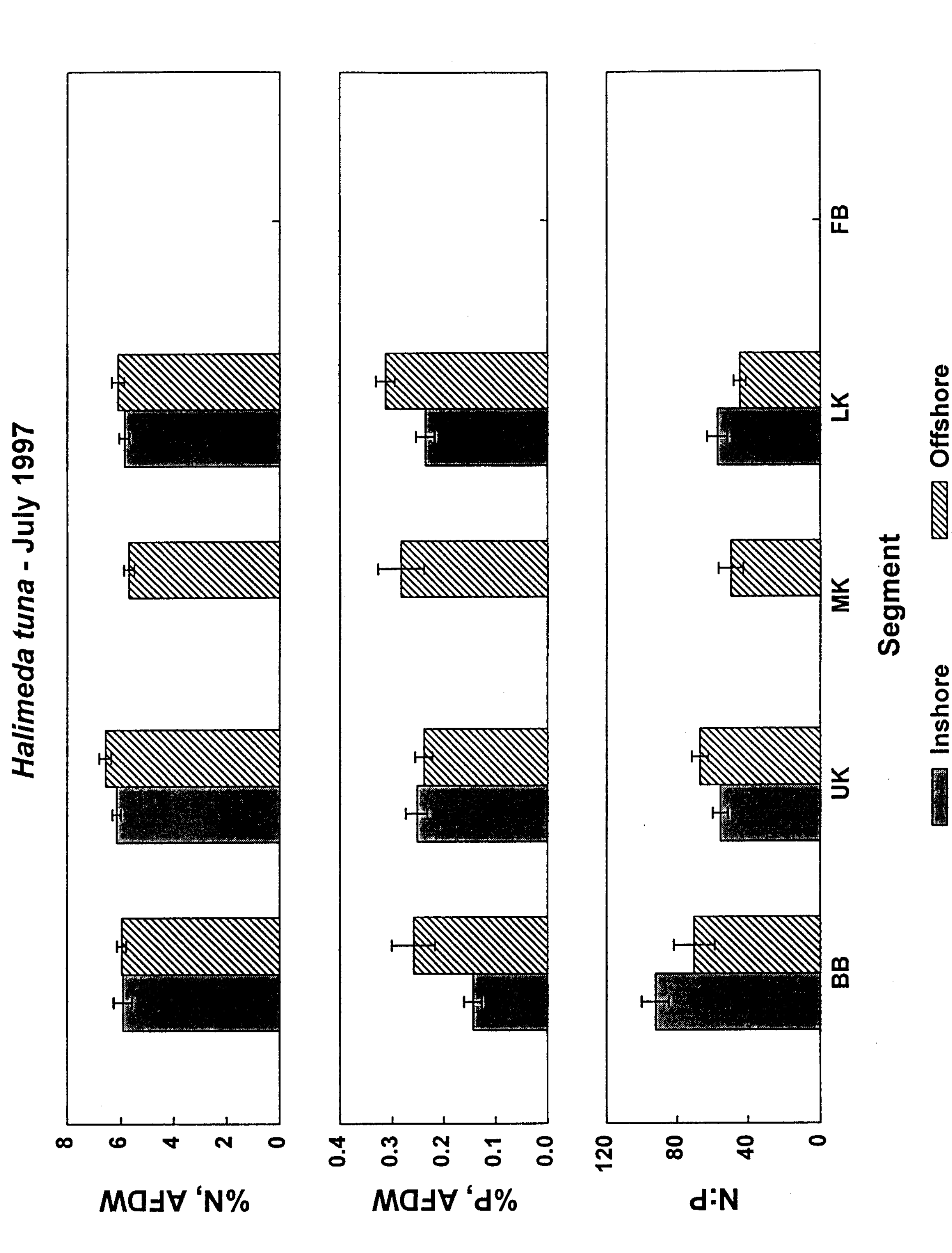

Fig. 138 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda tuna*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

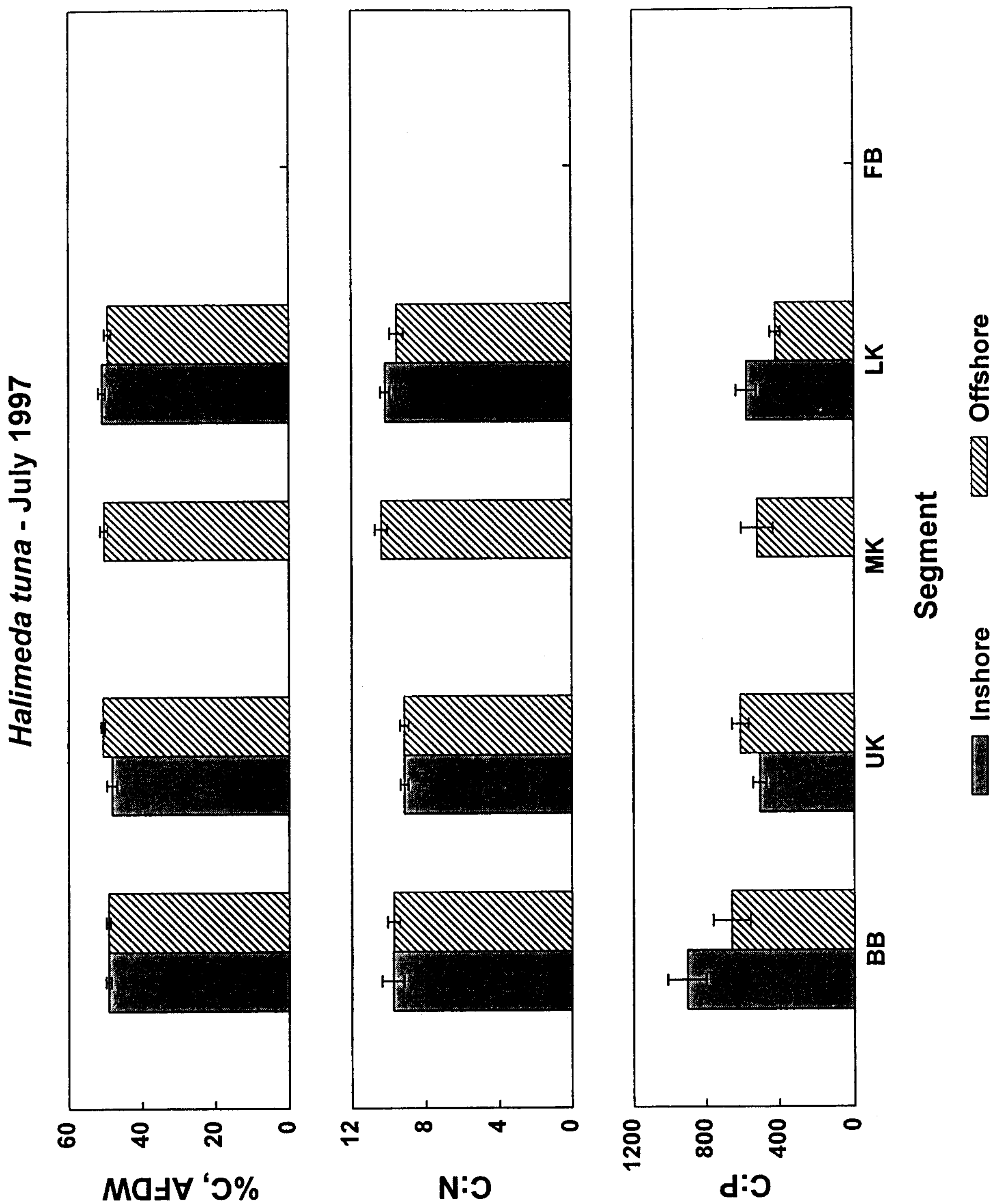

Fig. 139 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Halimeda tuna*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

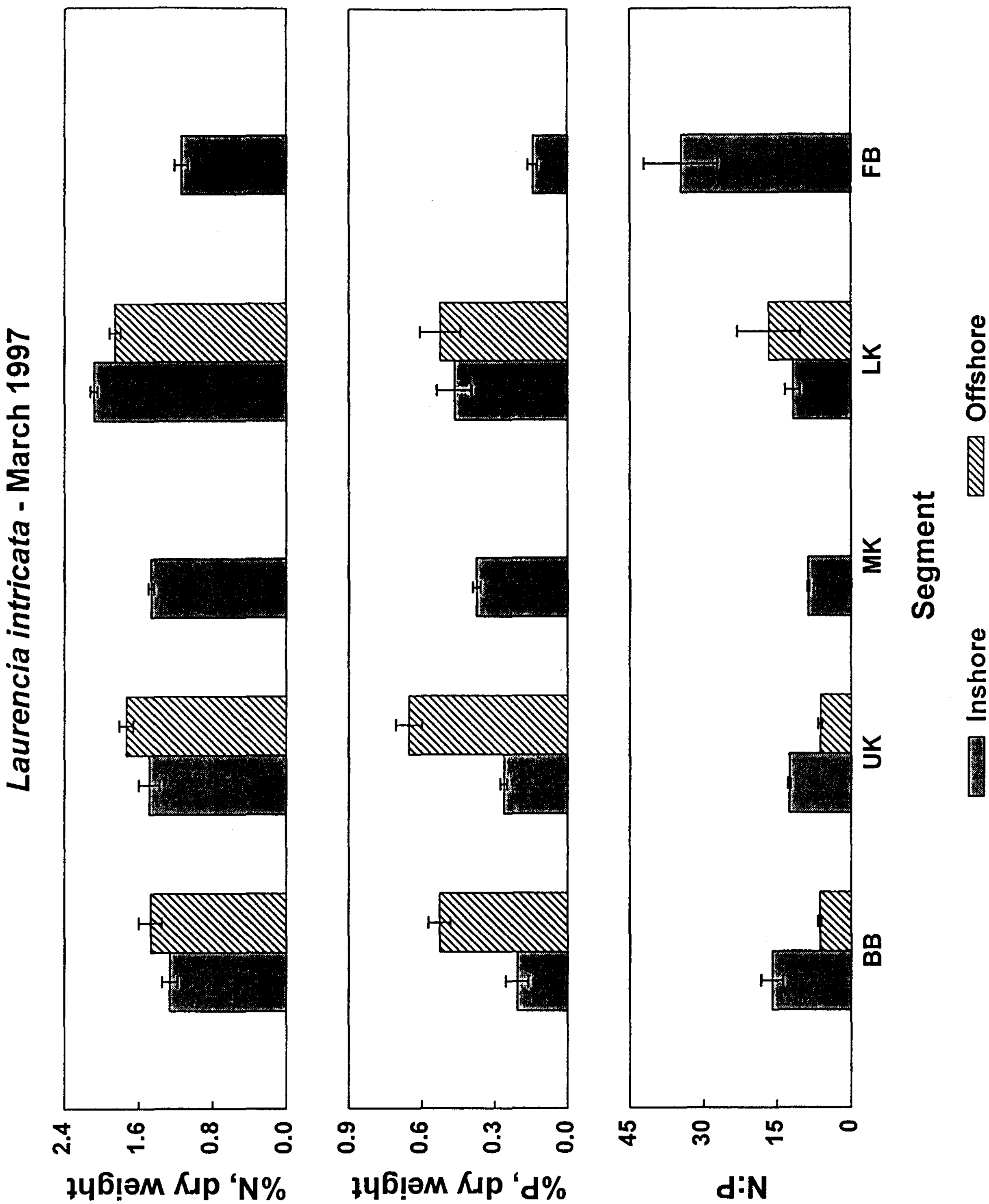

Fig. 140 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia intricata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

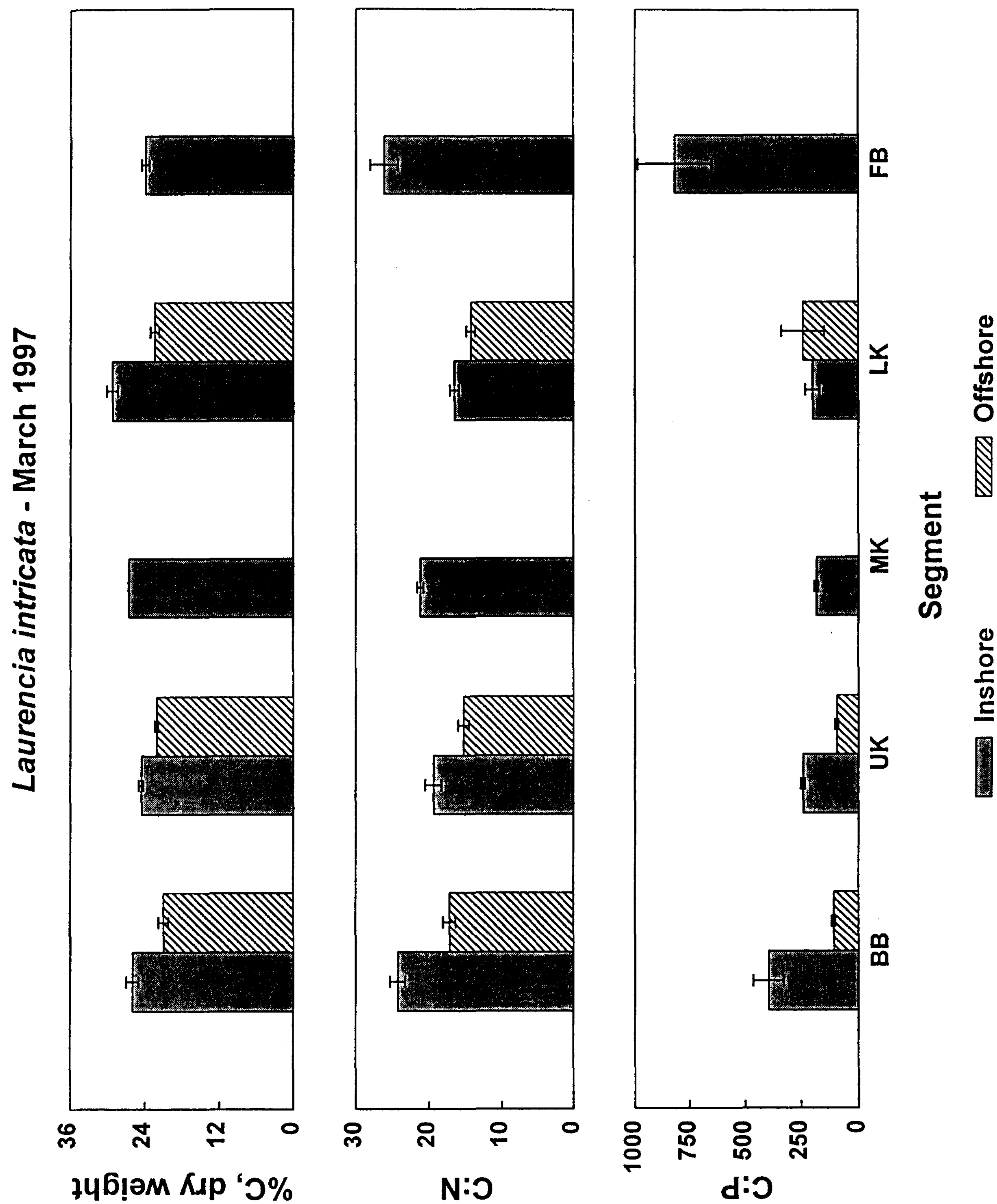

Fig. 141 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia intricata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

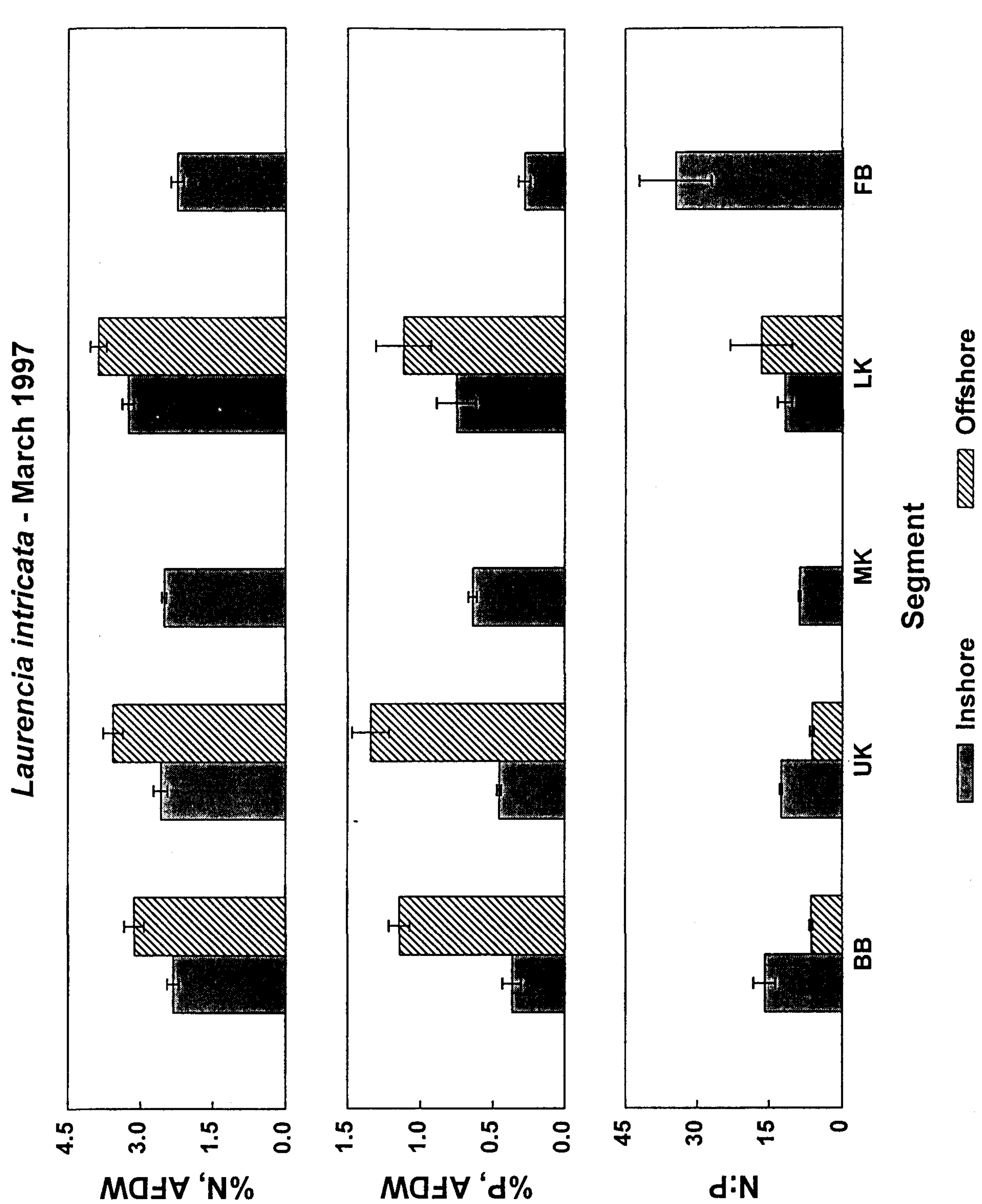

Fig. 142 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia intricata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

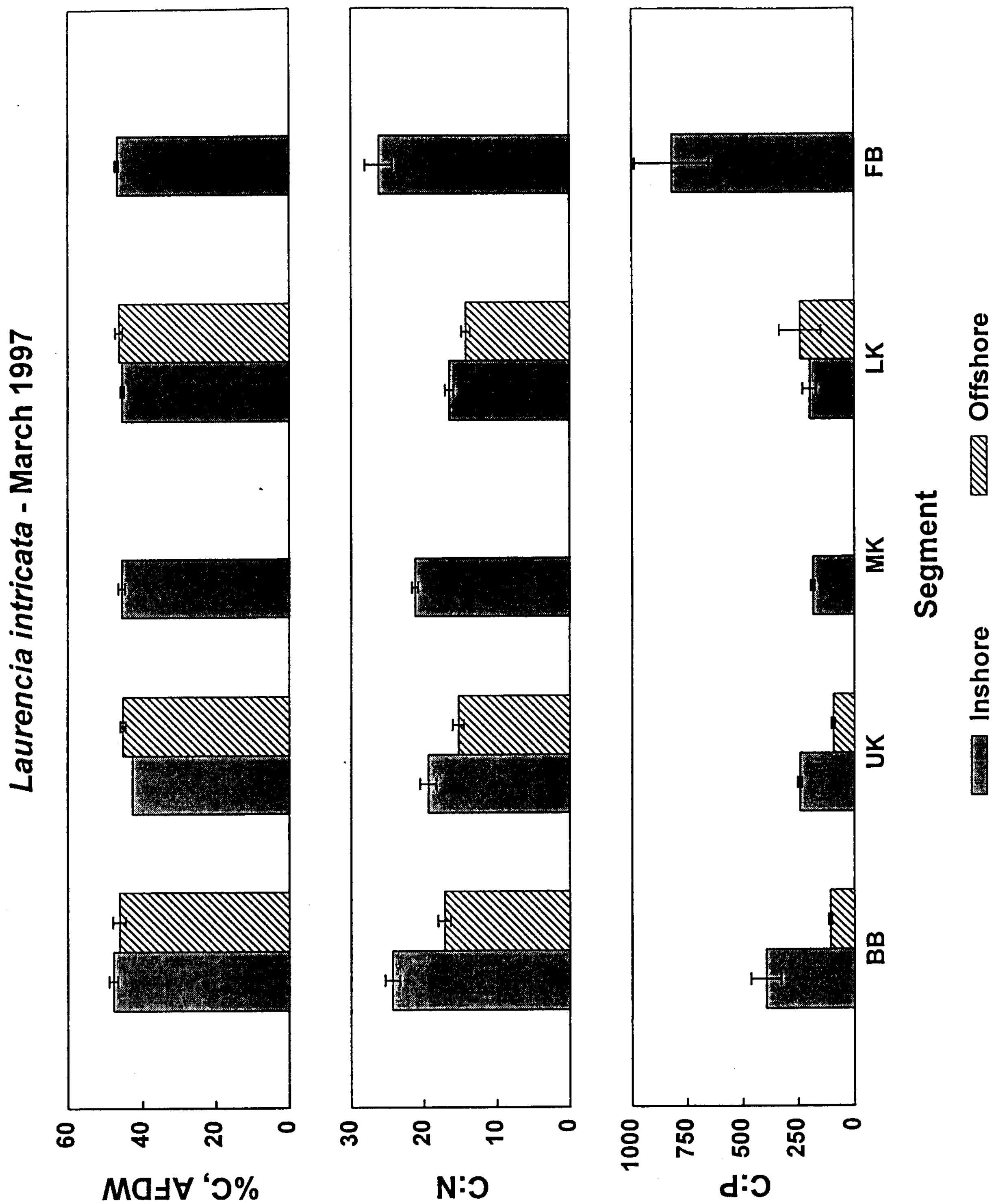

Fig. 143 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia intricata*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

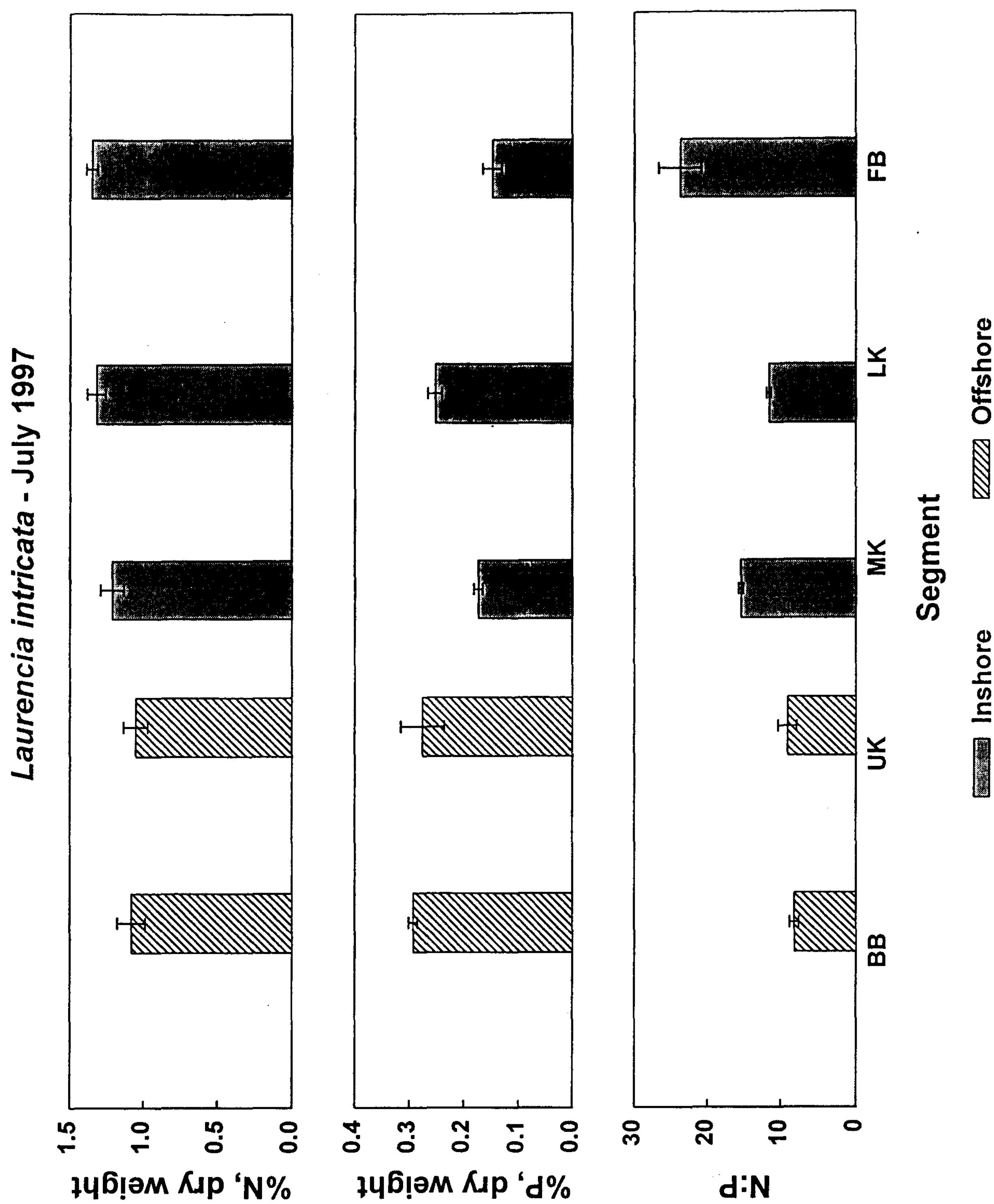

Fig. 144 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia intricata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

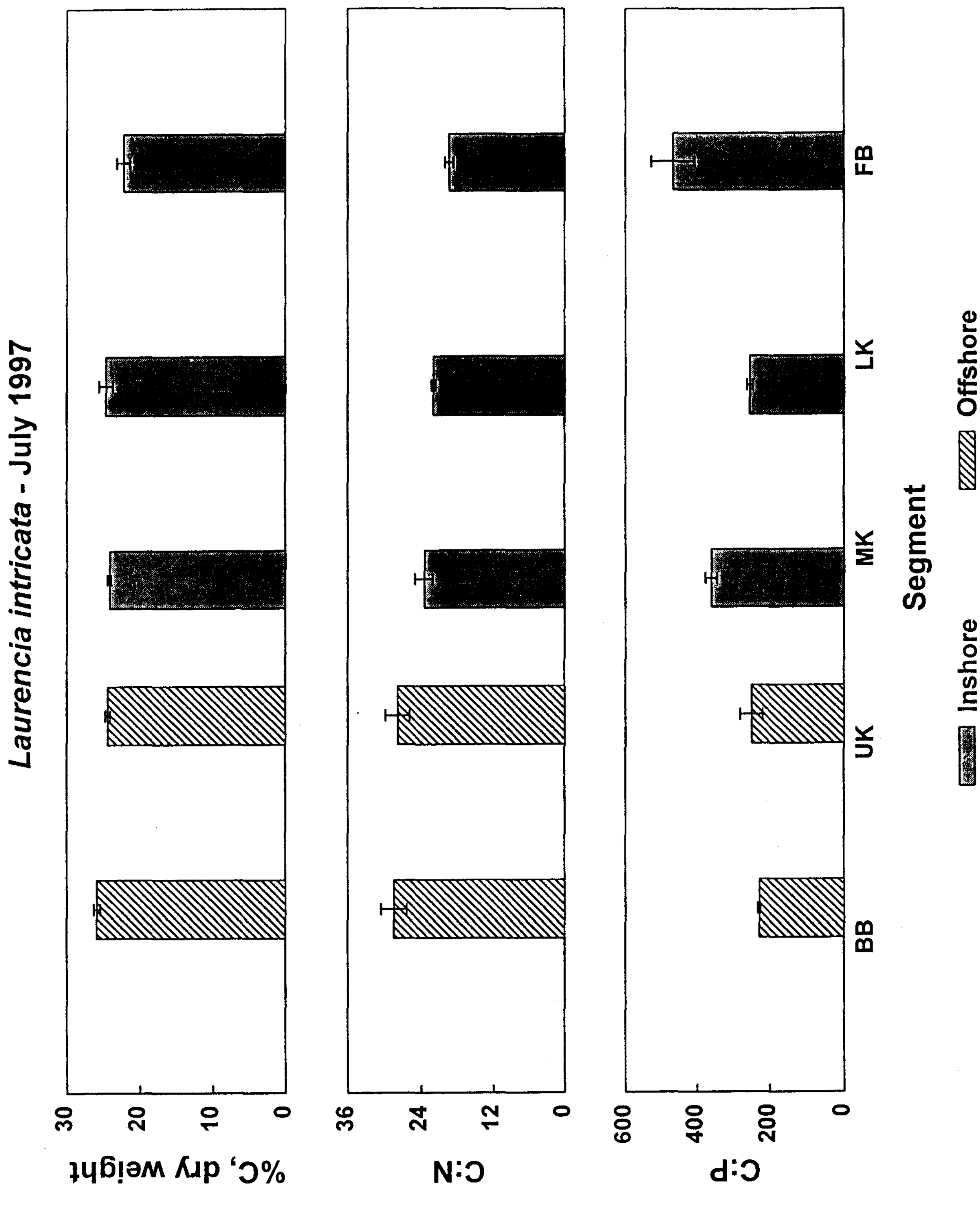

Fig. 145 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia intricata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

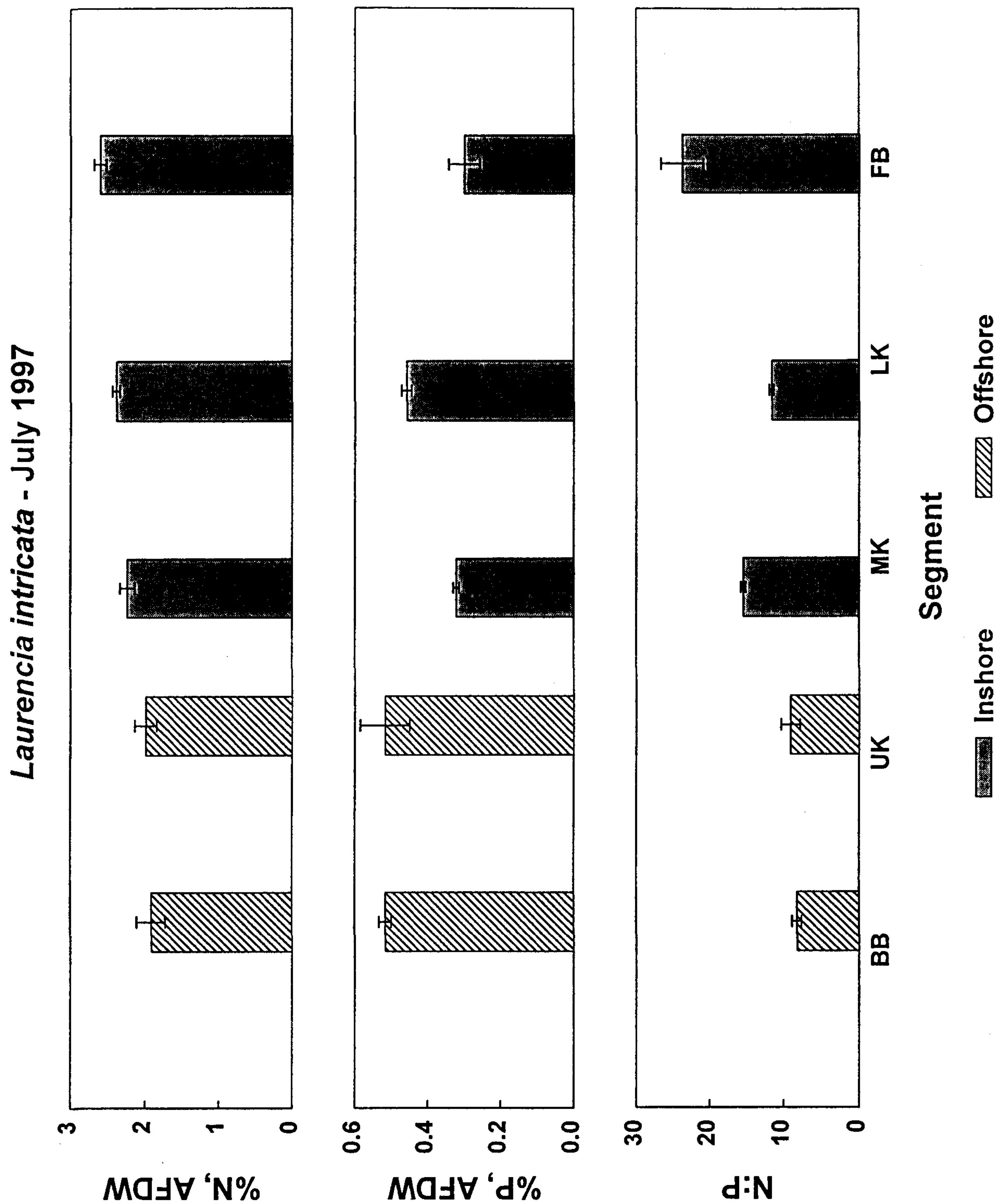

Fig. 146 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia intricata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

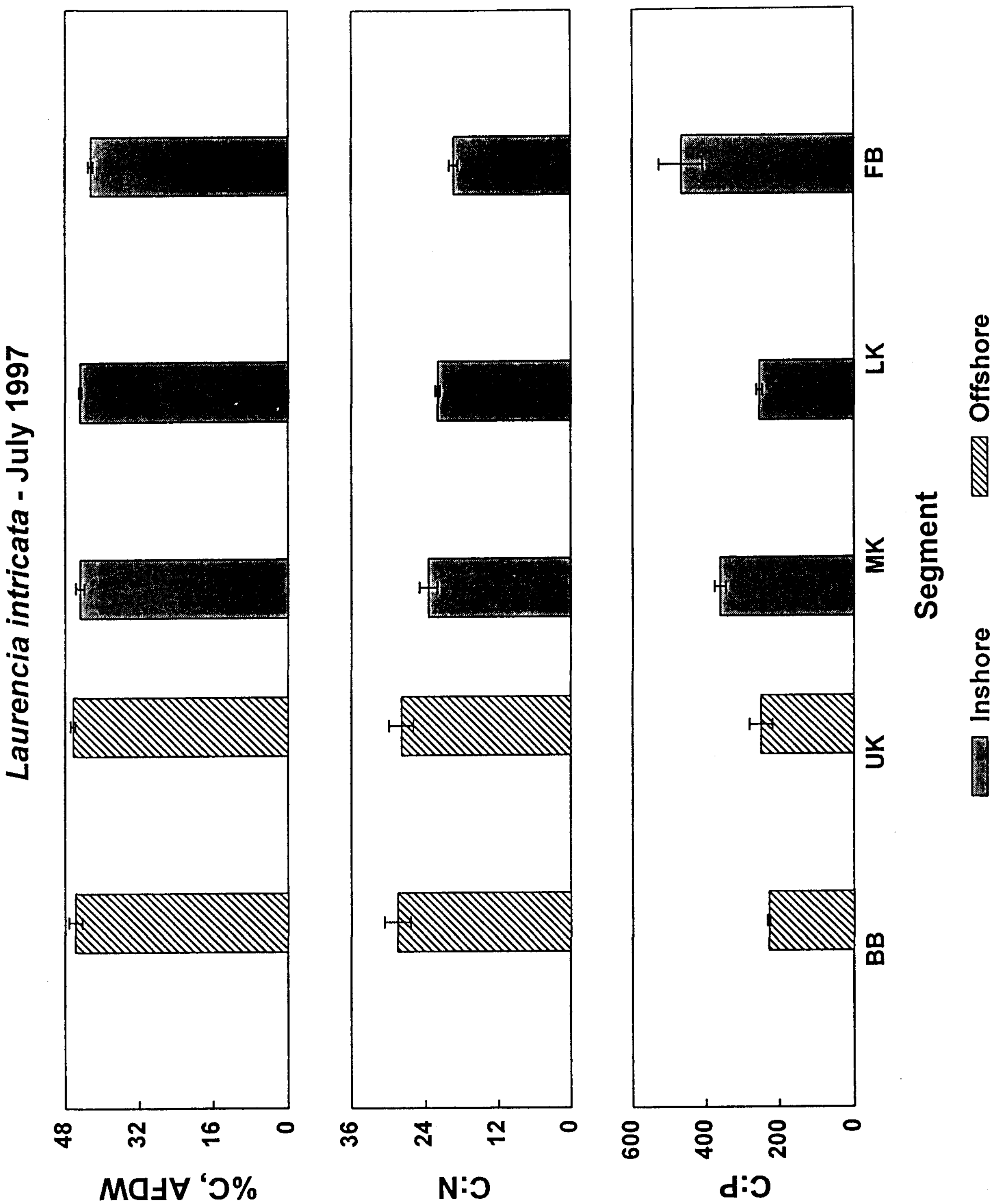

Fig. 147 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia intricata*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

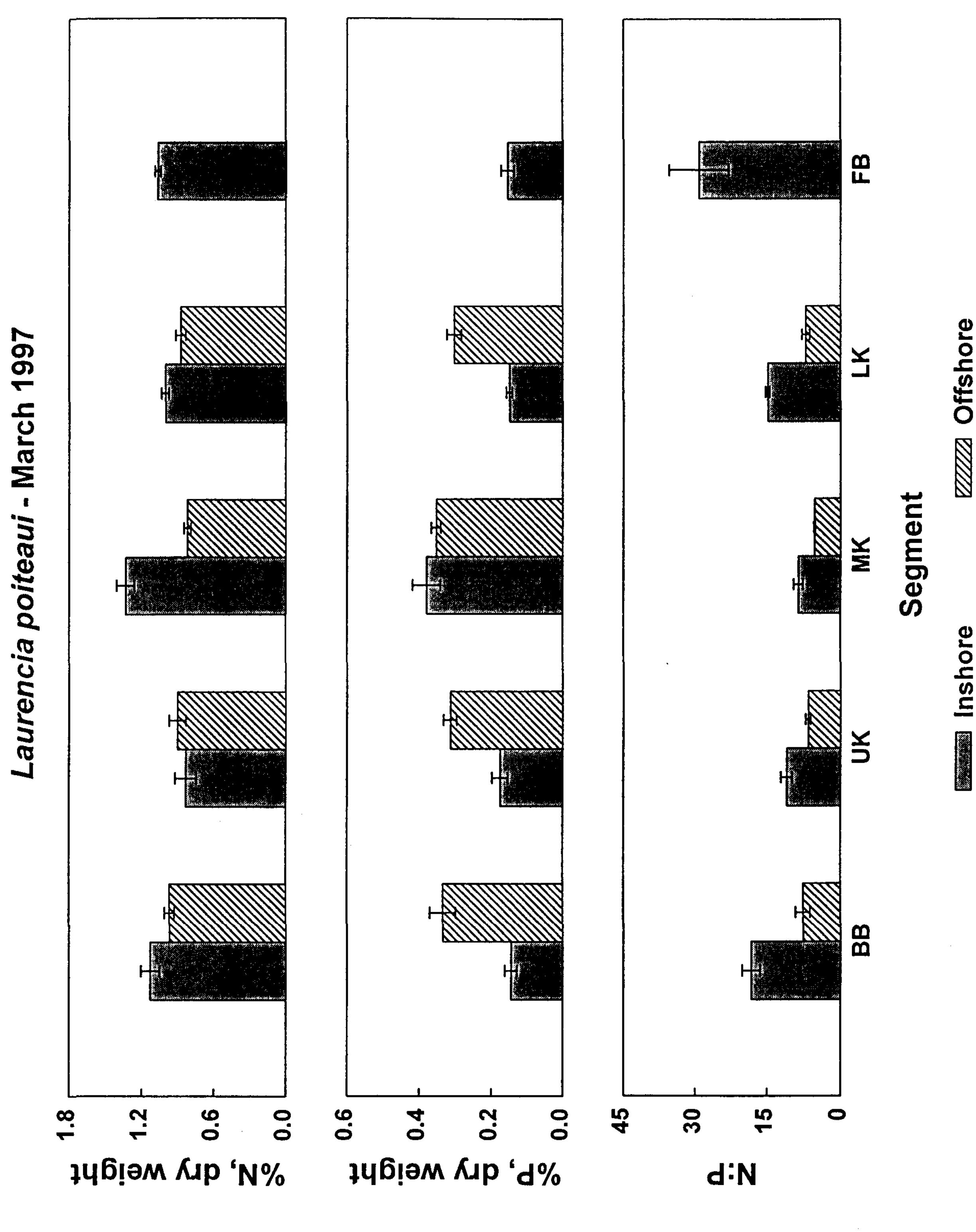

Fig. 148 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia poiteaui*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

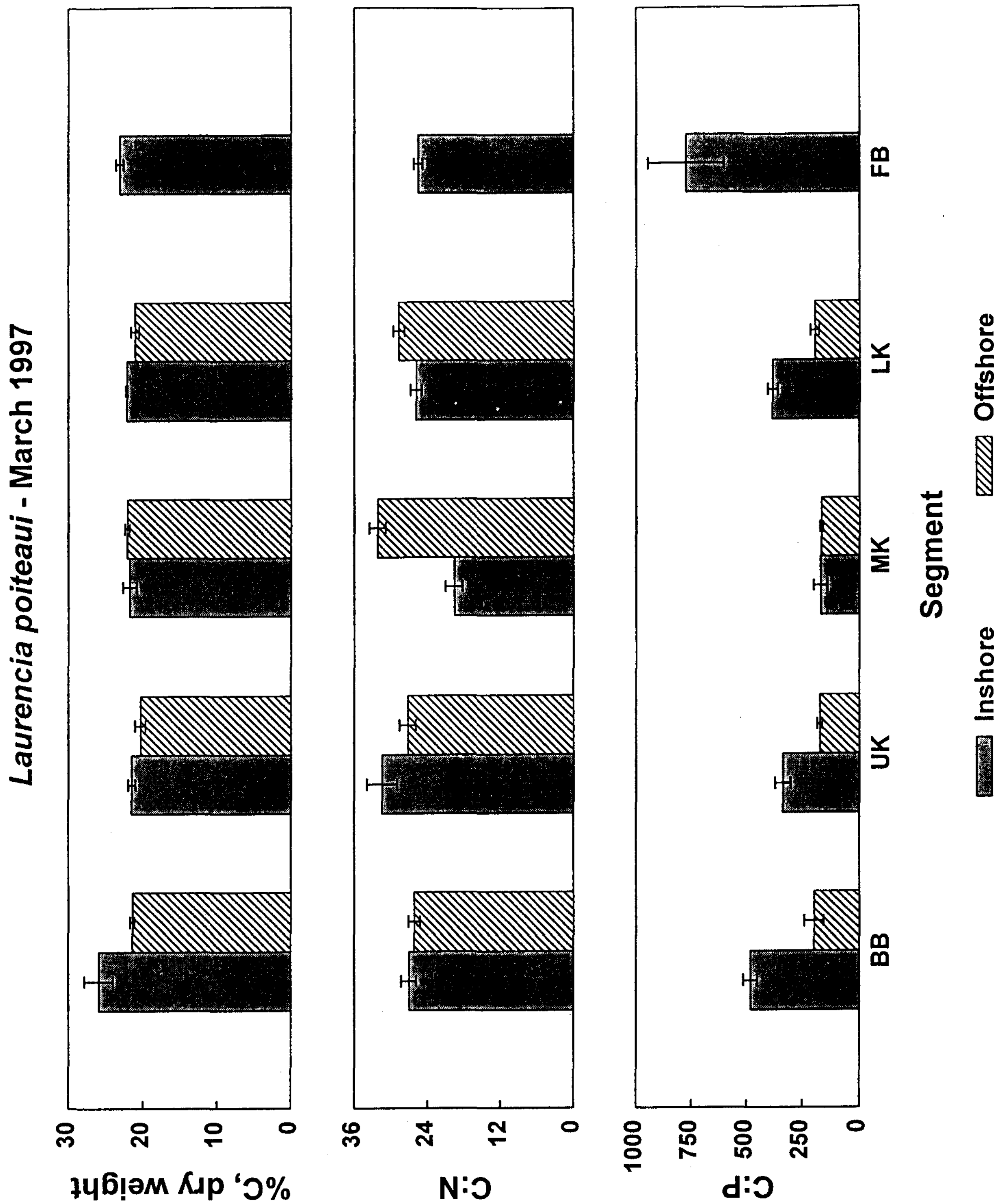

Fig. 149 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia poiteaui*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

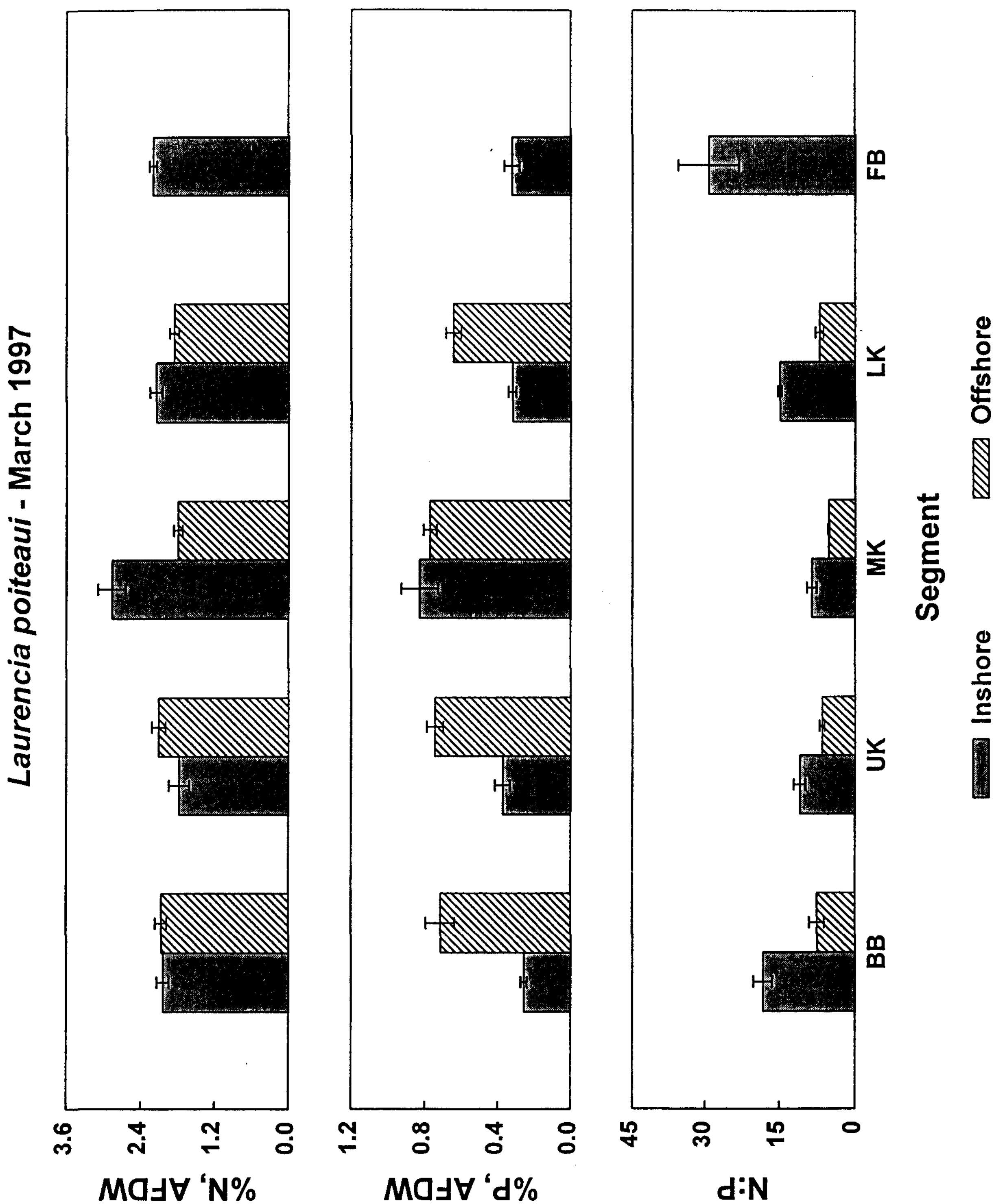

Fig. 150 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia poiteaui*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

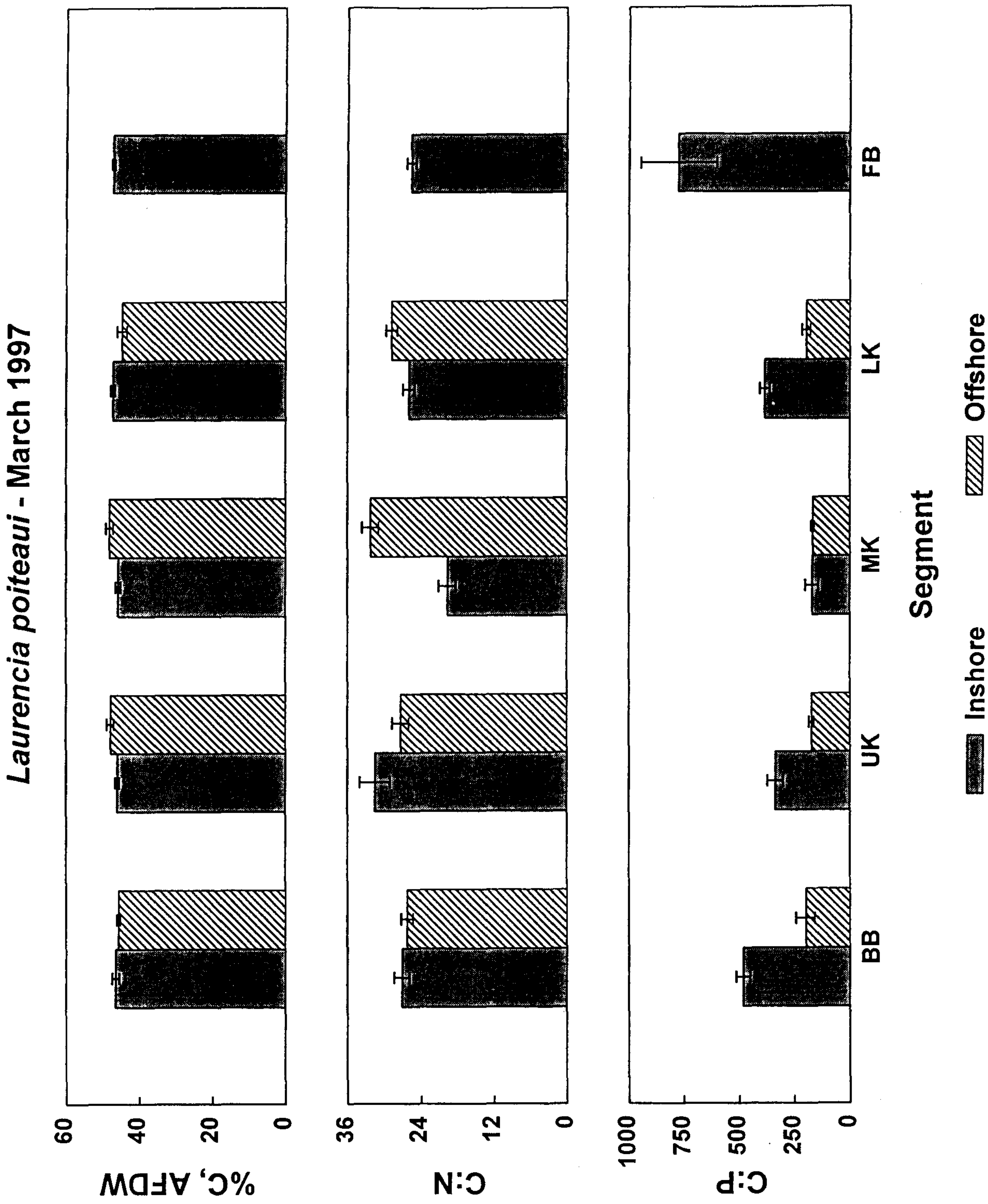

Fig. 151 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia poiteaui*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

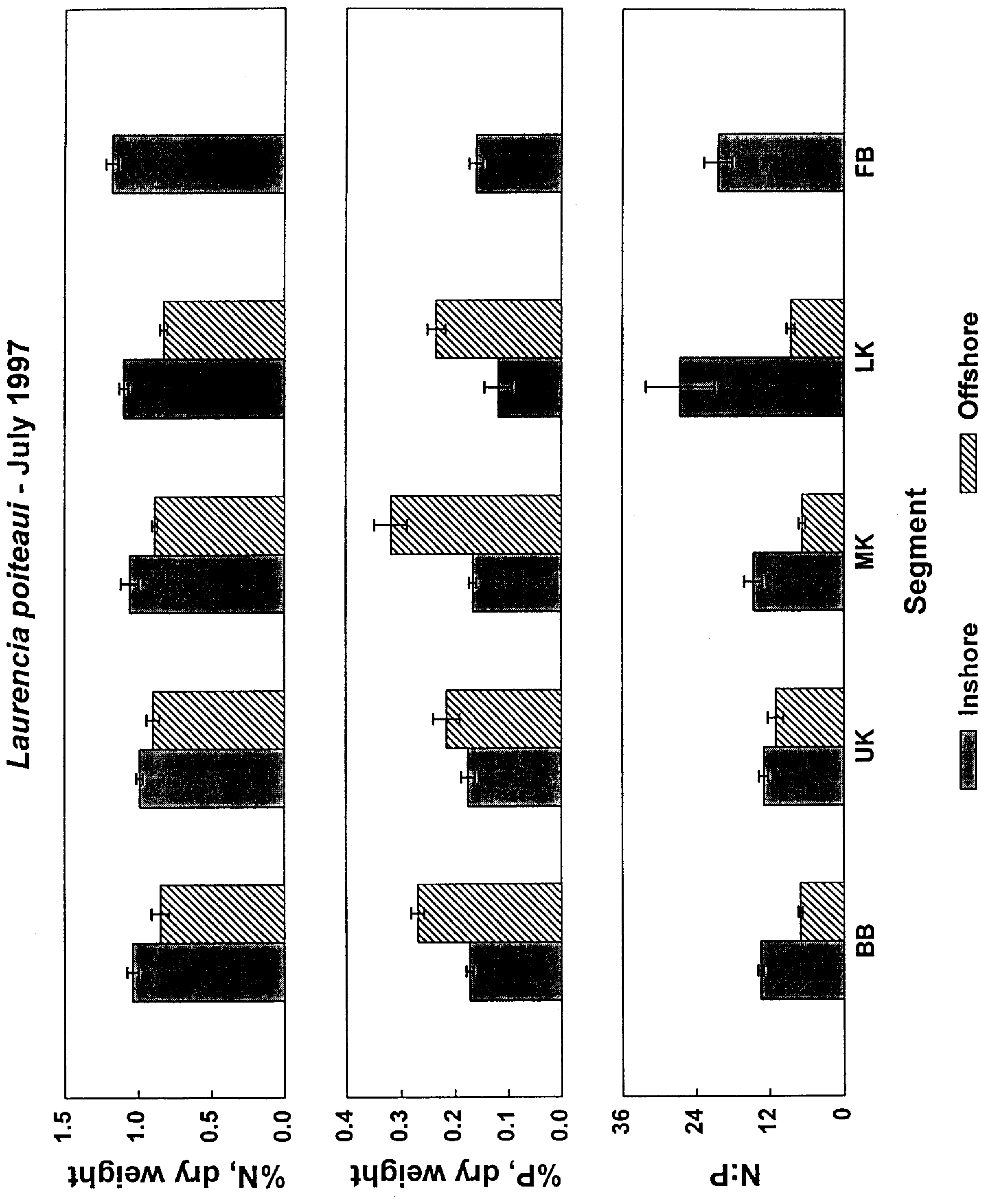

Fig. 152 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia poiteaui*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

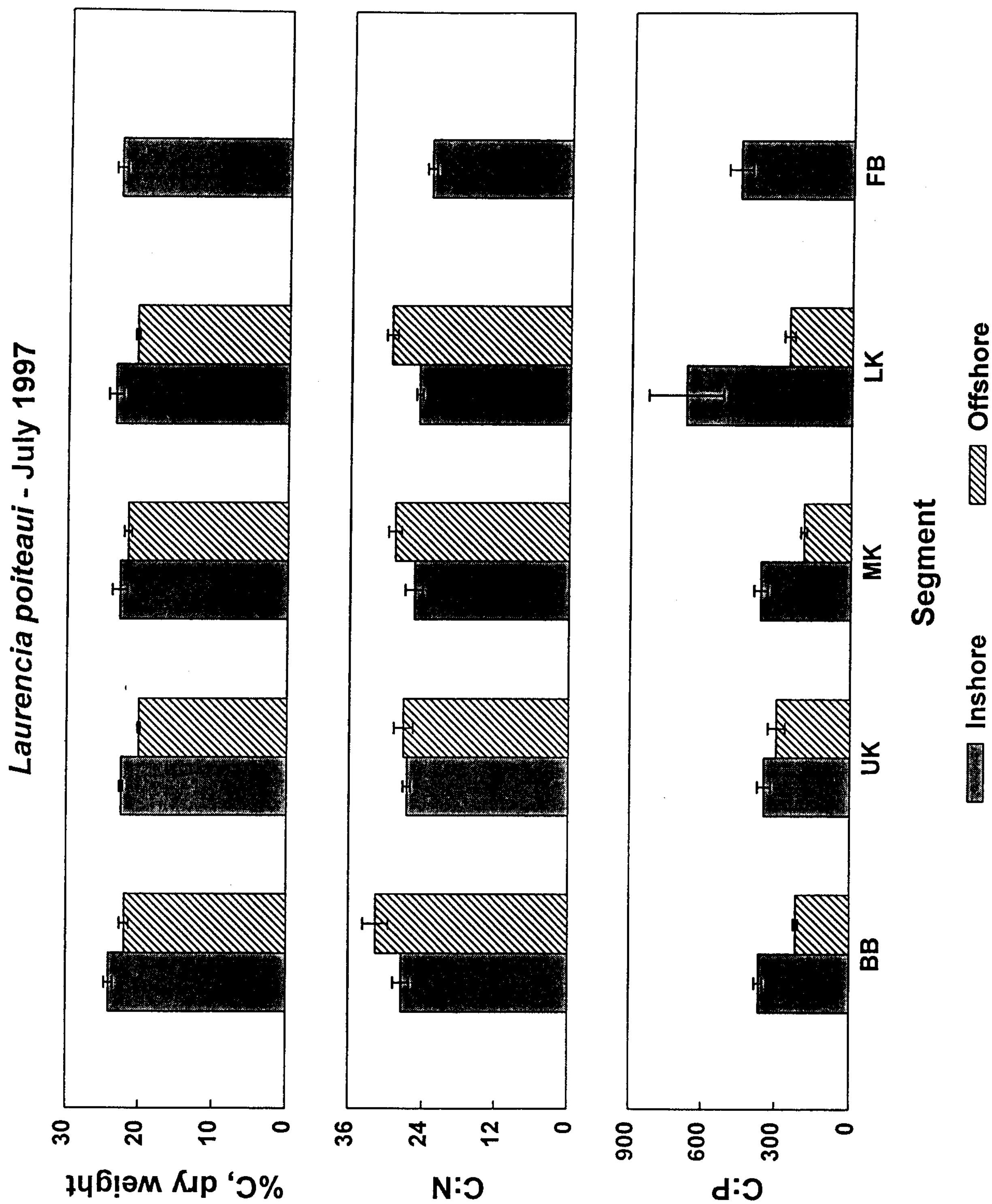

Fig. 153 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for inshore and offshore samples of *Laurencia poiteaui*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

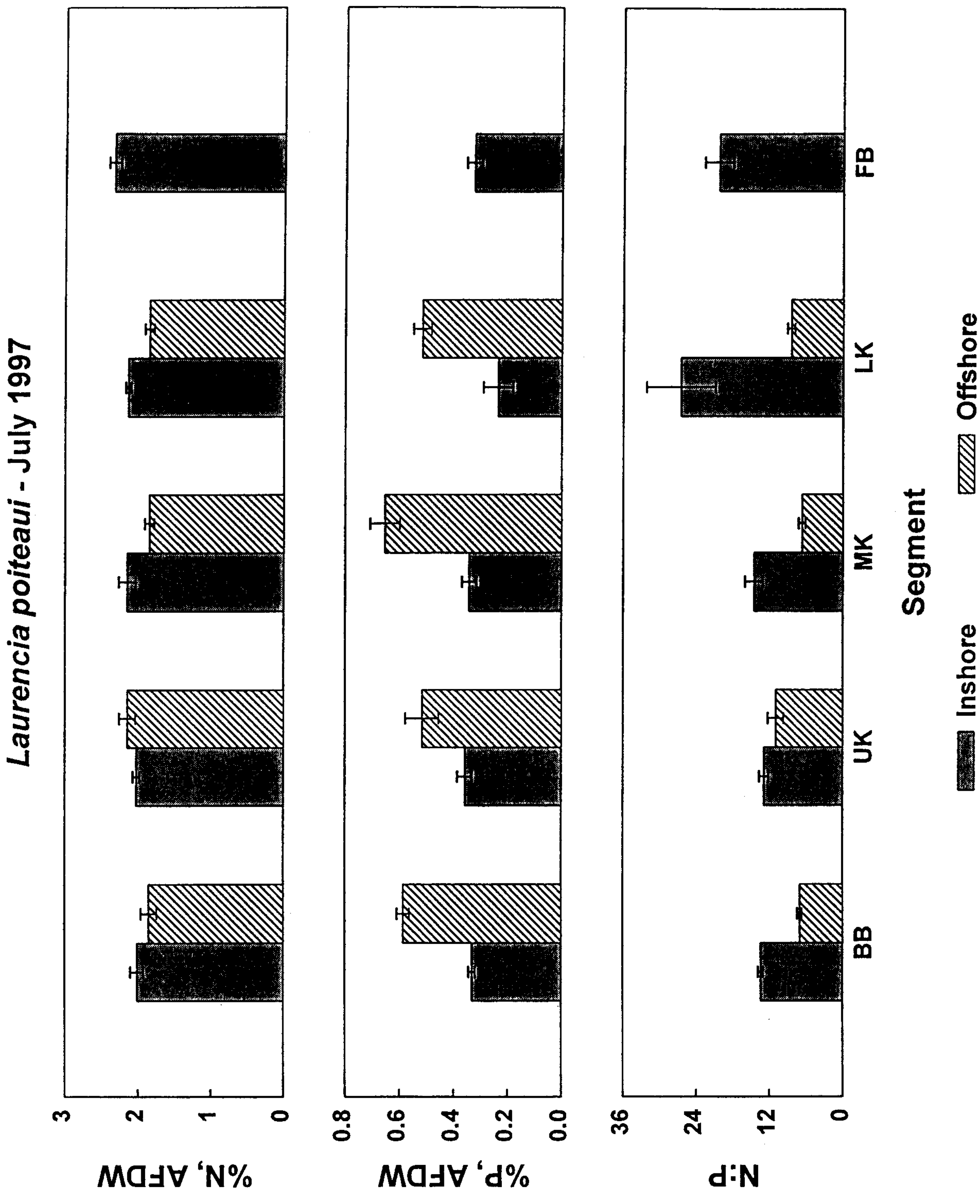

Fig. 154 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia poiteaui*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

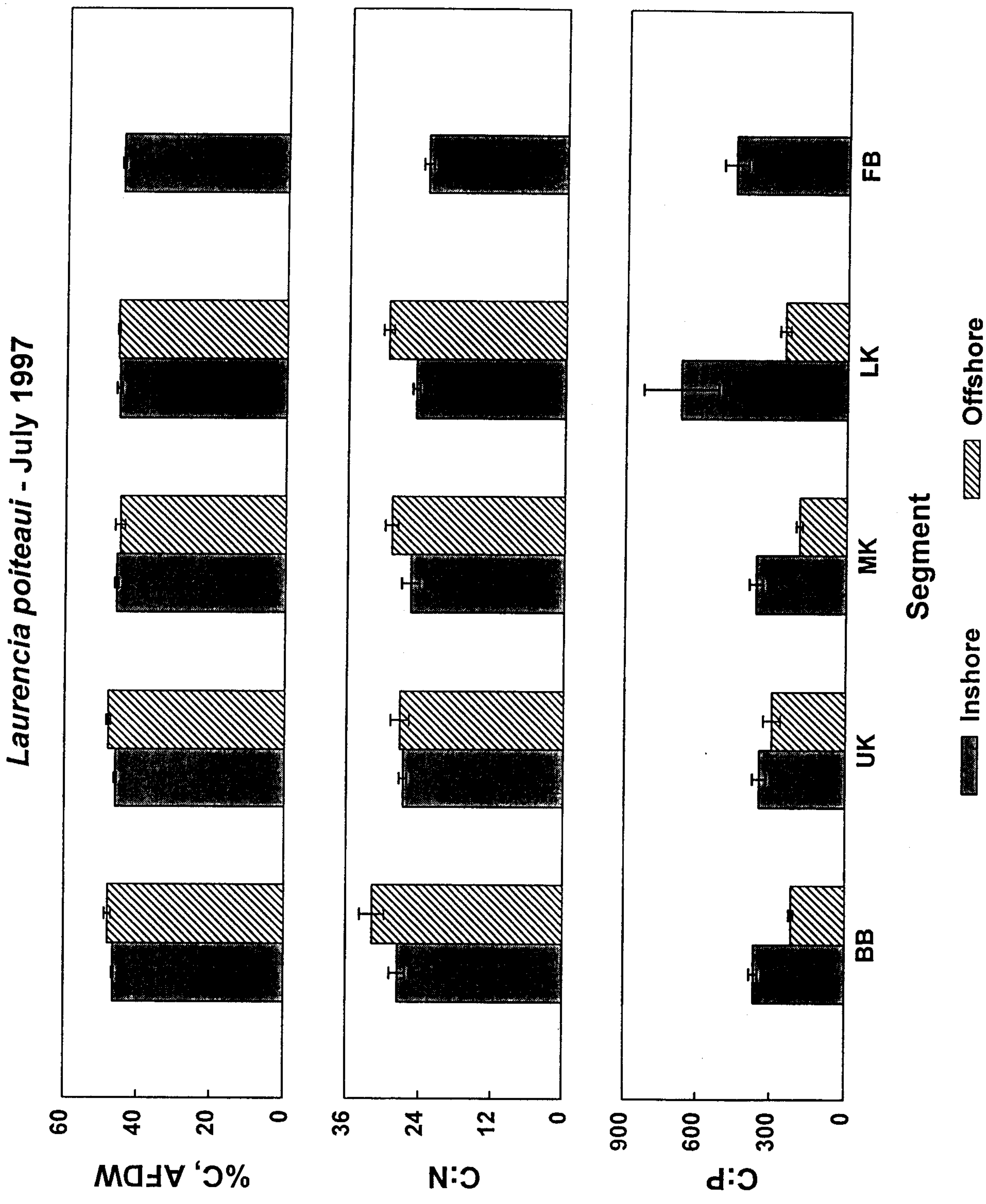

Fig. 155 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Laurencia poiteaui*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

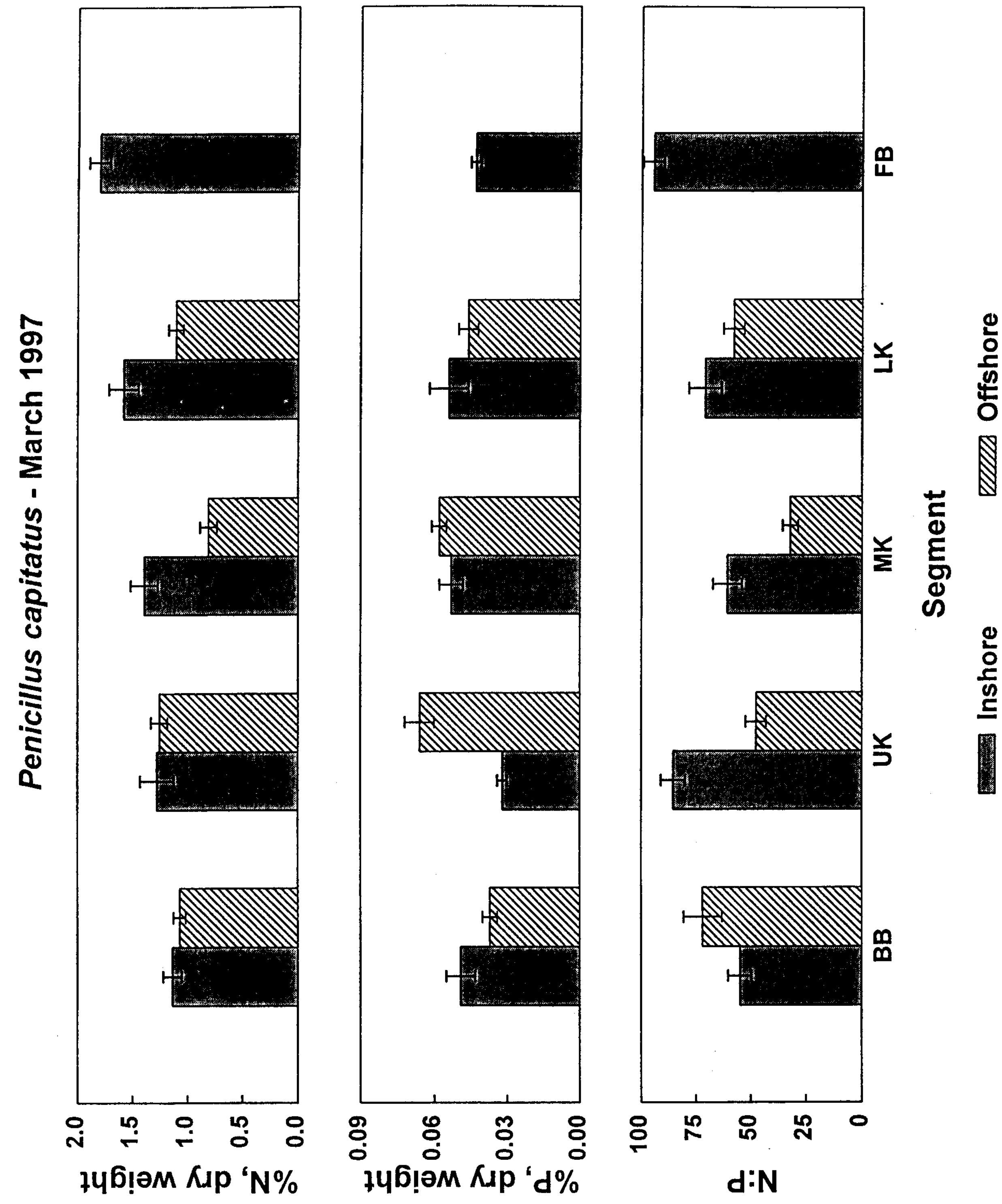

Fig. 156 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Penicillus capitatus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

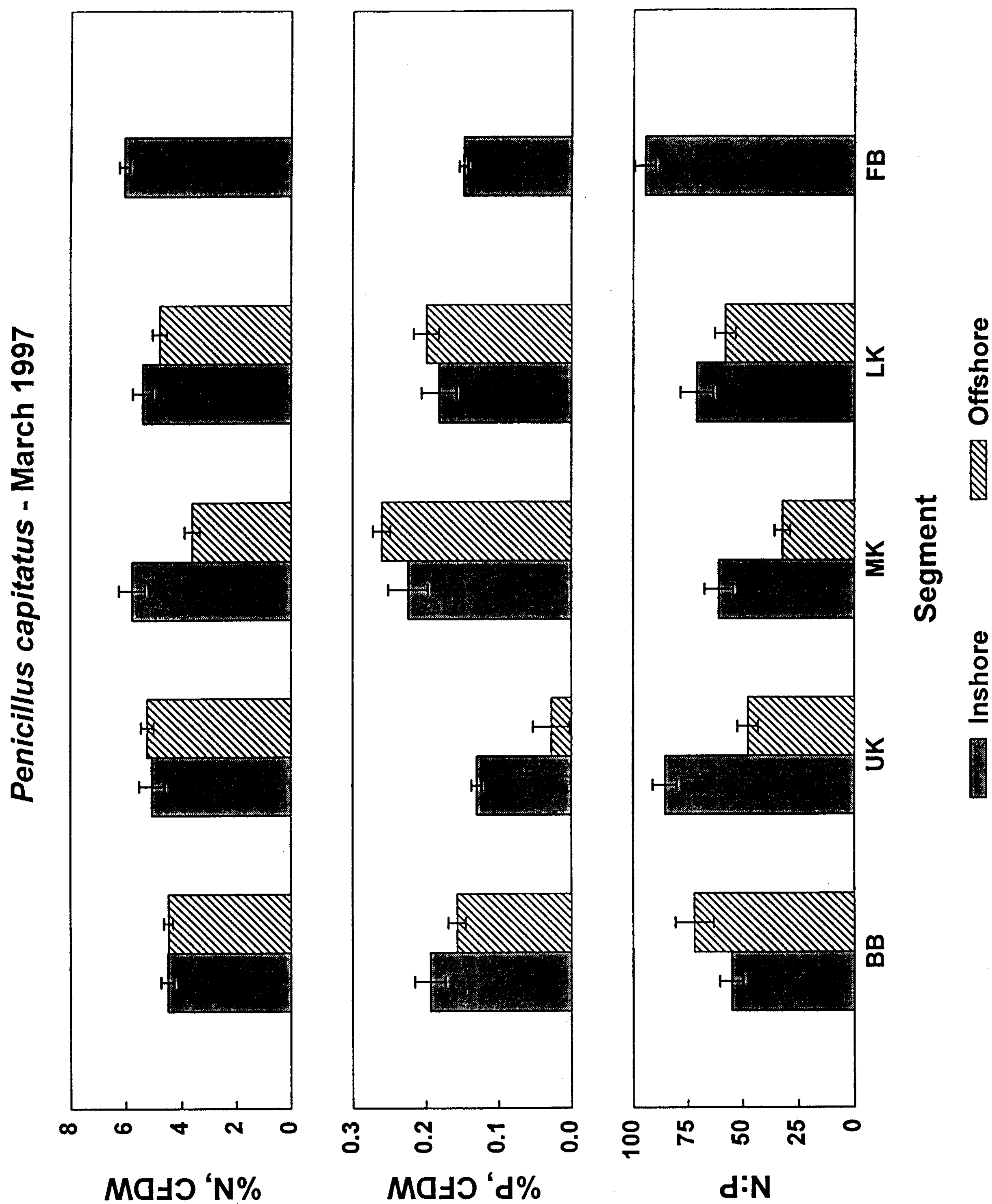

Fig. 157 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus capitatus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

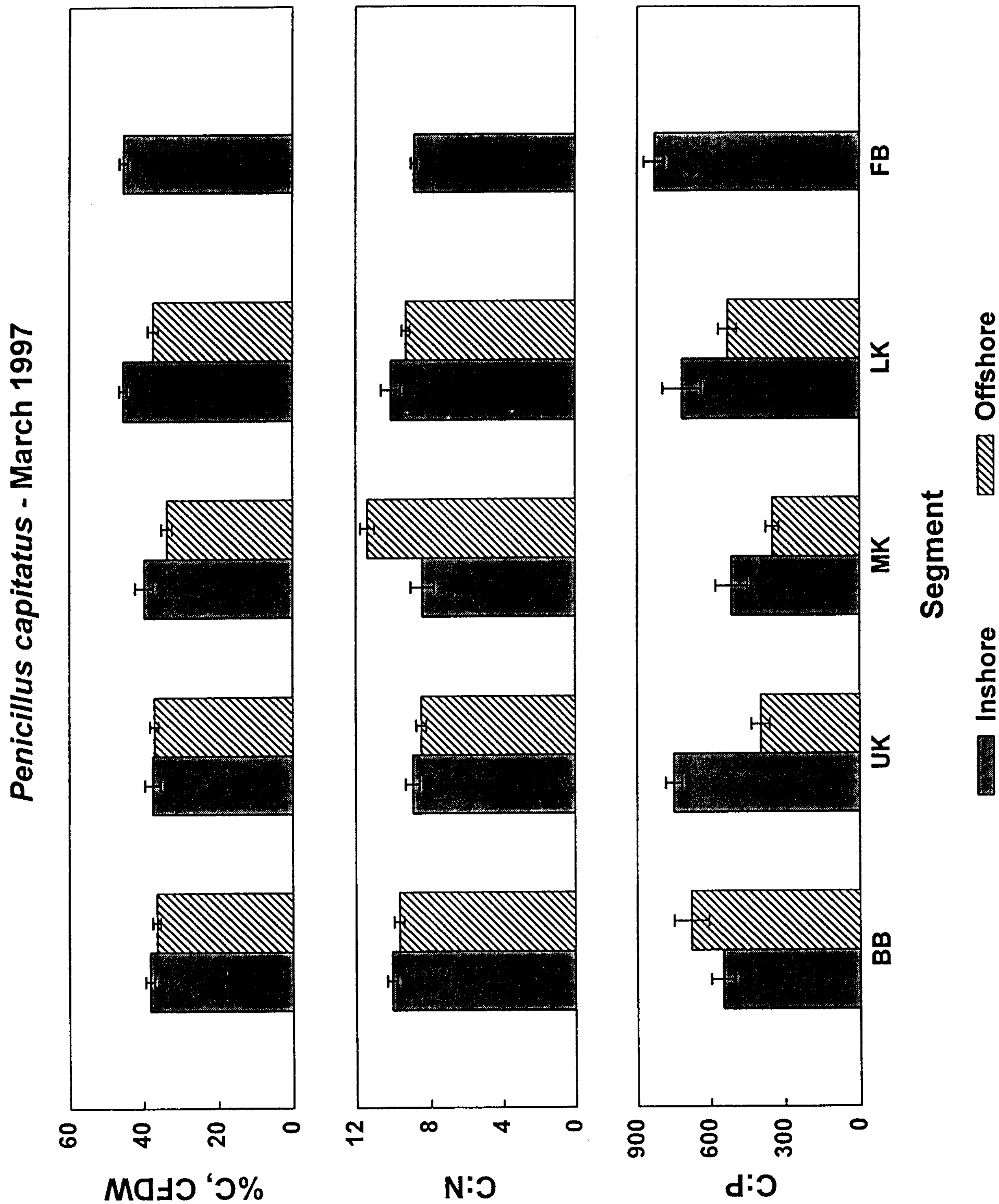

Fig. 158 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus capitatus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

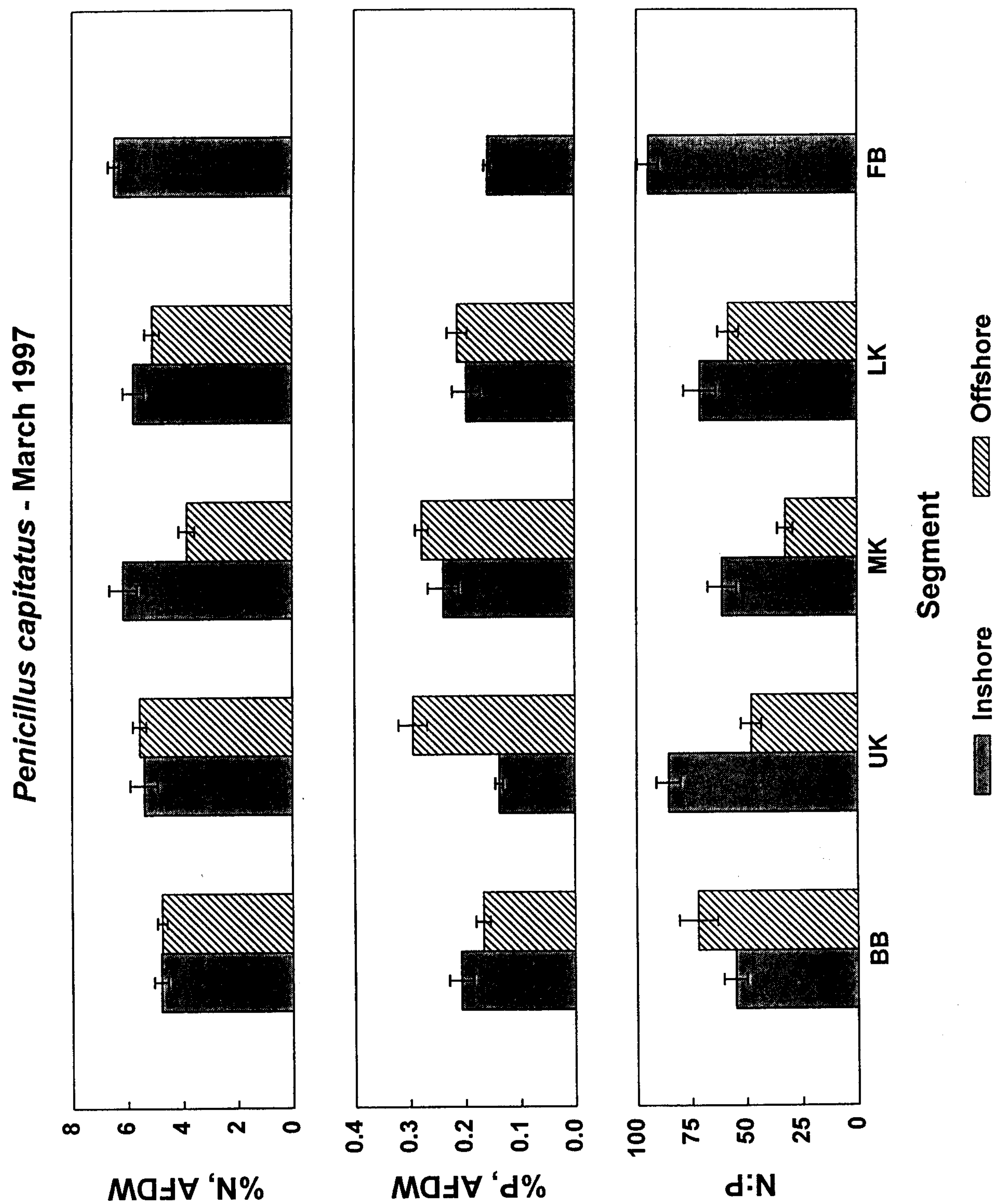

Fig. 159 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus capitatus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

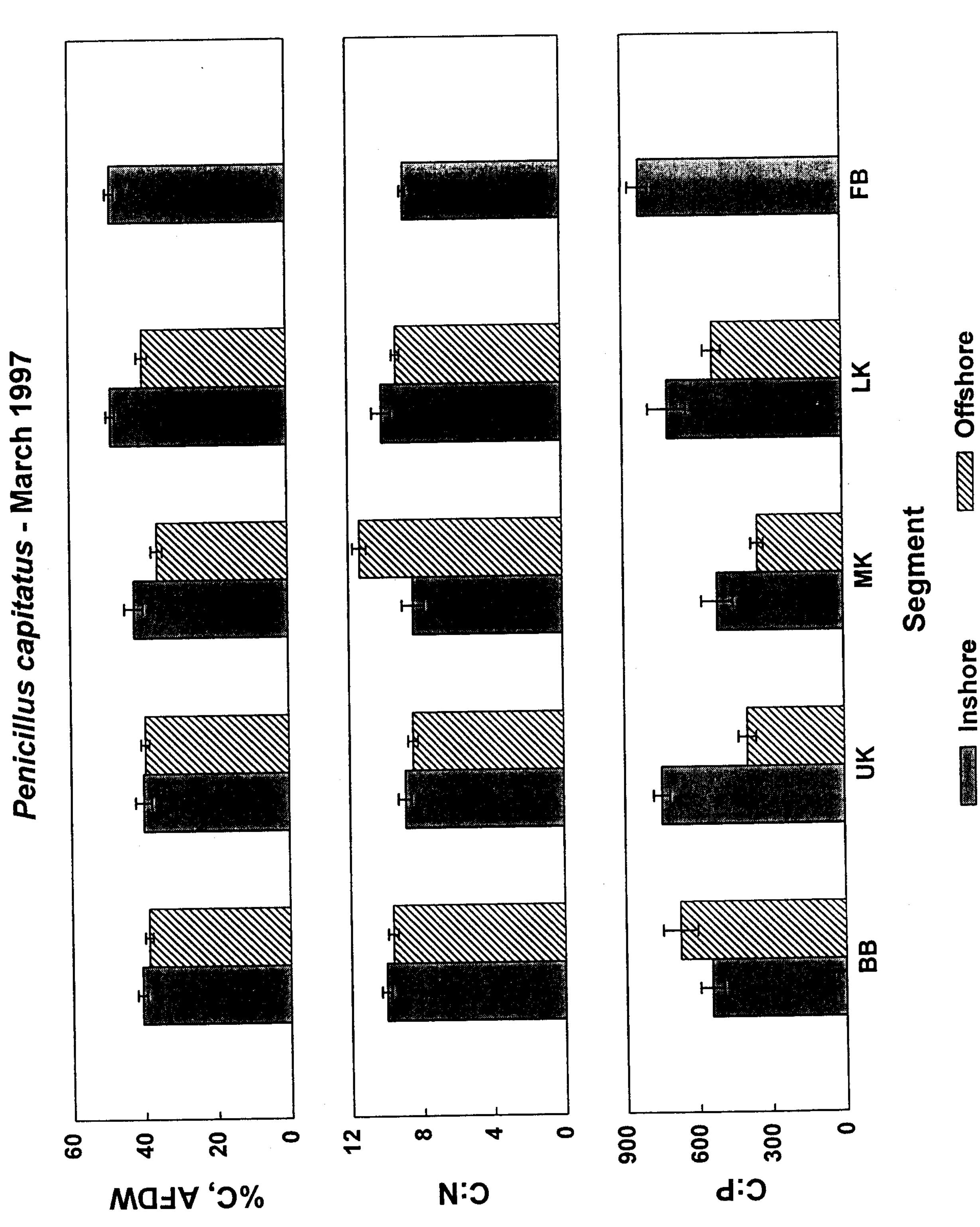

Fig. 160 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus capitatus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

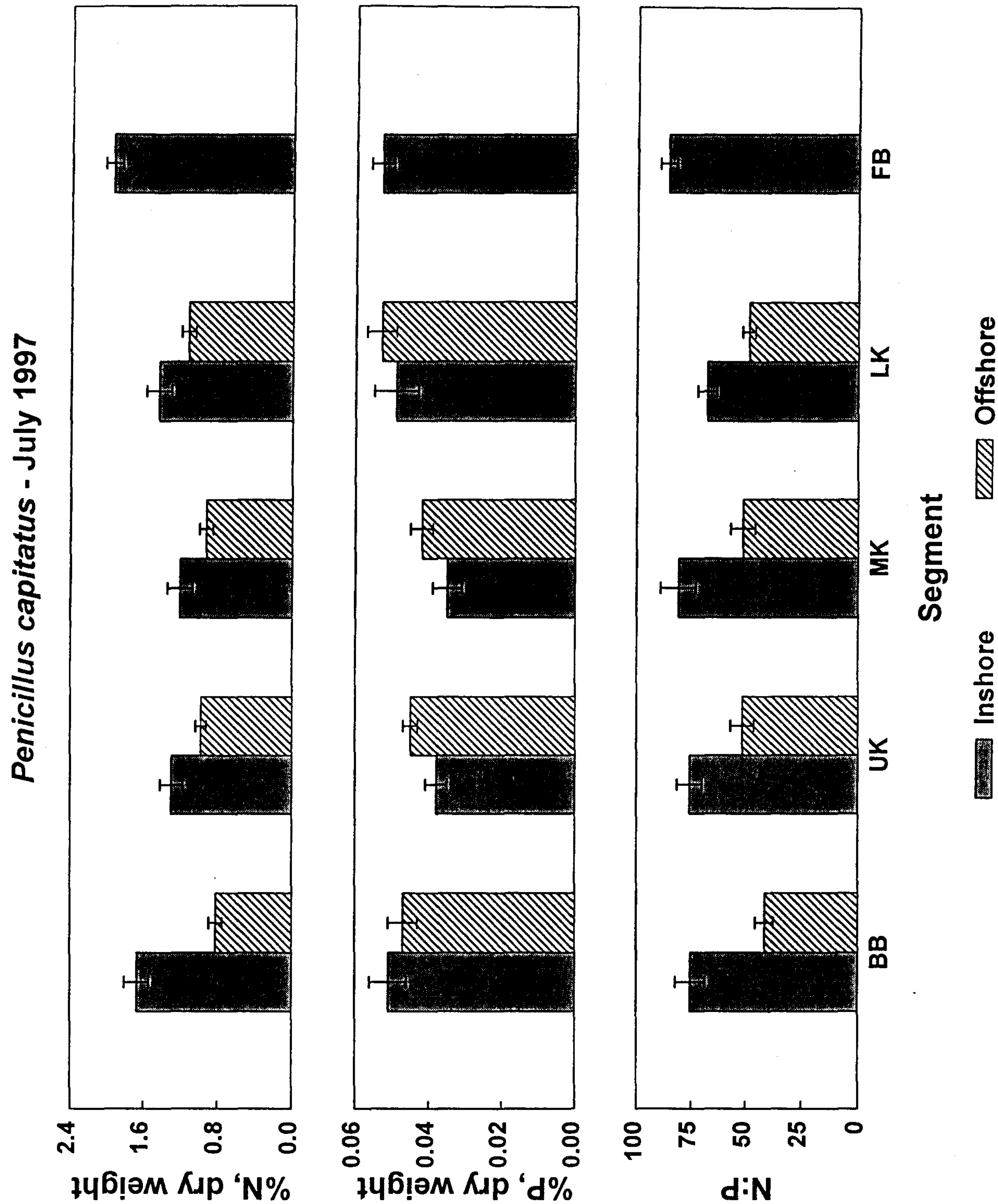

Fig. 161 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Penicillus capitatus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

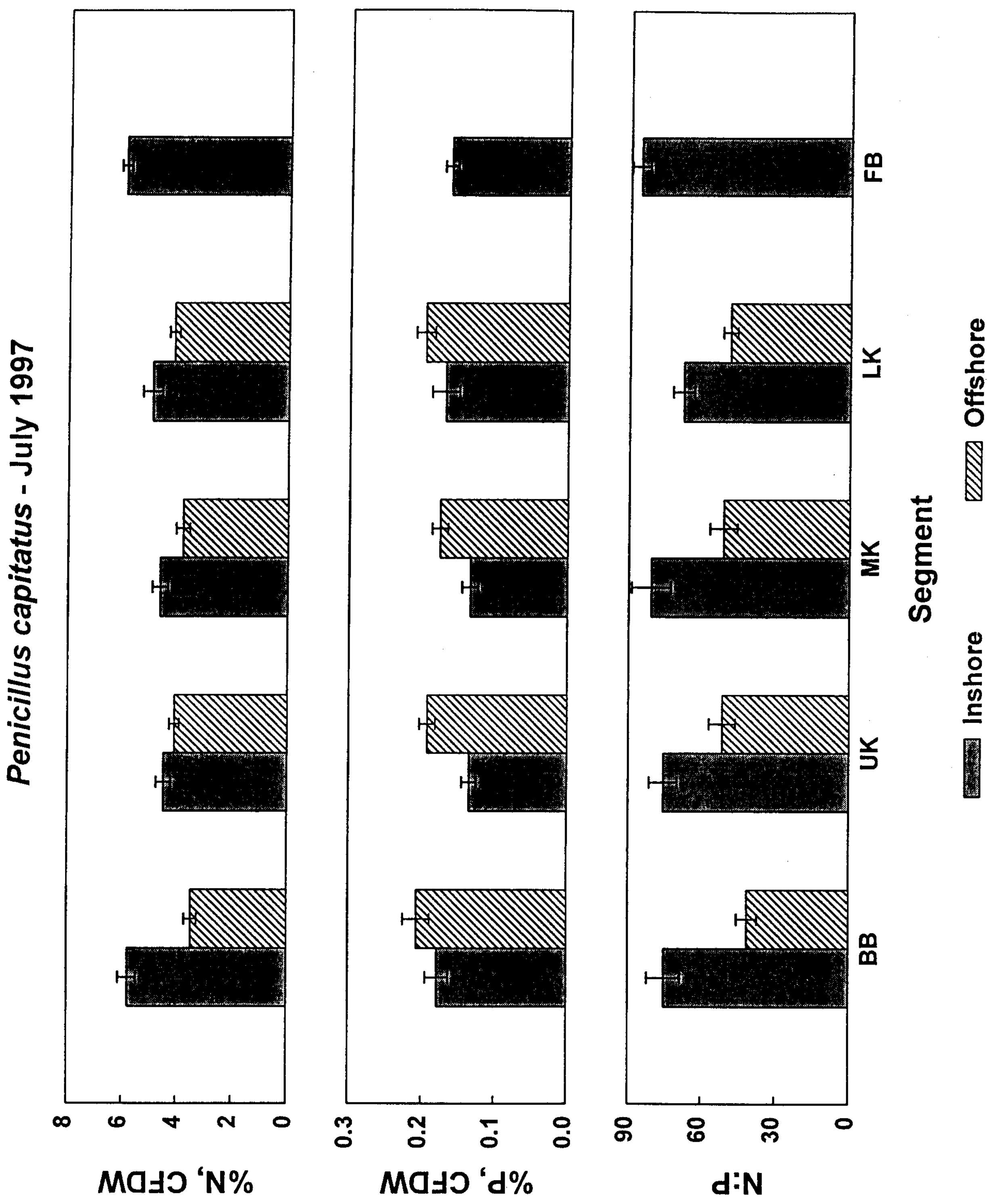

Fig. 162 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus capitatus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

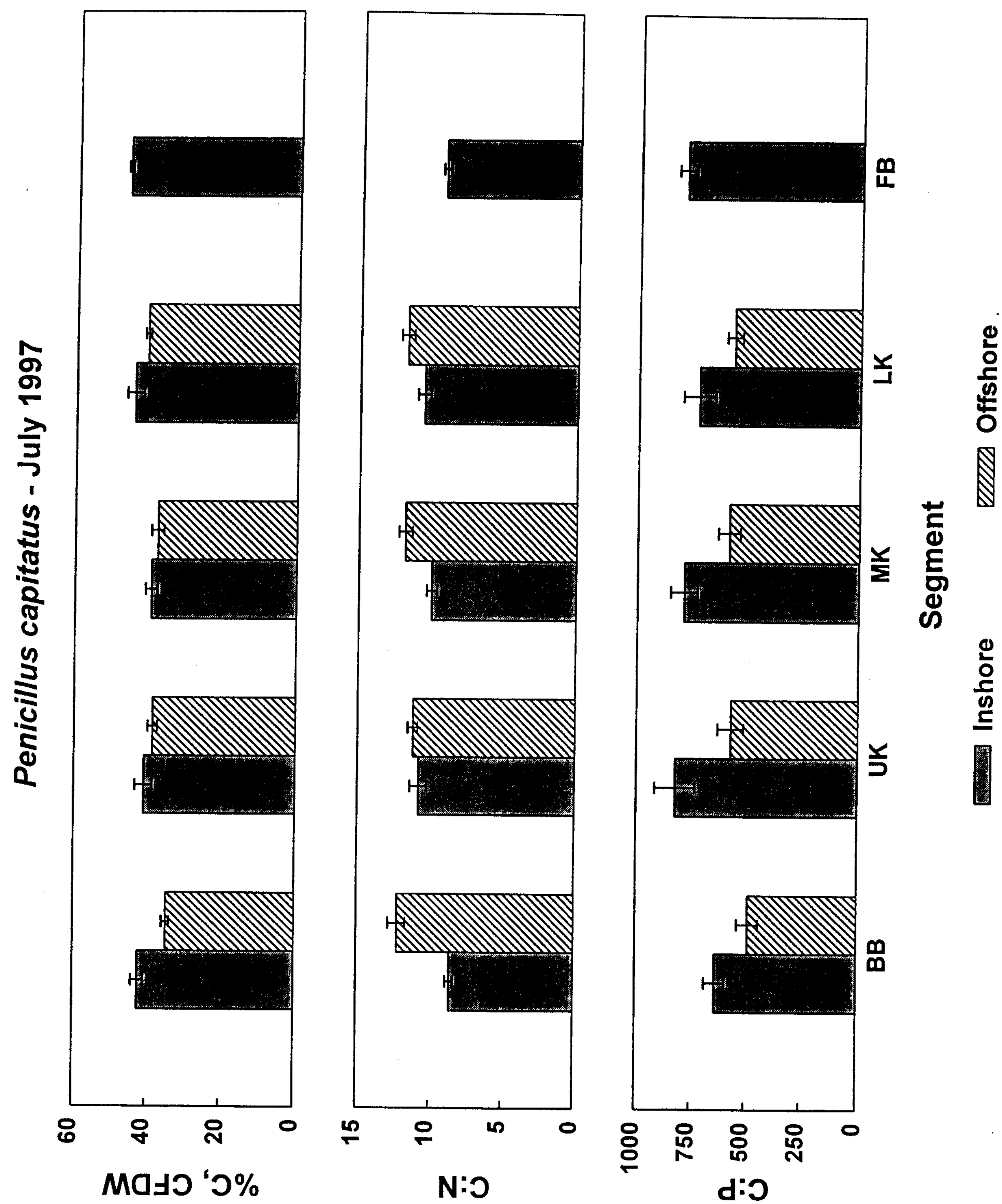

Fig. 163 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus capitatus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

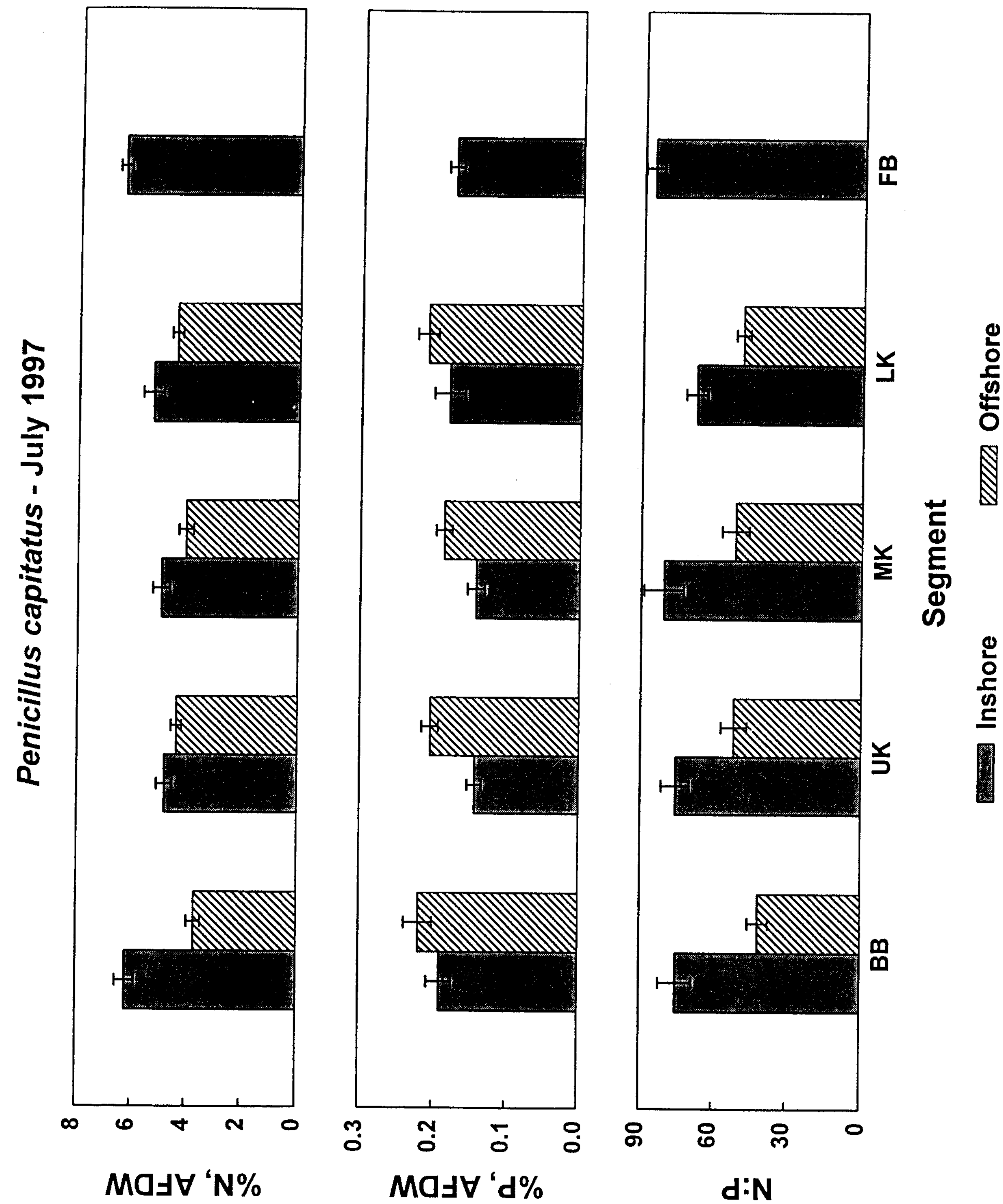

Fig. 164 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus capitatus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

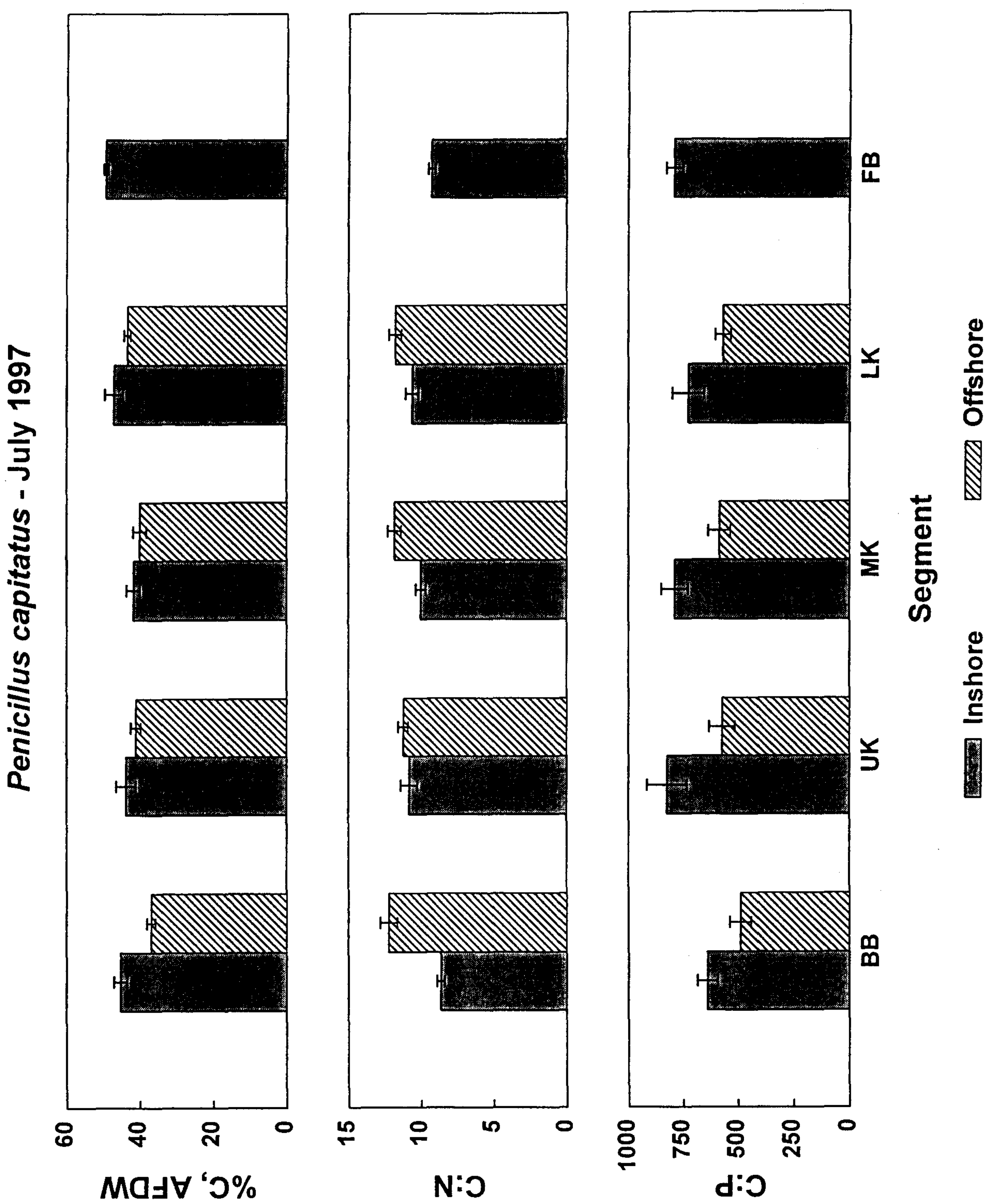

Fig. 165 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus capitatus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

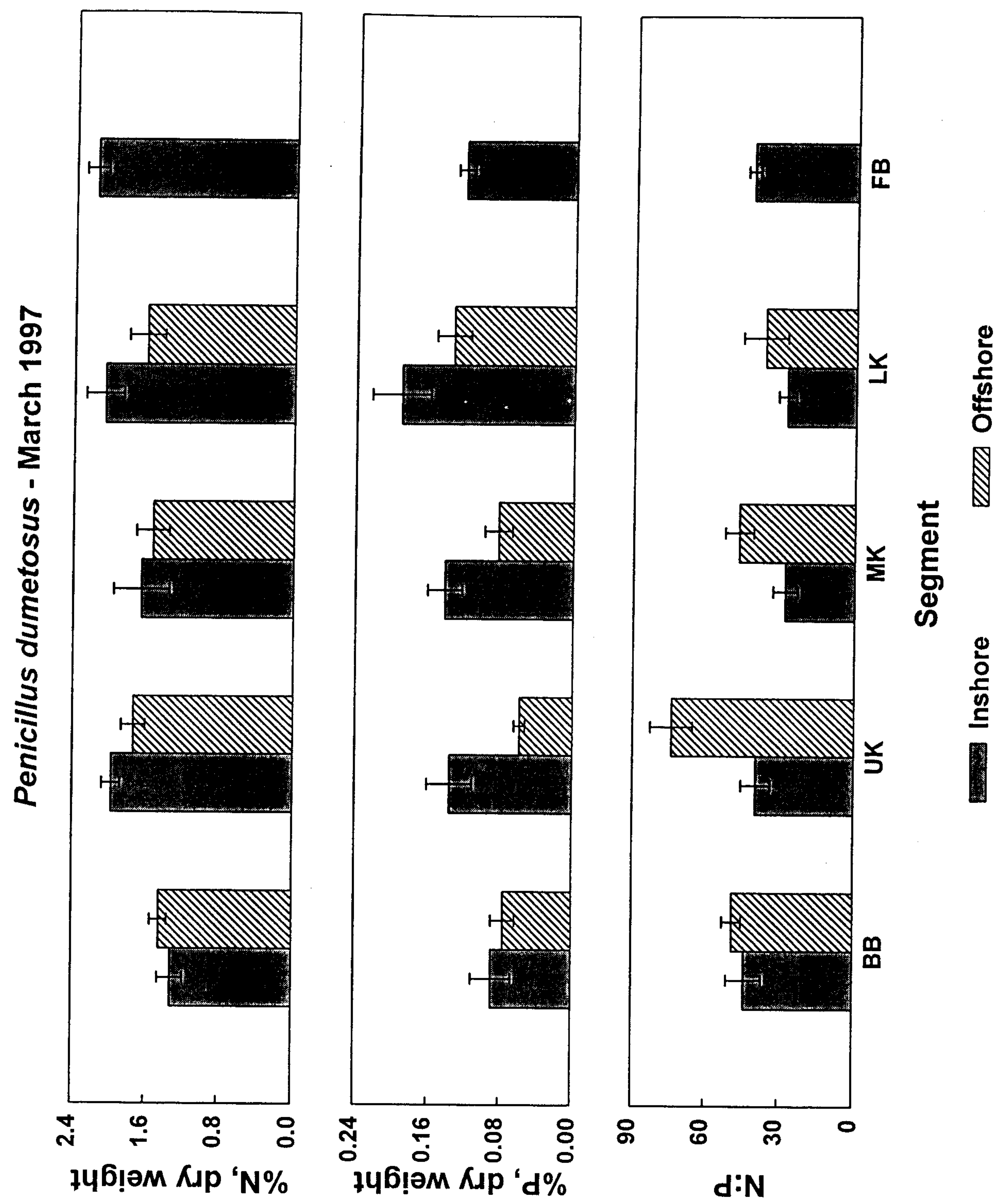

Fig. 166 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Penicillus dumetosus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

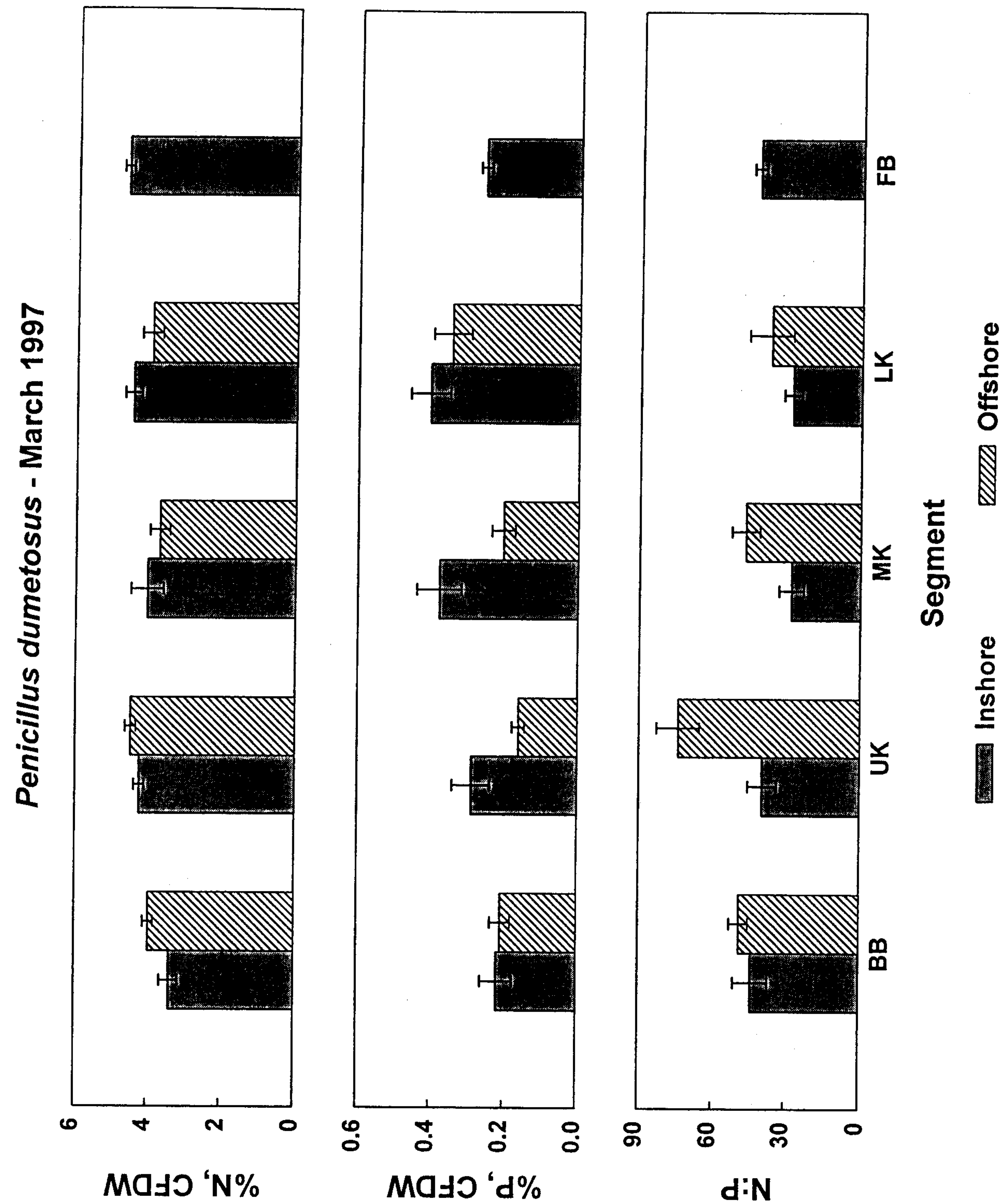

Fig. 167 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus dumetosus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

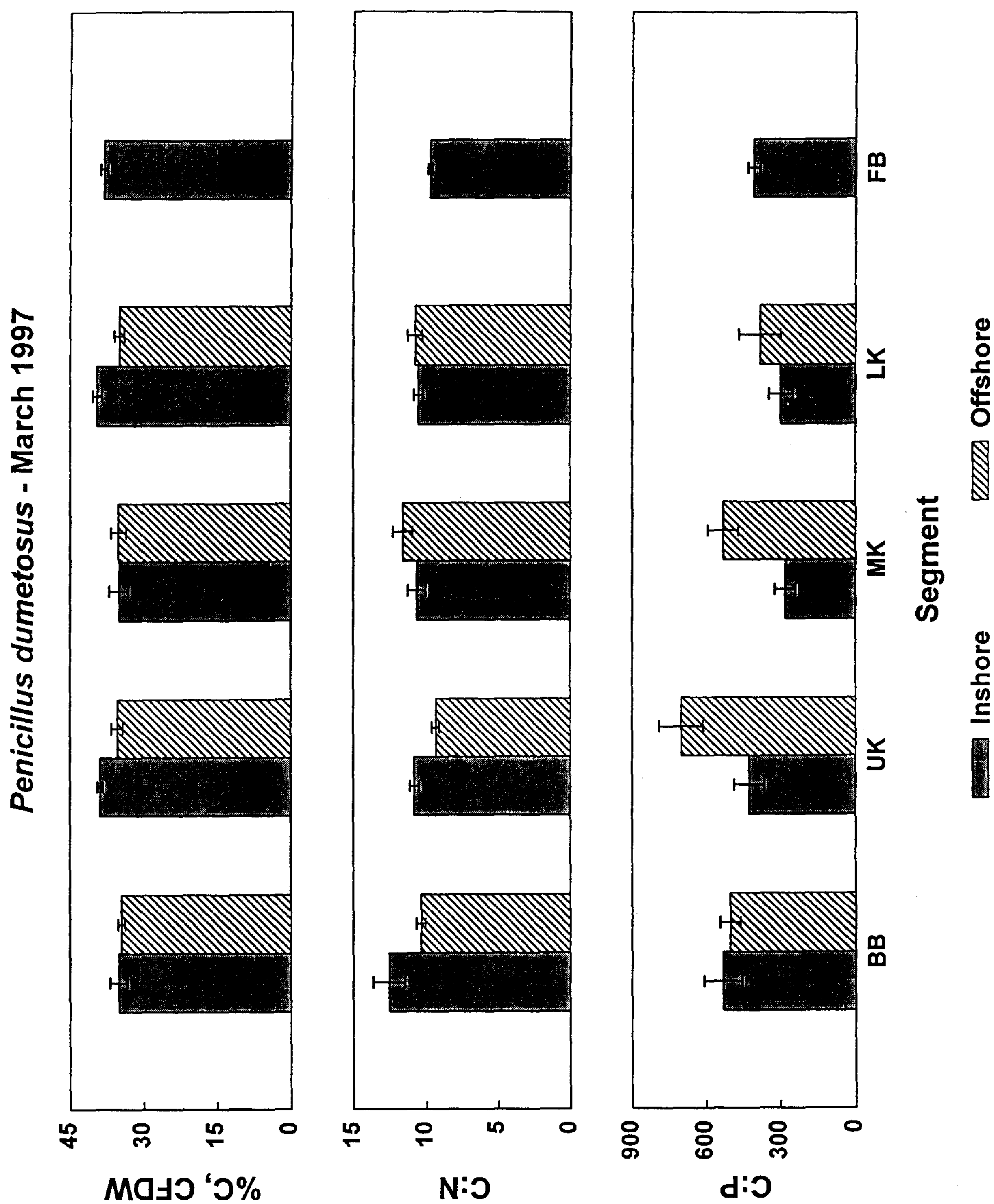

Fig. 168 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus dumetosus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

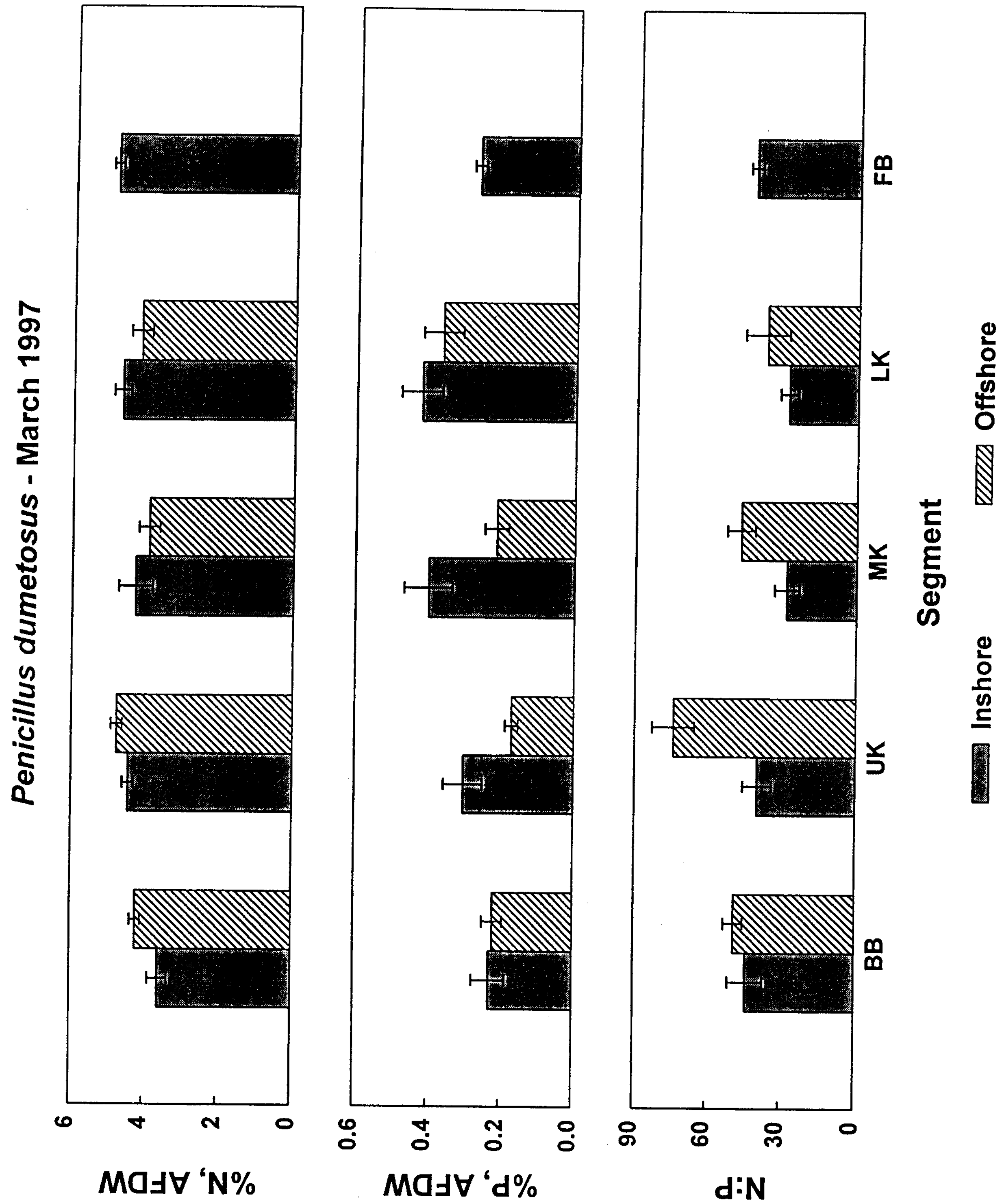

Fig. 169 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus dumetosus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

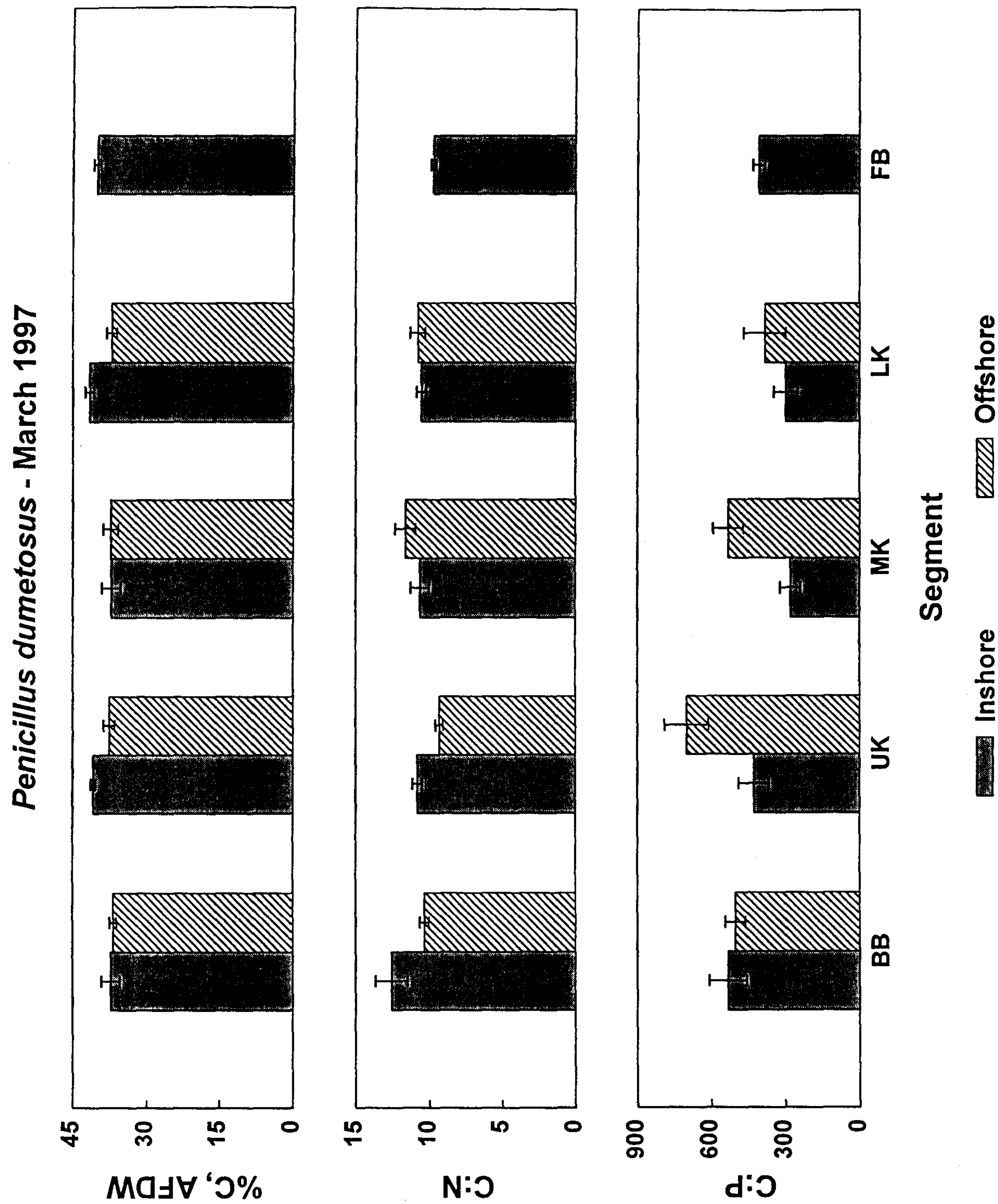

Fig. 170 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus dumetosus*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

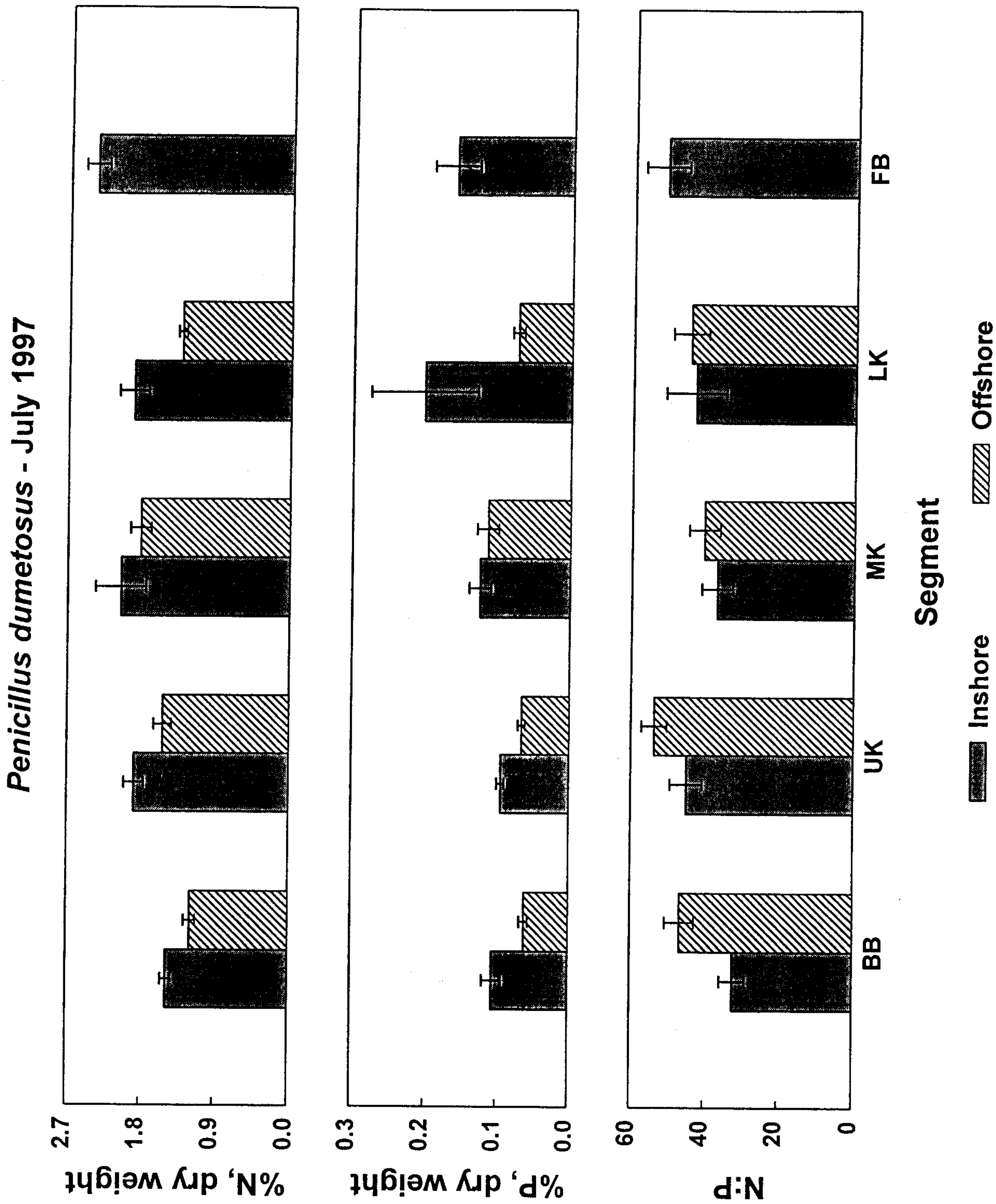

Fig. 171 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Penicillus dumetosus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

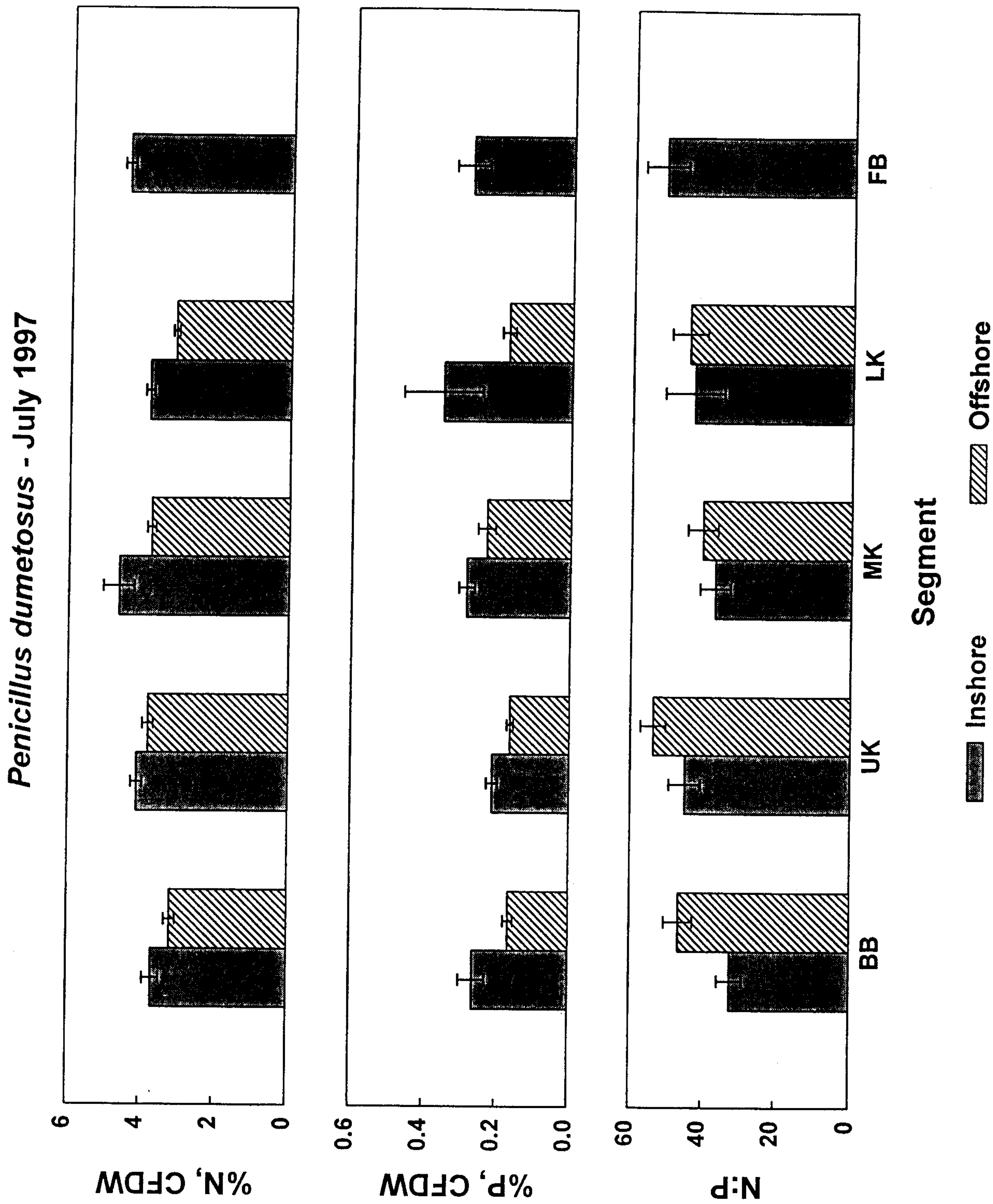

Fig. 172 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus dumetosus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

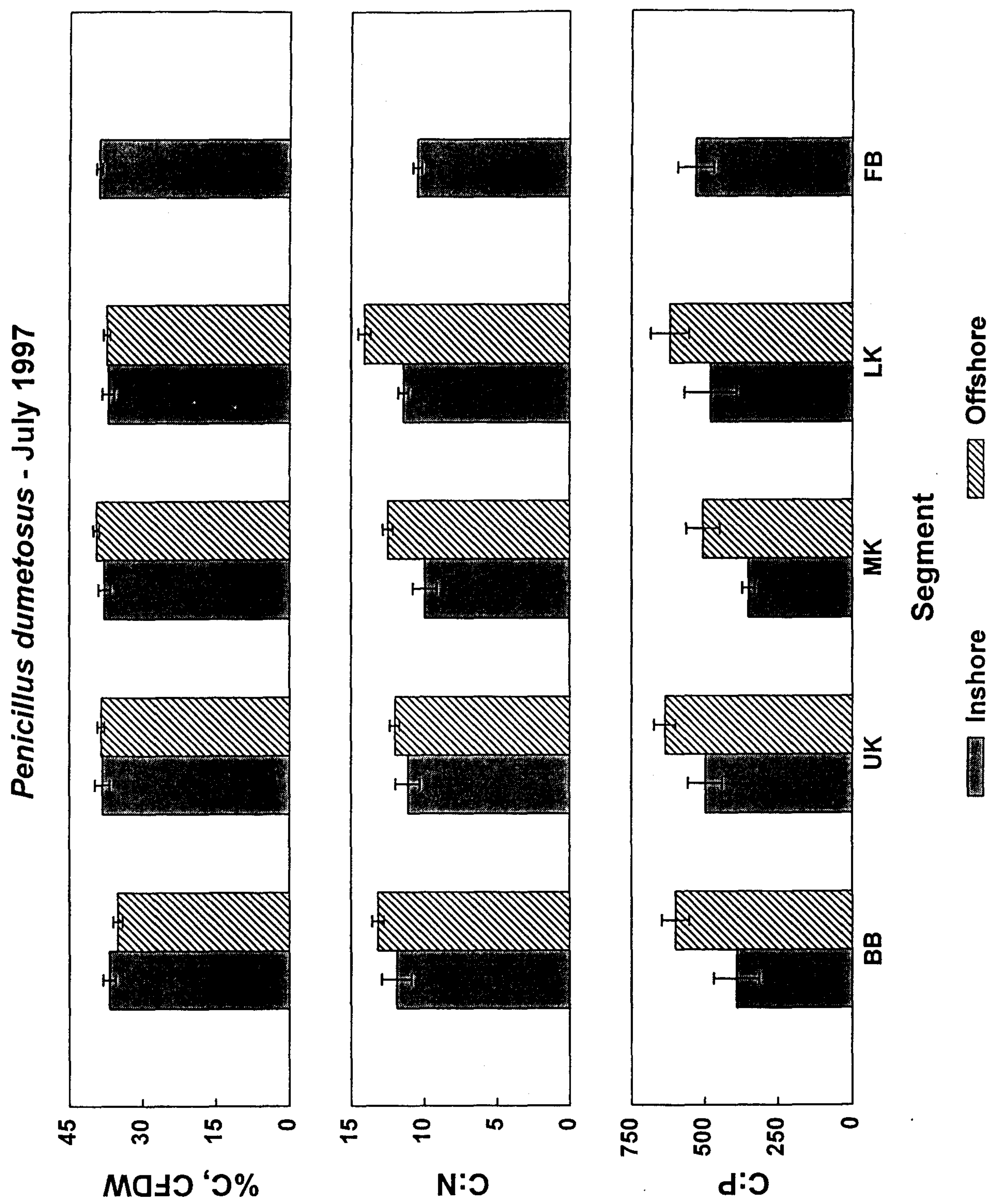

Fig. 173 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Penicillus dumetosus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

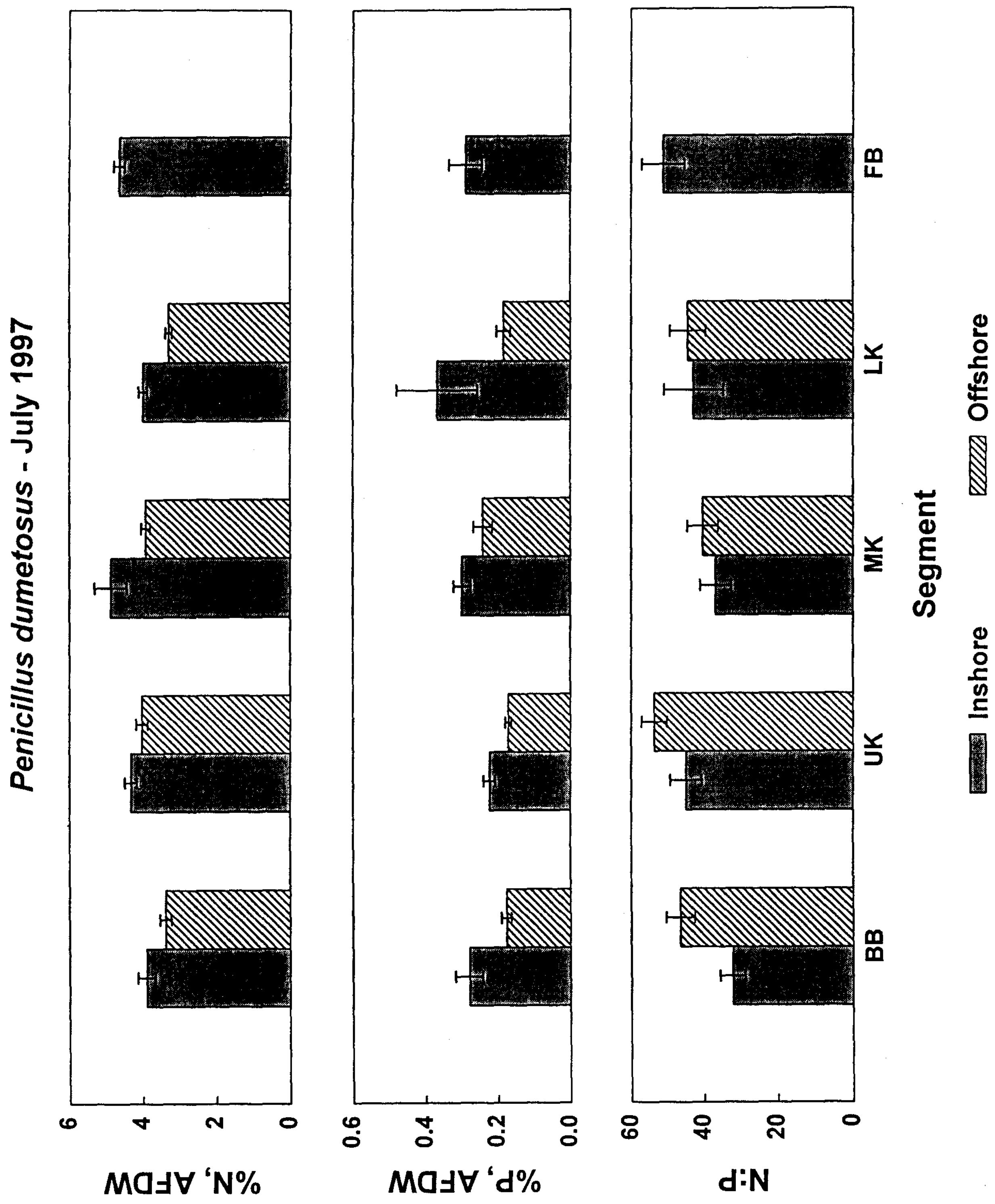

Fig. 174 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus dumetosus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

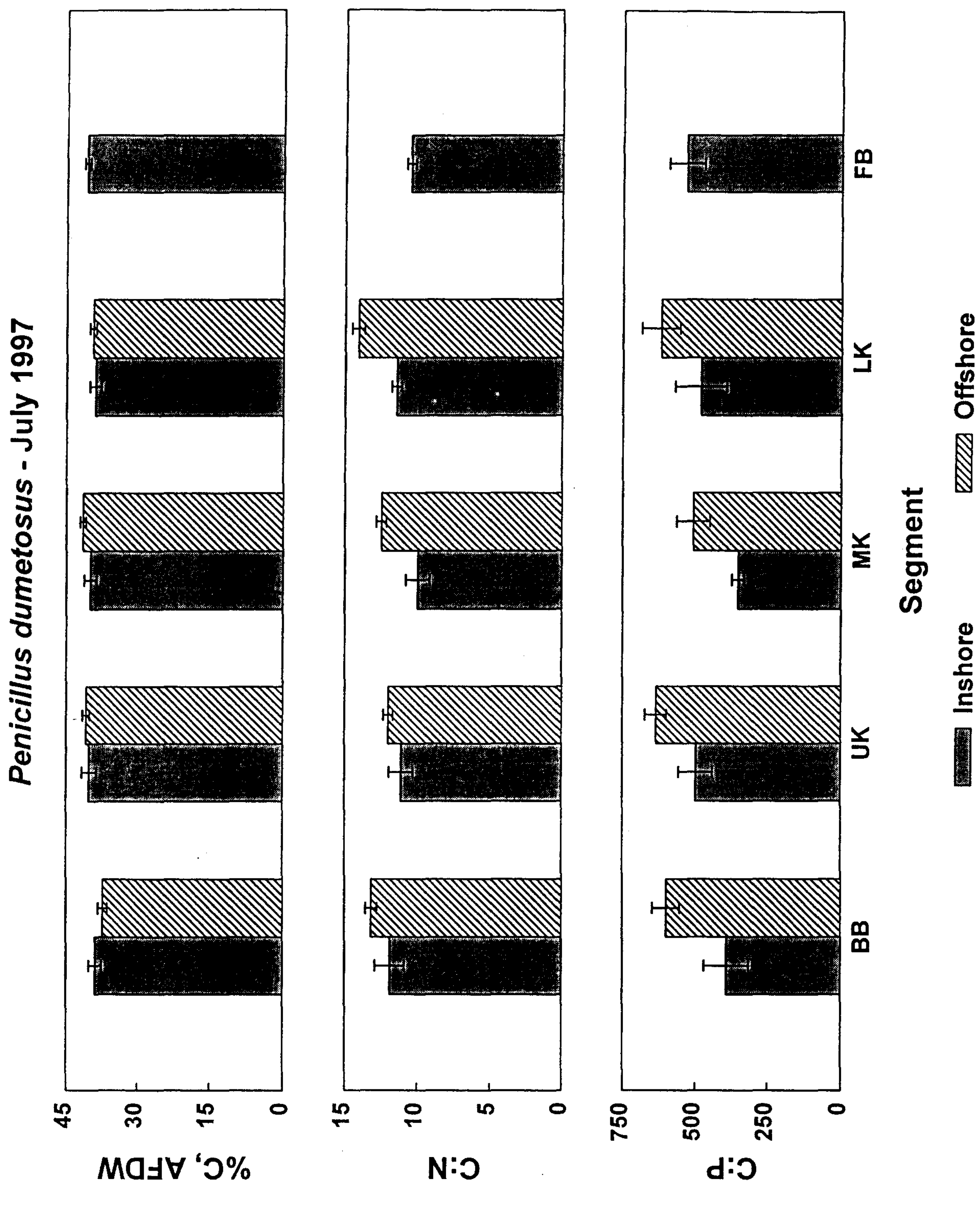

Fig. 175 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Penicillus dumetosus*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

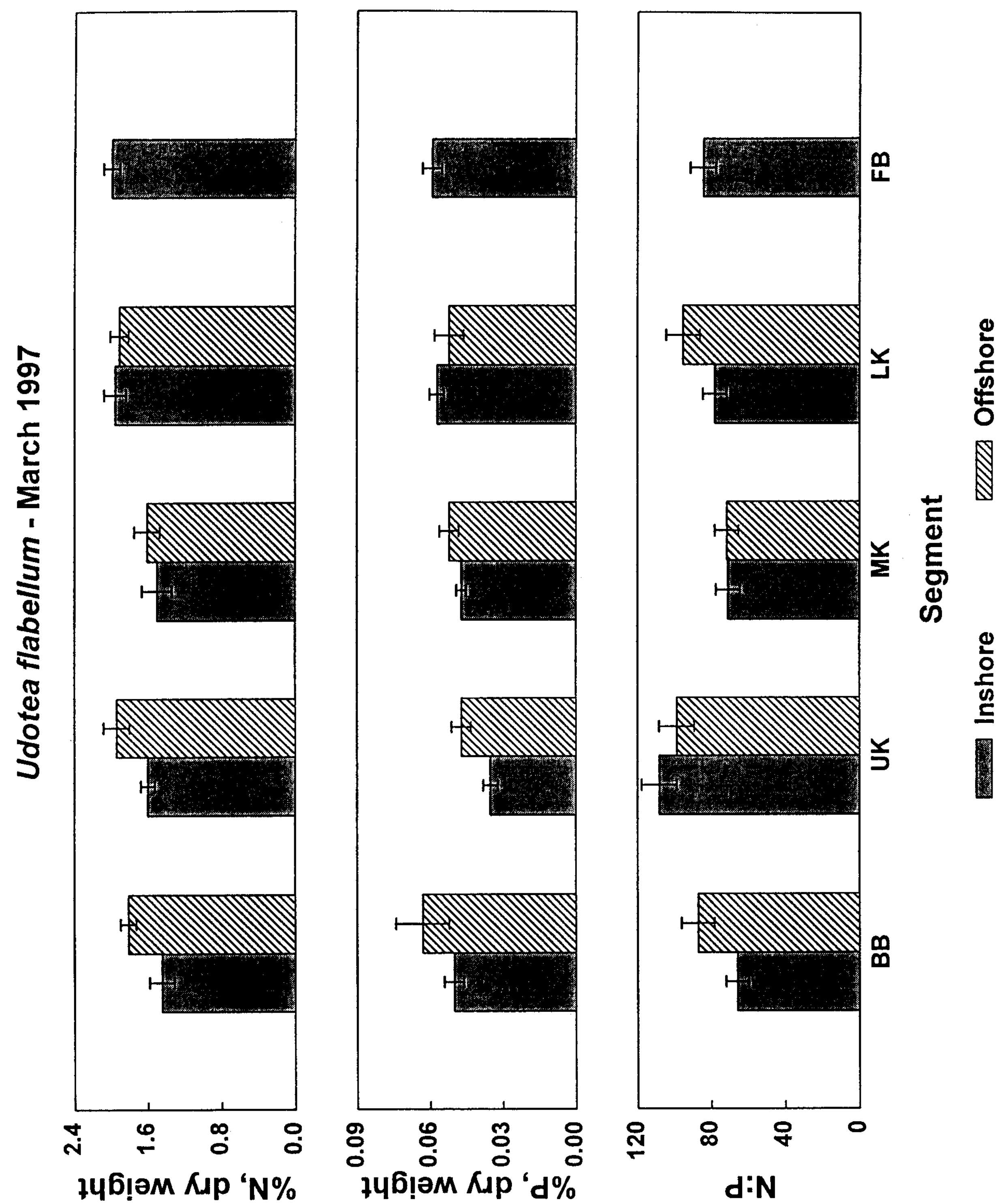

Fig. 176 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Udotea flabellum*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

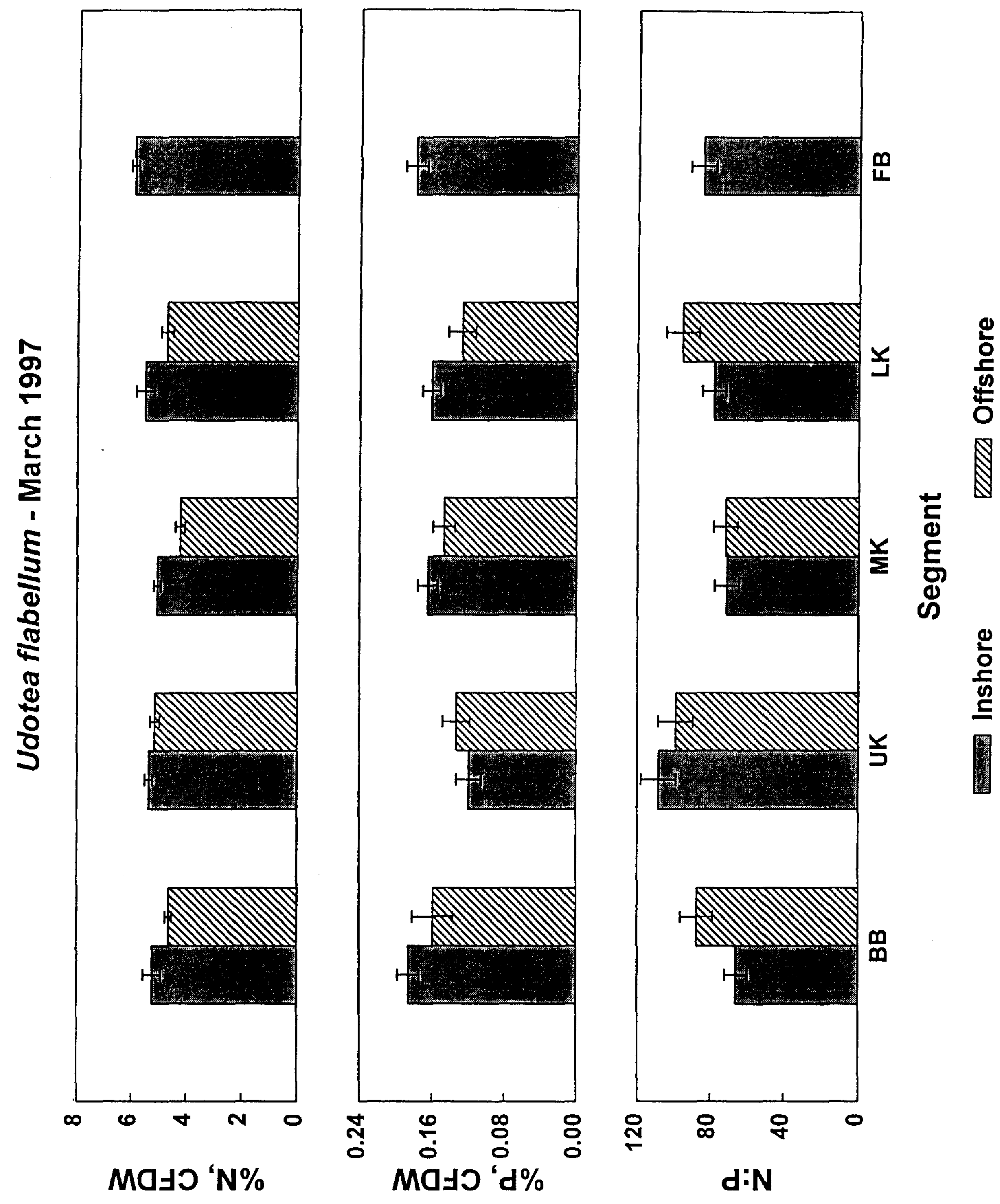

Fig. 177 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Udotea flabellum*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

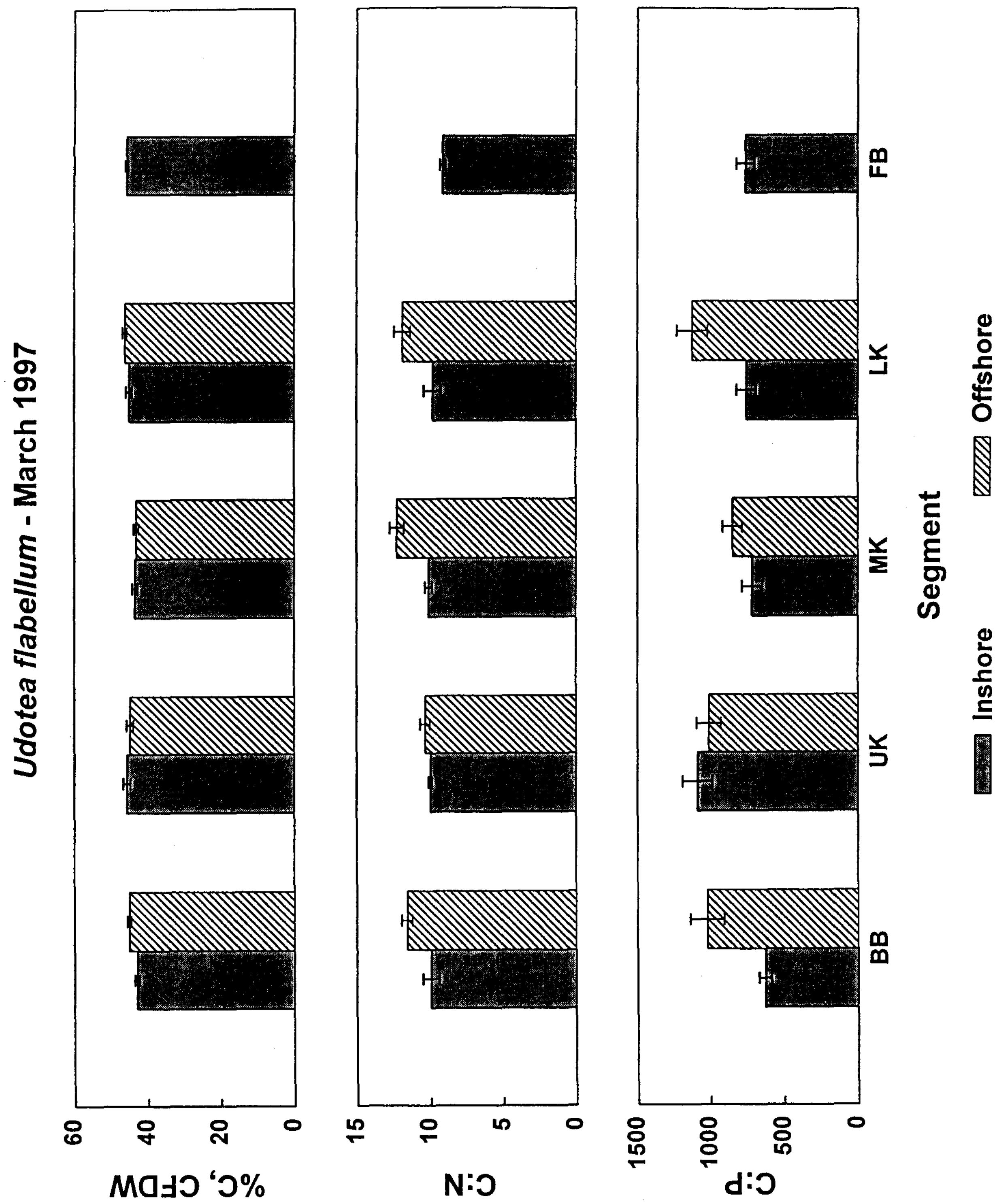

Fig. 178 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Udotea flabellum*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

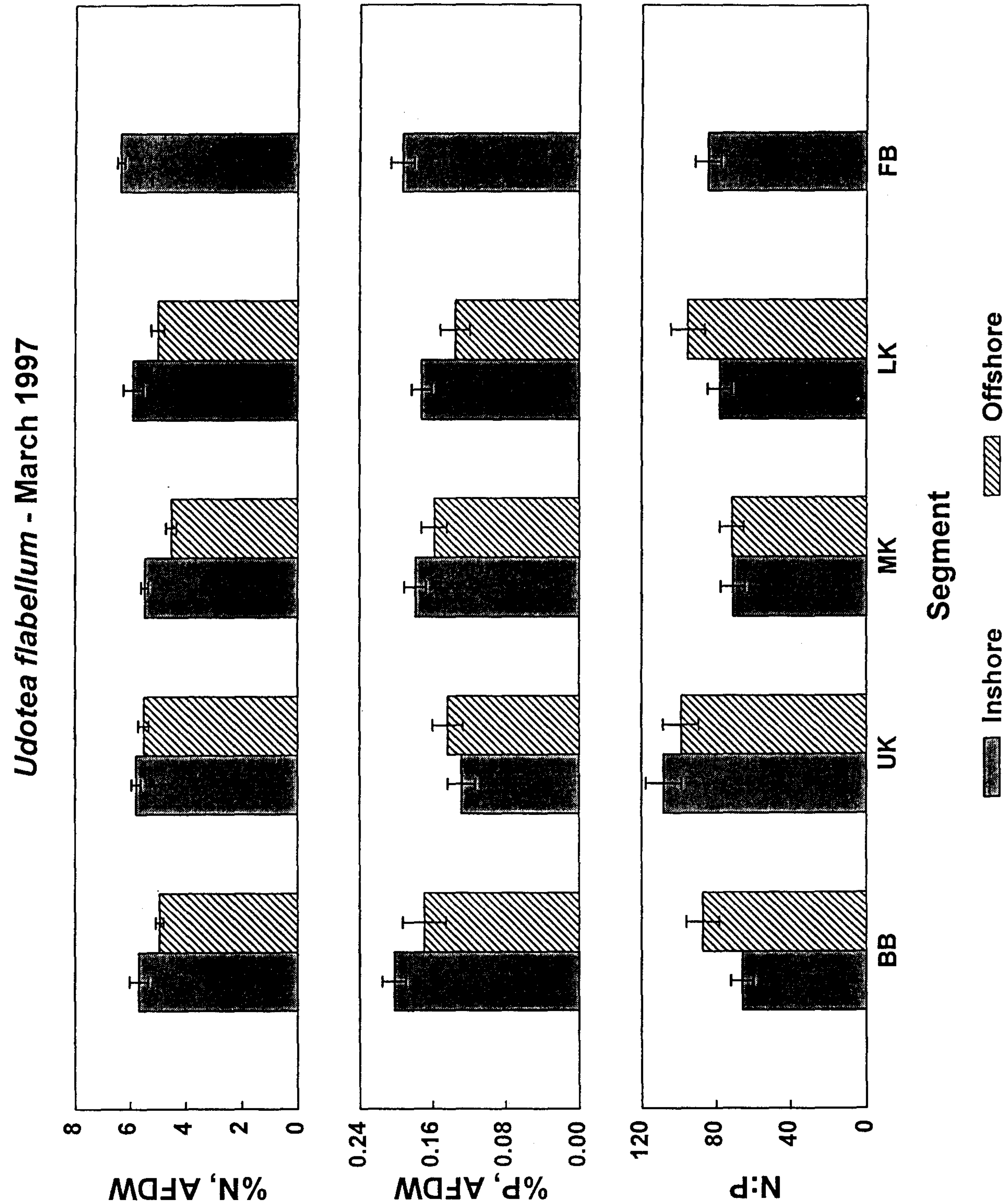

Fig. 179 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Udotea flabellum*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

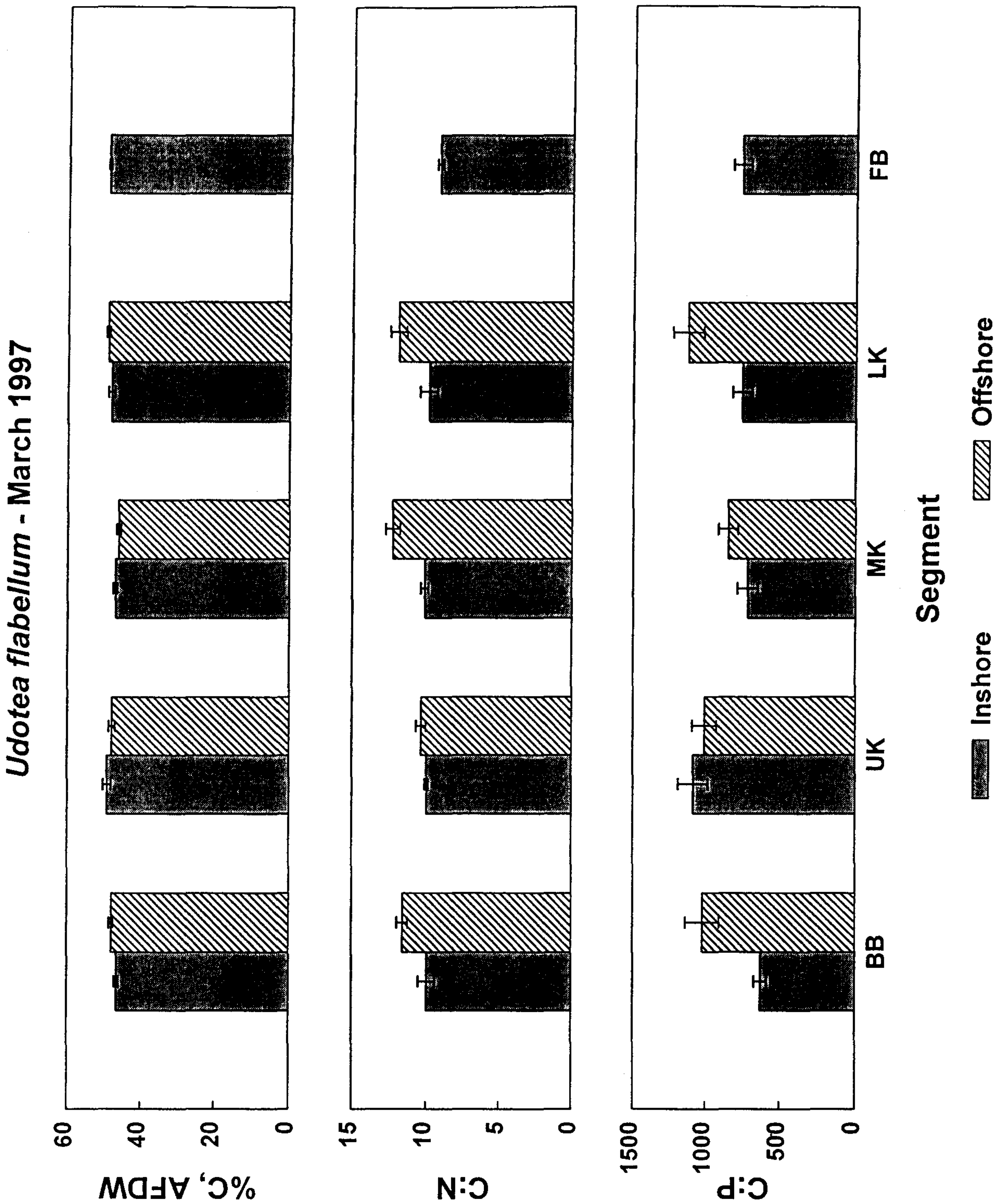

Fig. 180 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Udotea flabellum*, March 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

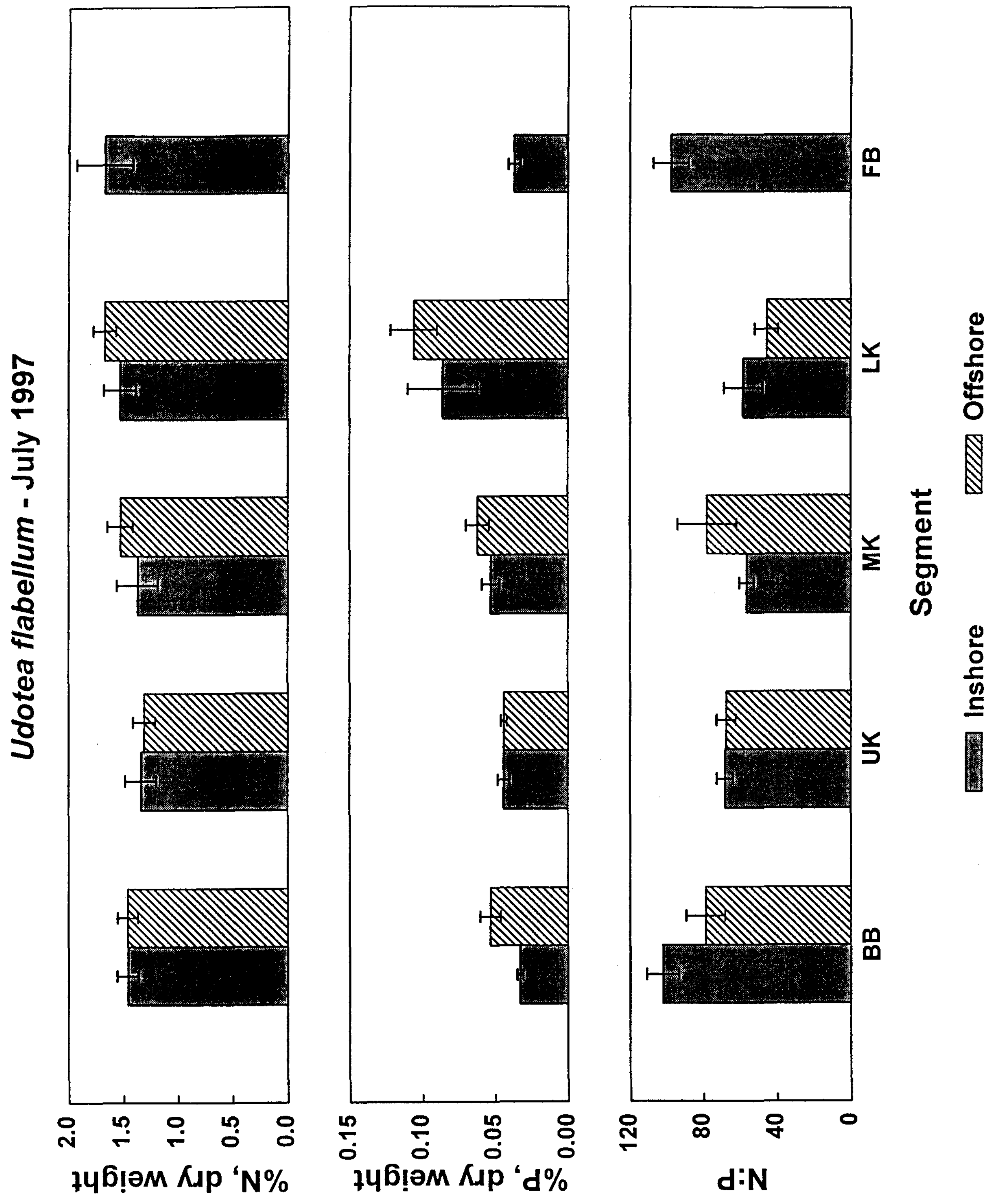

Fig. 181 Segment means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for inshore and offshore samples of *Udotea flabellum*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

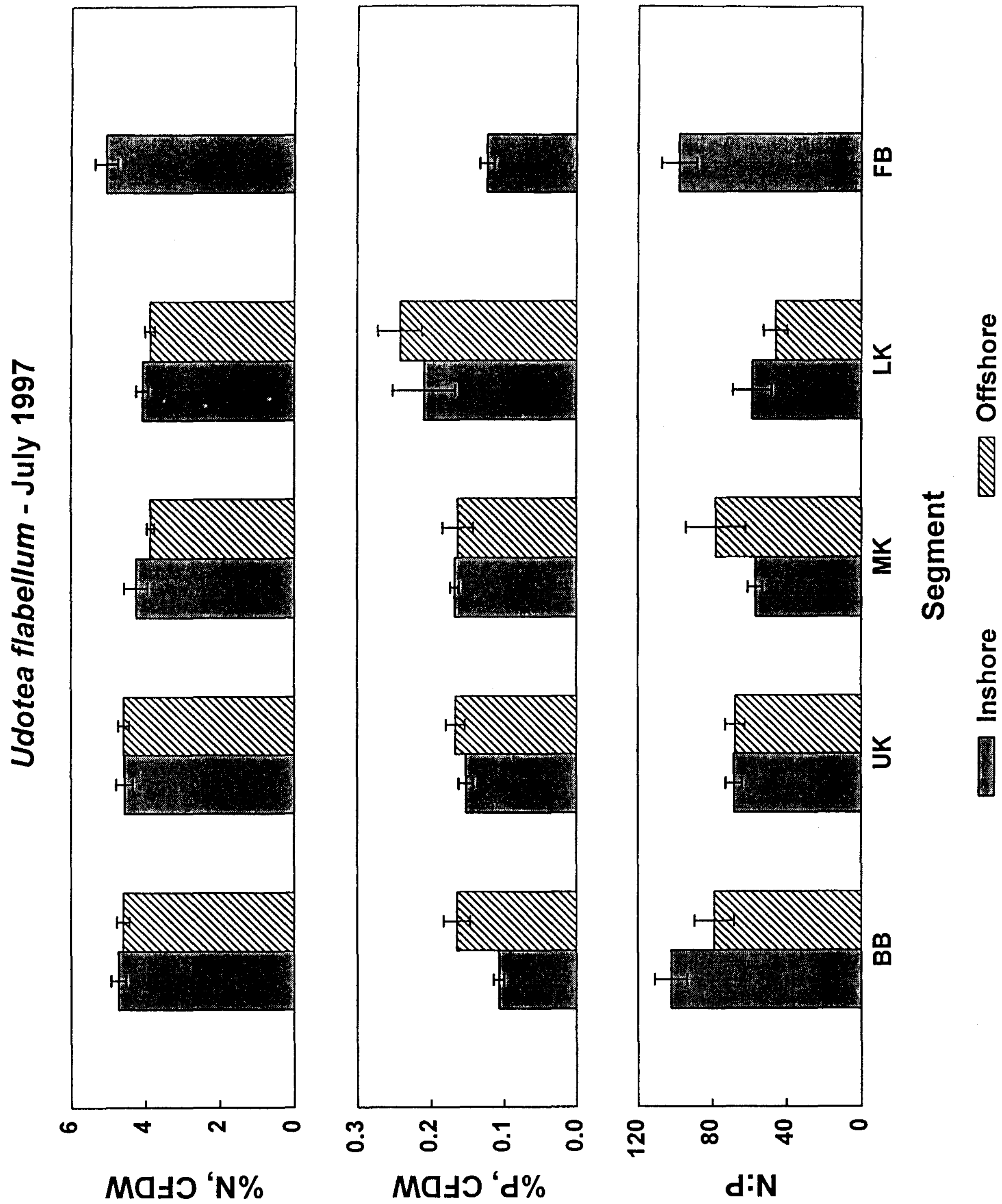

Fig. 182 Segment means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Udotea flabellum*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

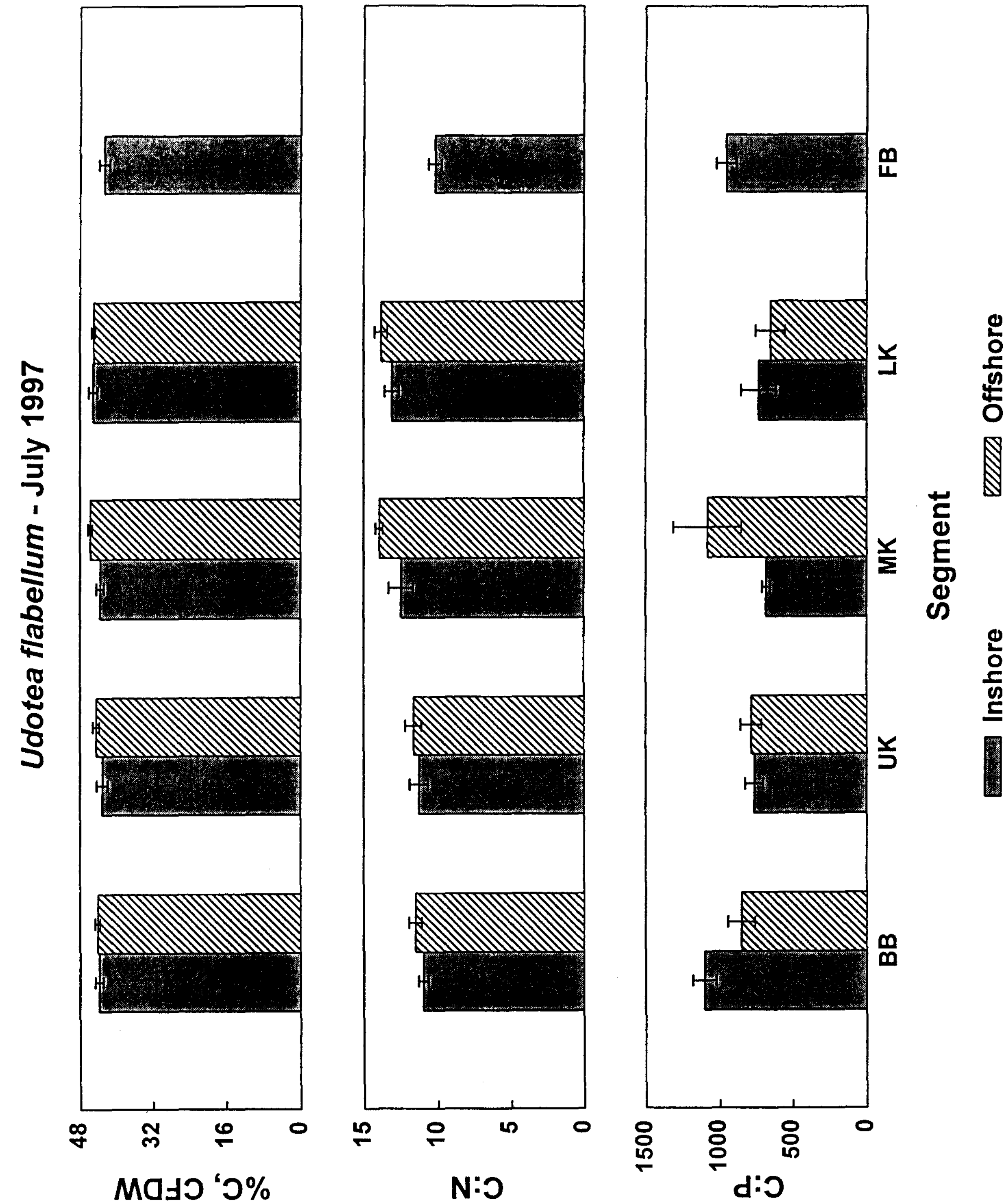

Fig. 183 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for inshore and offshore samples of *Udotea flabellum*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

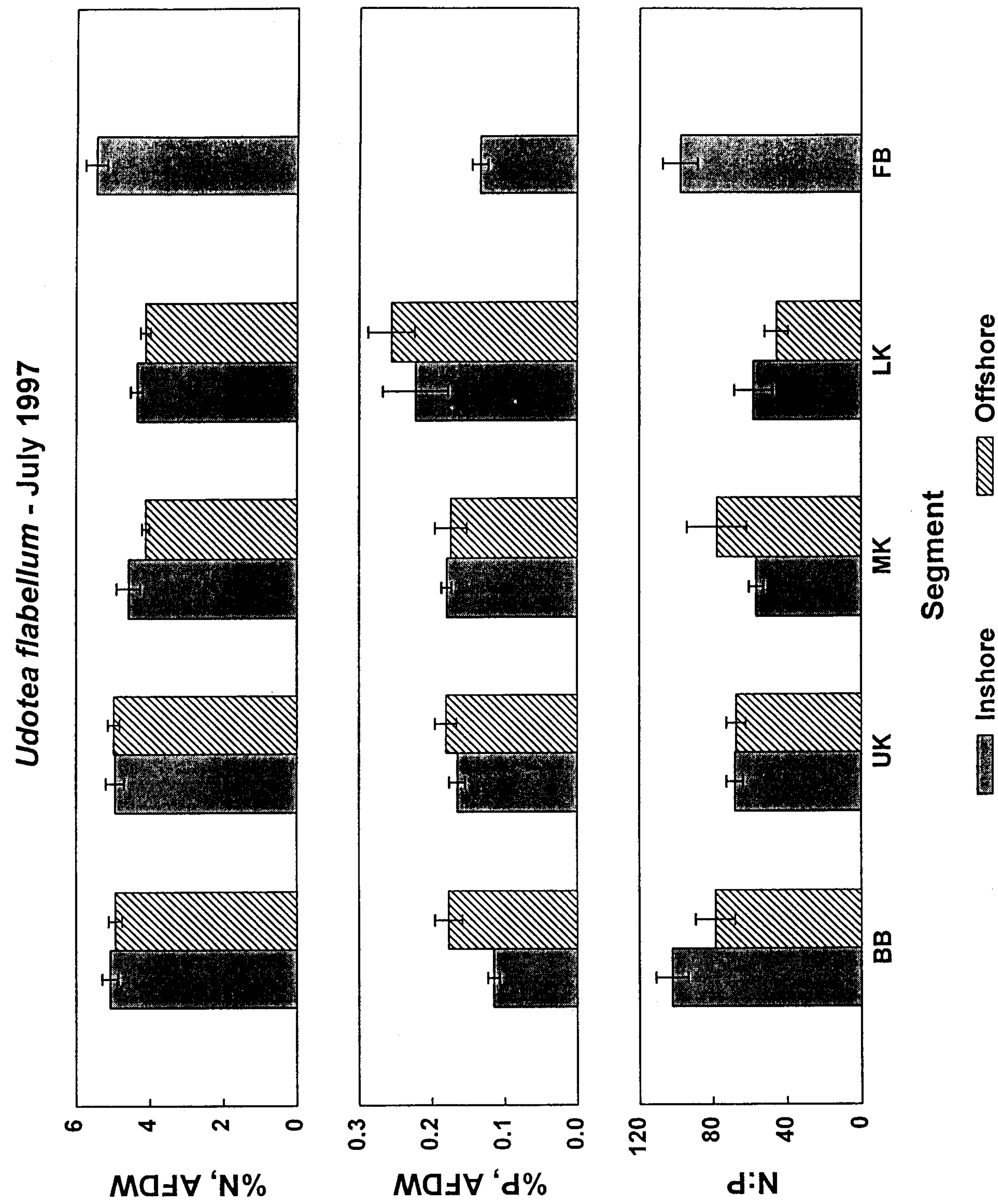

Fig. 184 Segment means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Udotea flabellum*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

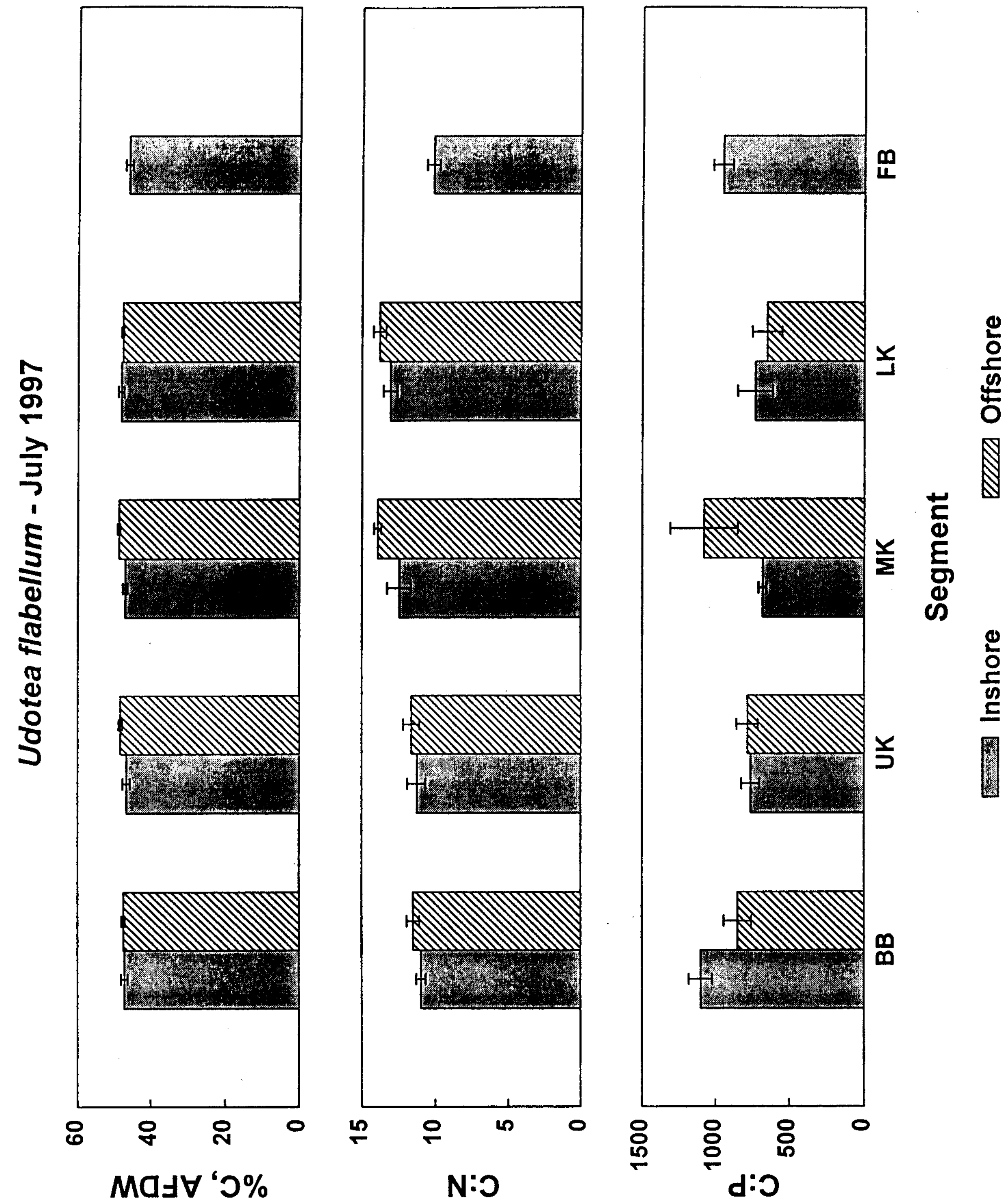

Fig. 185 Segment means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for inshore and offshore samples of *Udotea flabellum*, July 1997. Codes for segments: BB = Biscayne Bay, UK = Upper Keys, MK = Middle Keys, LK = Lower Keys, FB = Florida Bay.

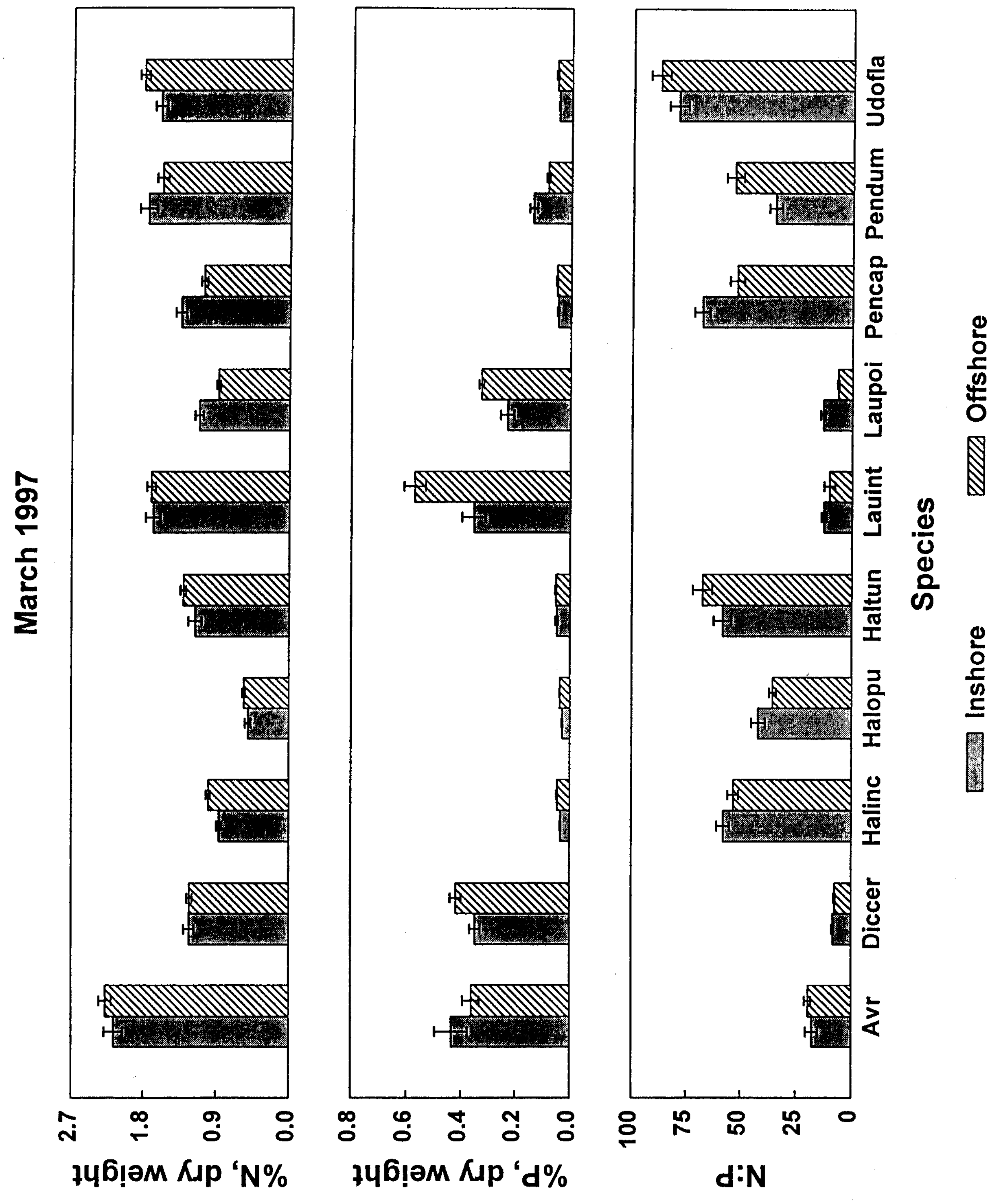

Fig. 186 Species means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for all inshore and offshore samples, March 1997. Codes for species are in Table 3.

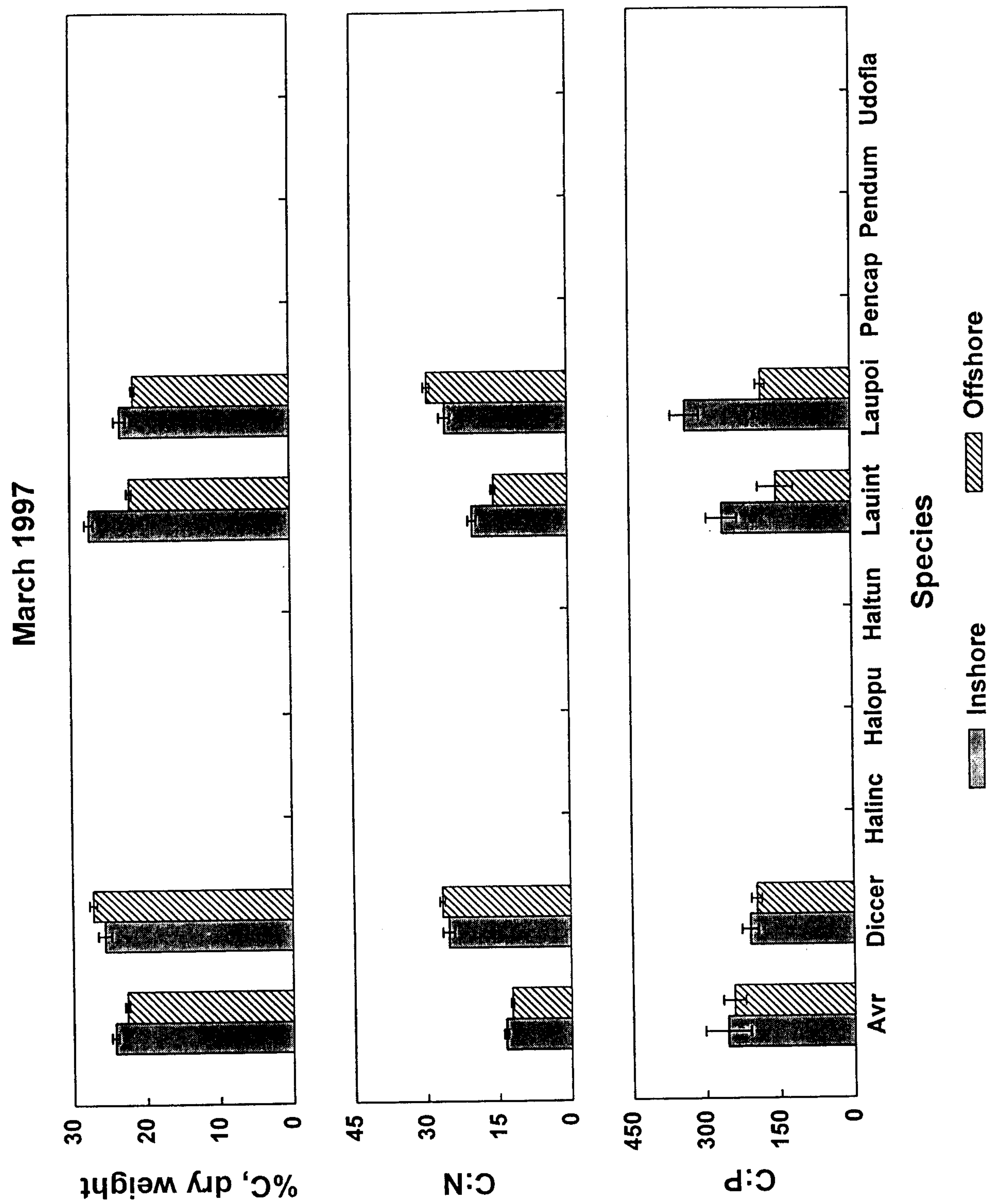

Fig. 187 Species means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for all inshore and offshore samples, March 1997. Codes for species are in Table 3. Values for calcified species are omitted.

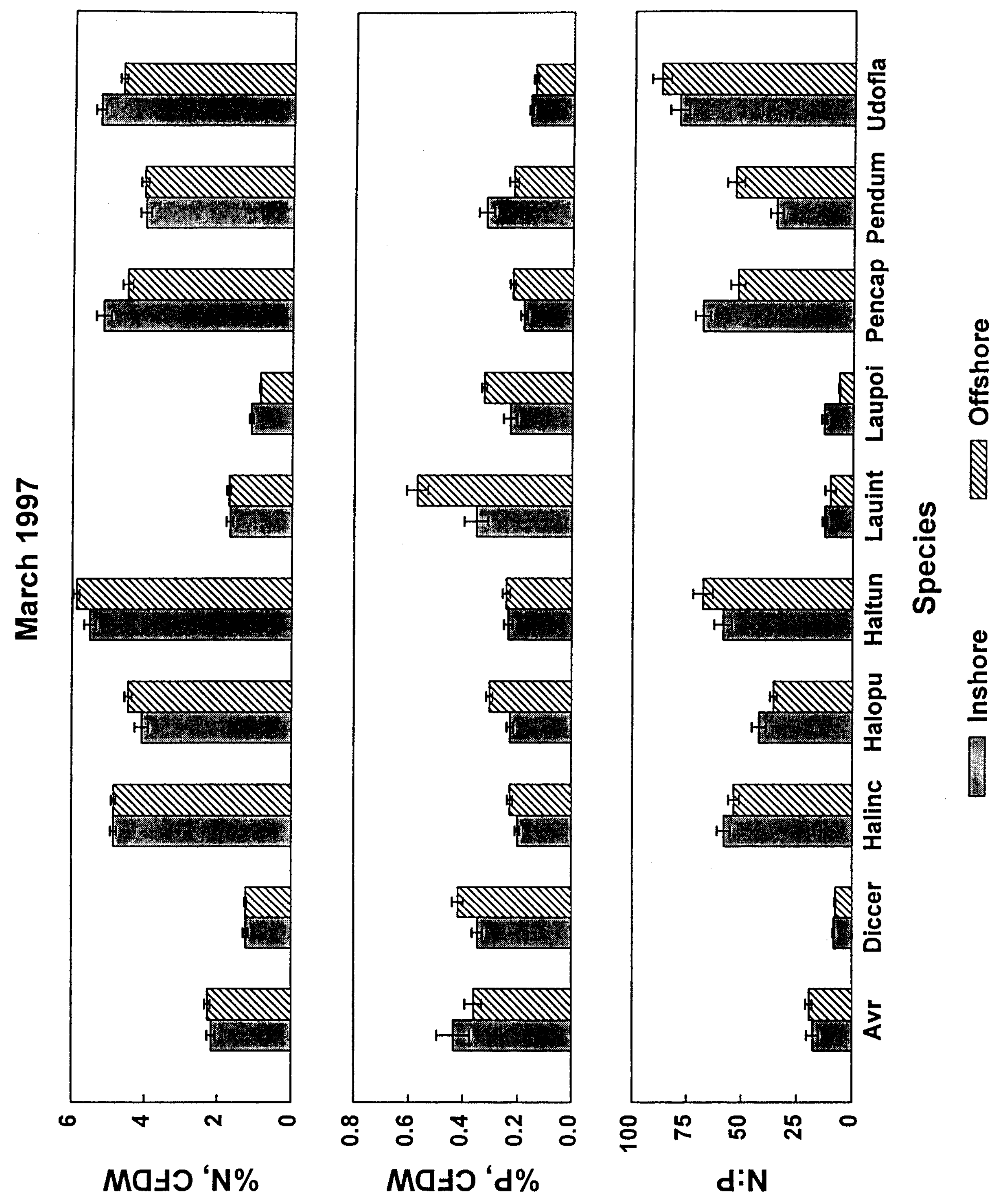

Fig. 188 Species means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for all inshore and offshore samples, March 1997. Codes for species are in Table 3.

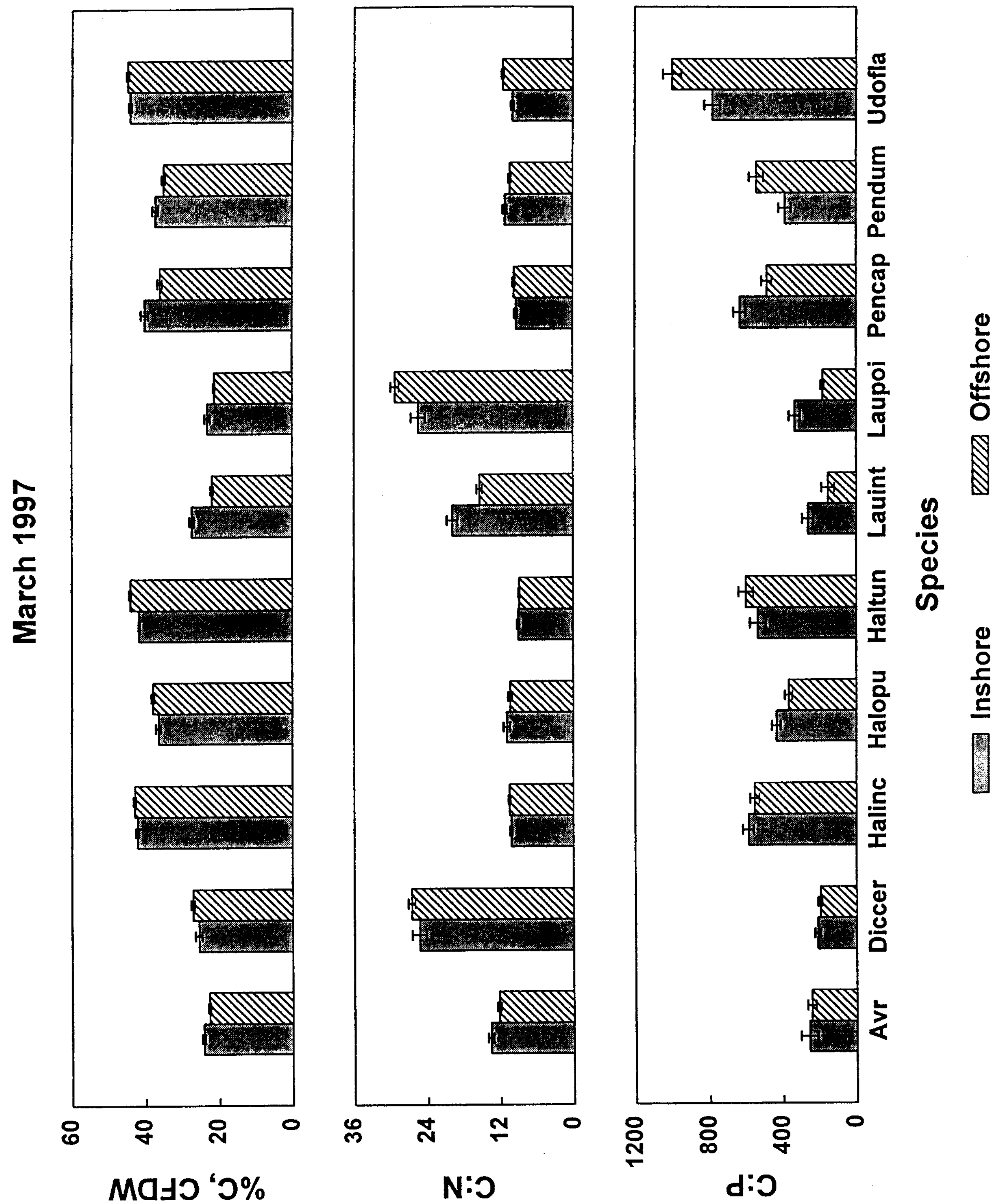

Fig. 189 Species means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for all inshore and offshore samples, March 1997. Codes for species are in Table 3.

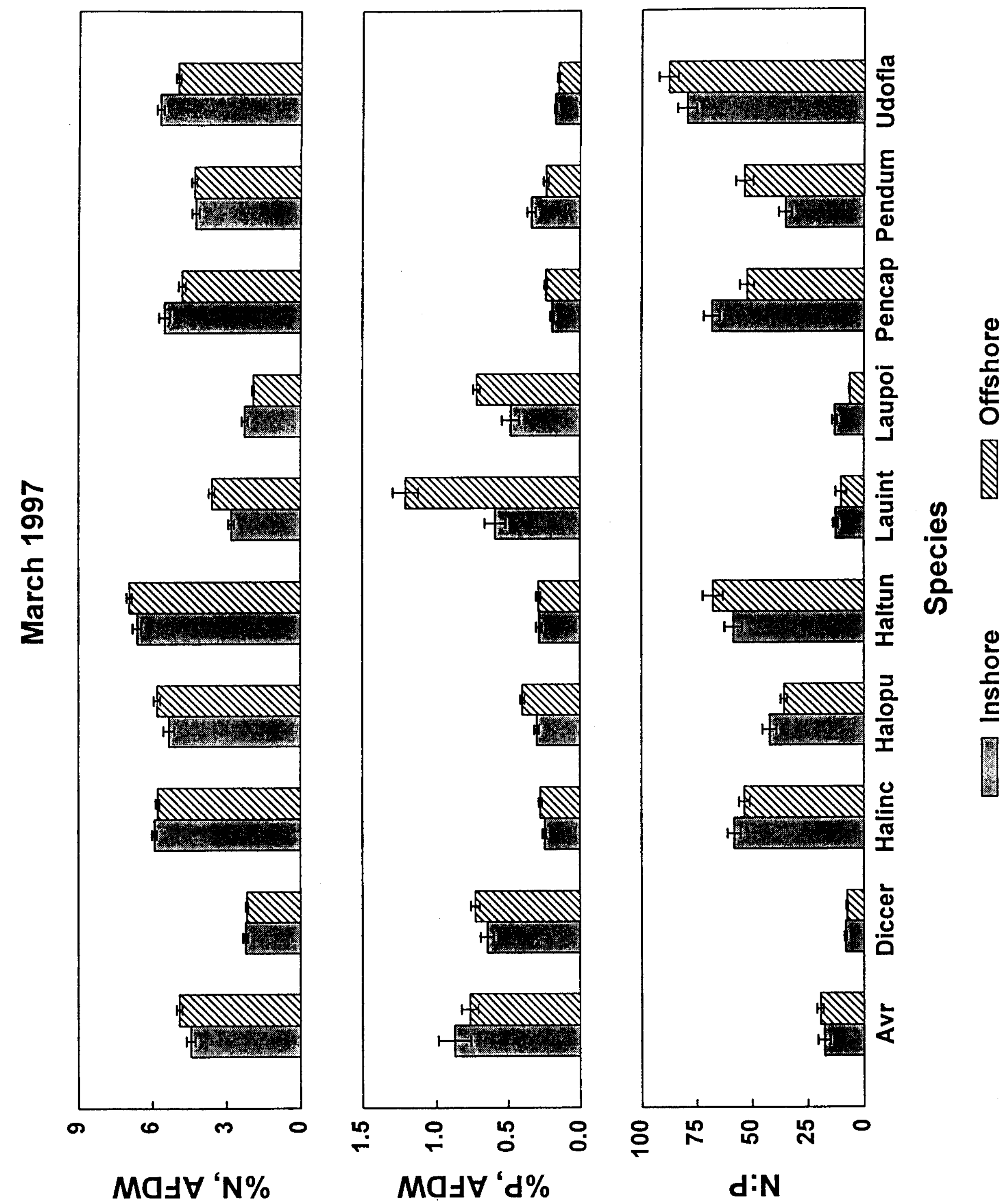

Fig. 190 Species means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for all inshore and offshore samples, March 1997. Codes for species are in Table 3.

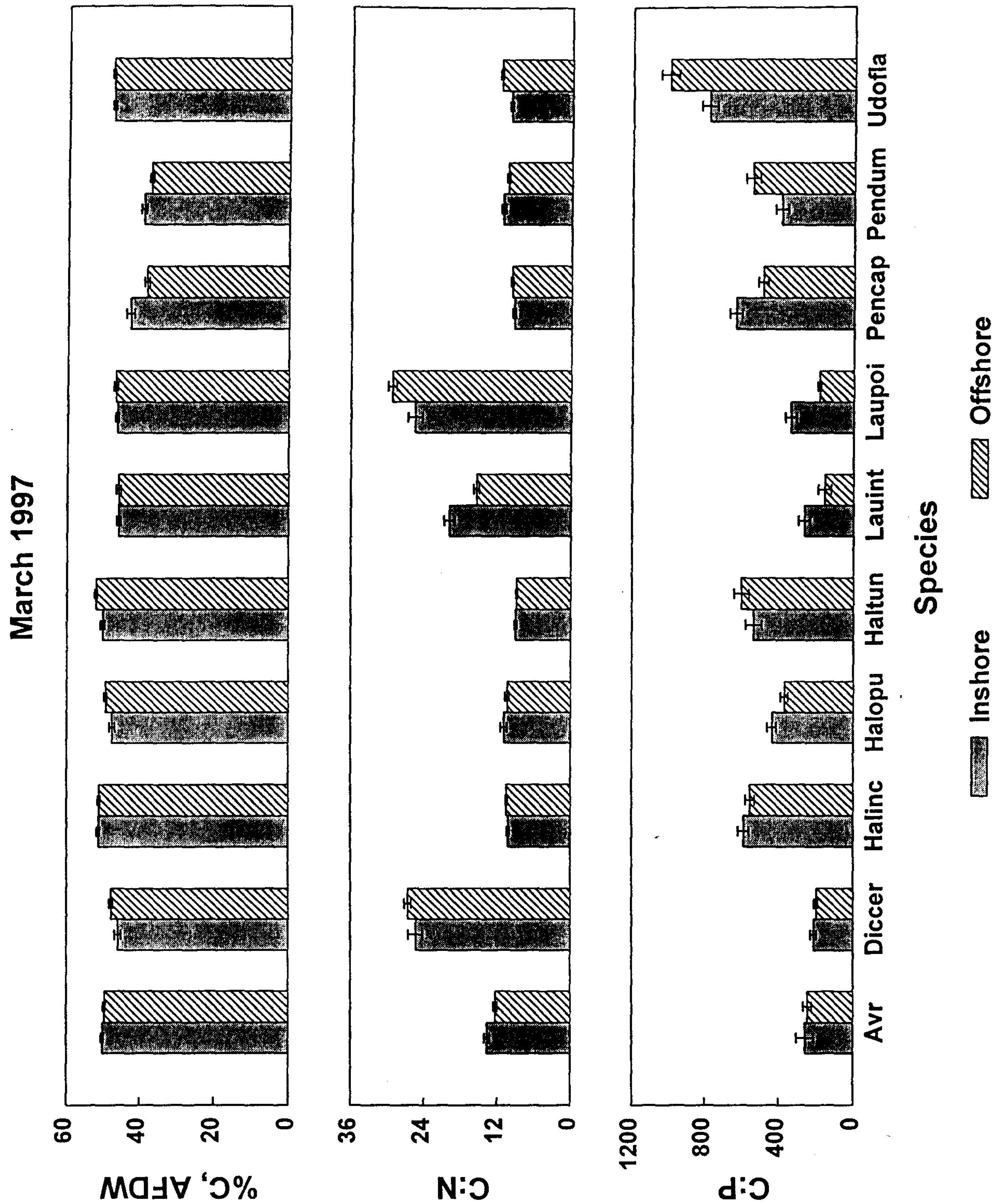

Fig. 191 Species means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for all inshore and offshore samples, March 1997. Codes for species are in Table 3.

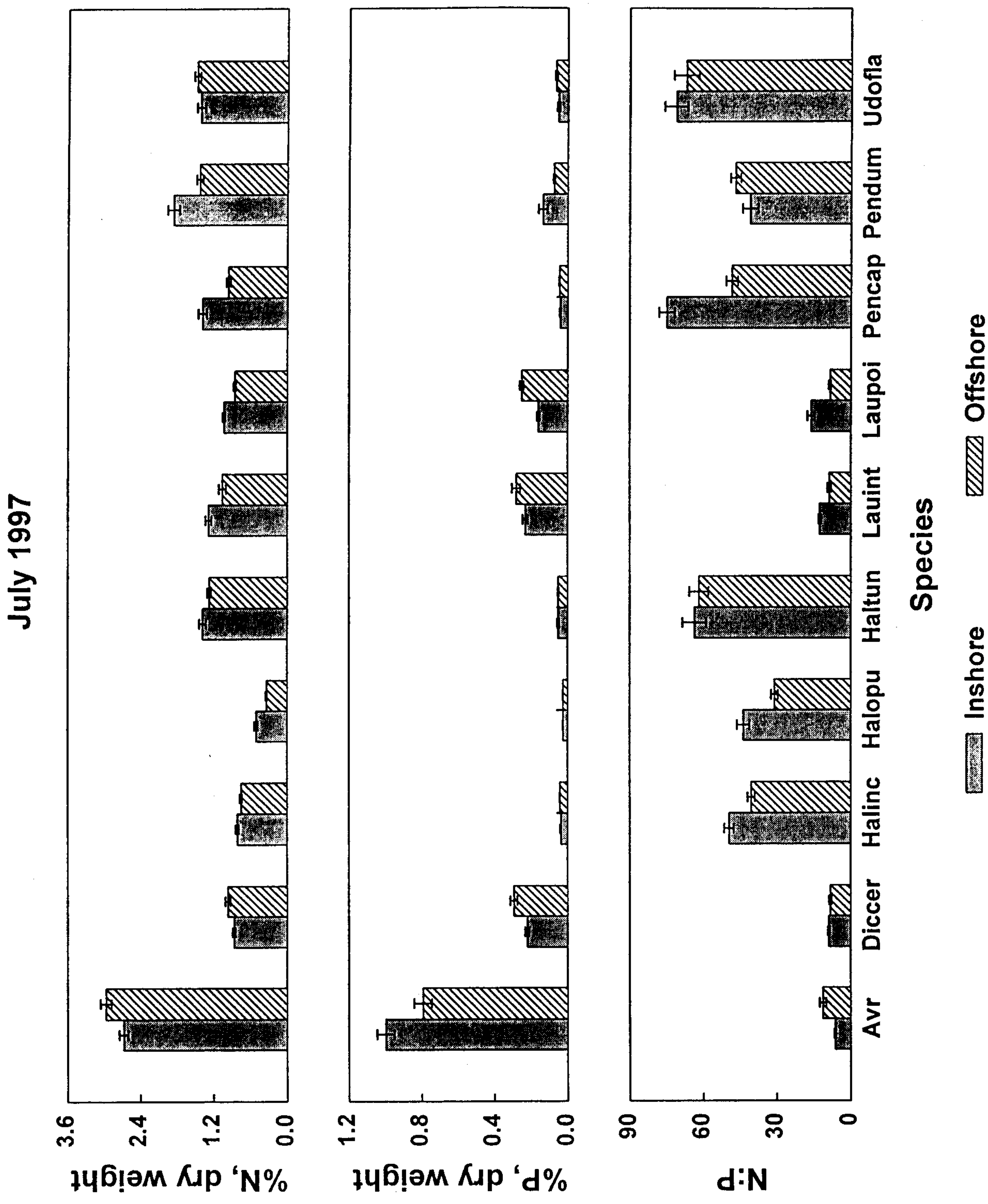

Fig. 192 Species means (±SE) for %N, %P, and N:P ratio, on a dry weight basis, for all inshore and offshore samples, July 1997. Codes for species are in Table 3.

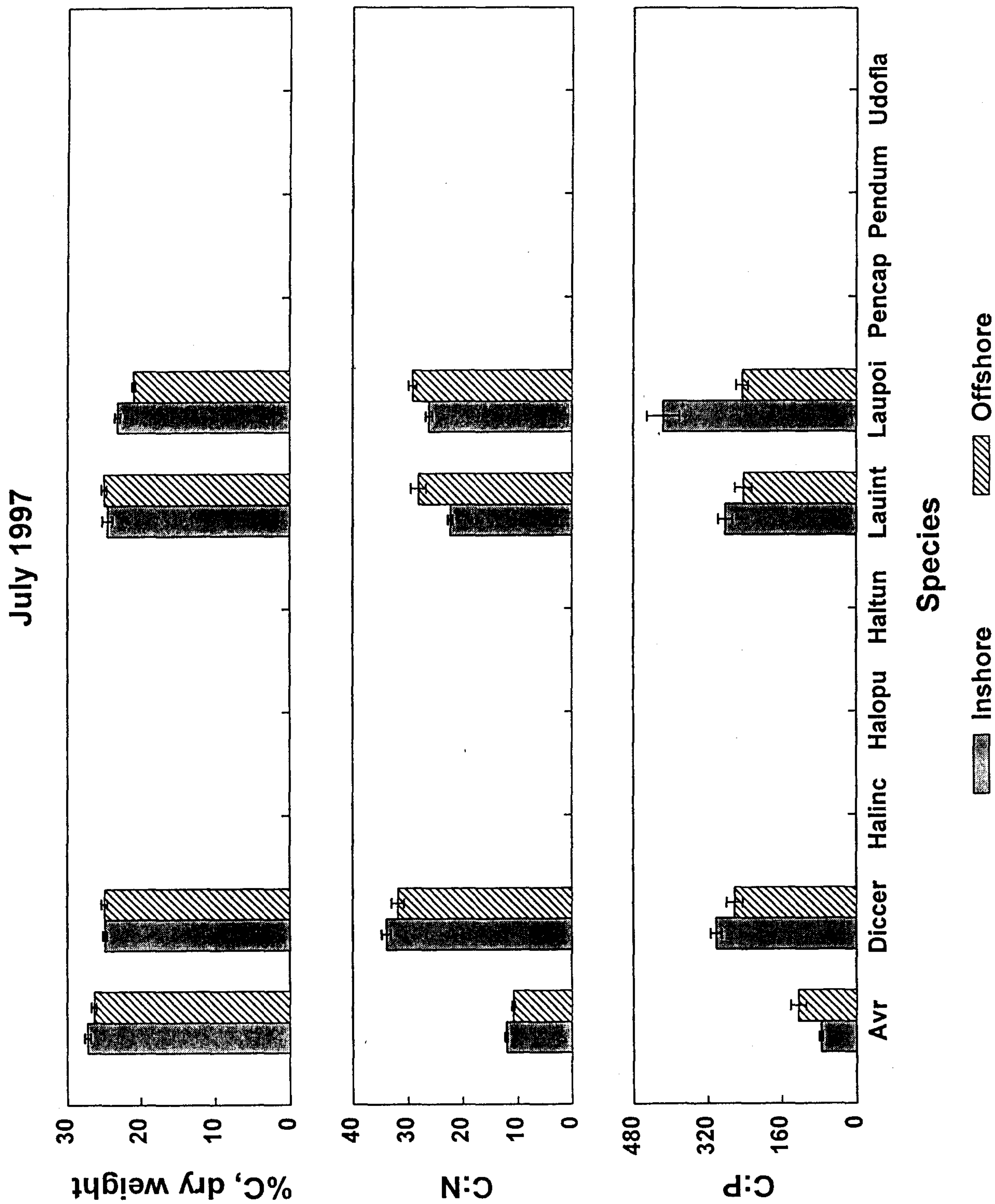

Fig. 193 Species means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for all inshore and offshore samples, July 1997. Codes for species are in Table 3. Values for calcified species are omitted.

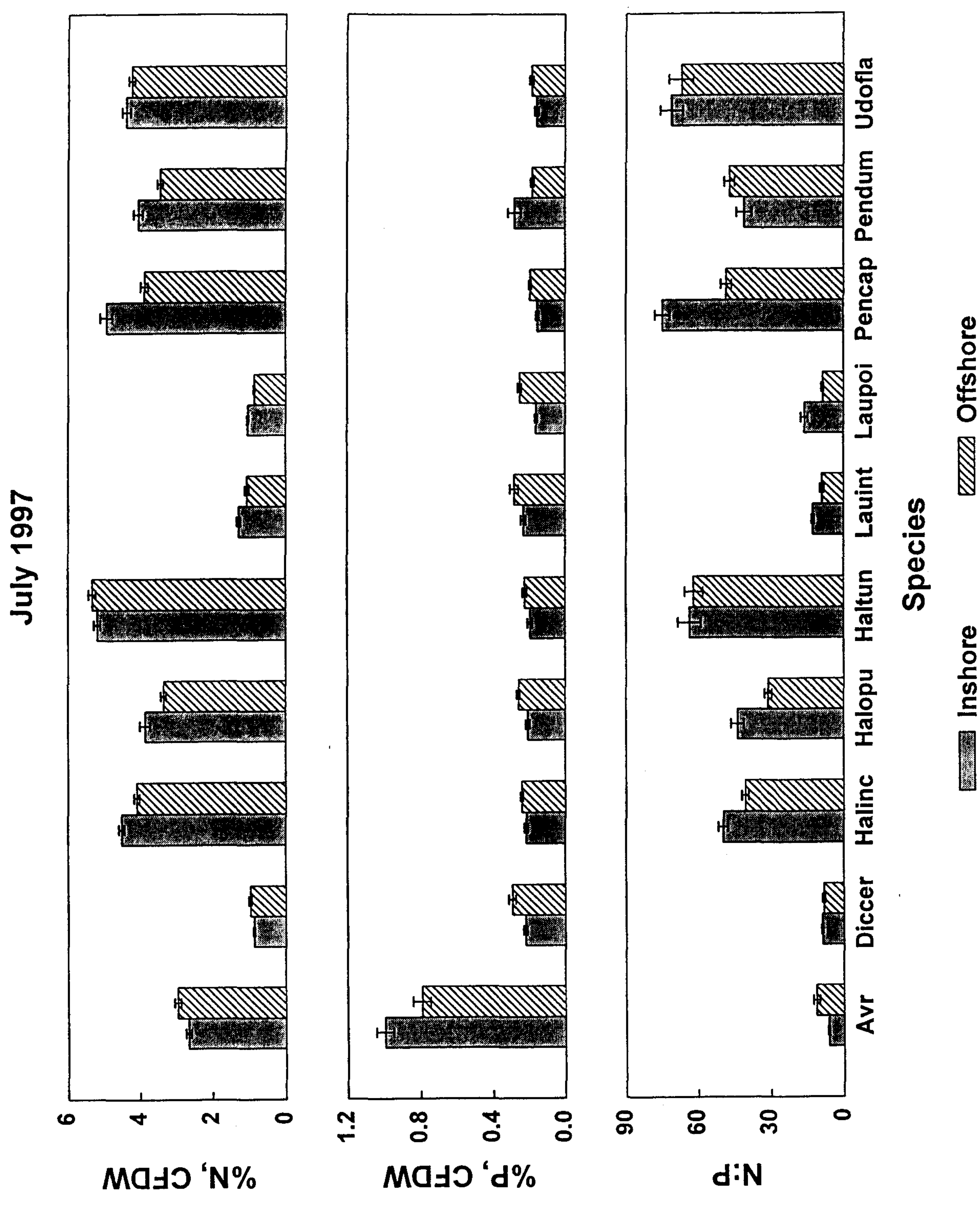

Fig. 194 Species means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for all inshore and offshore samples, July 1997. Codes for species are in Table 3.

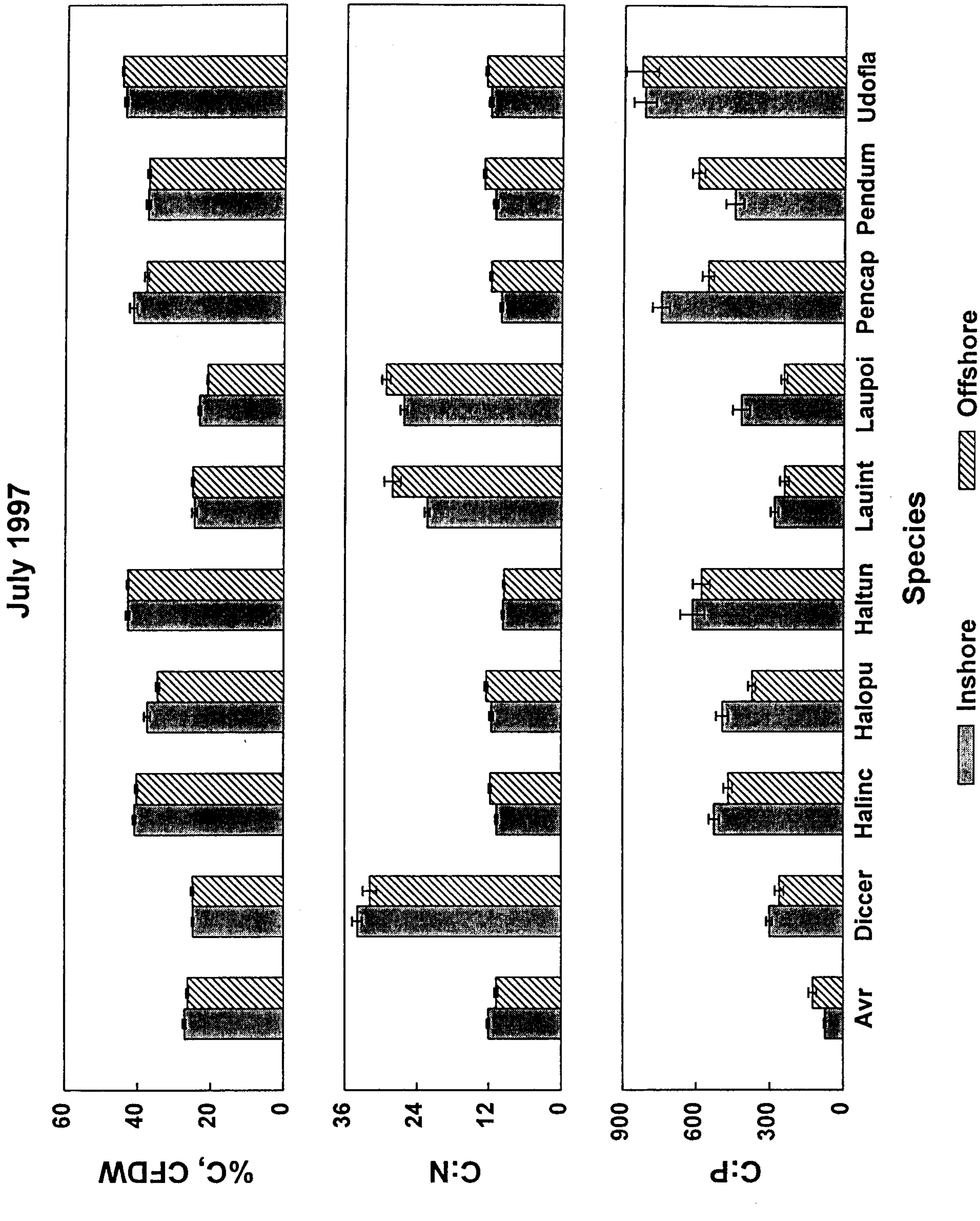

Fig. 195 Species means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for all inshore and offshore samples, July 1997. Codes for species are in Table 3.

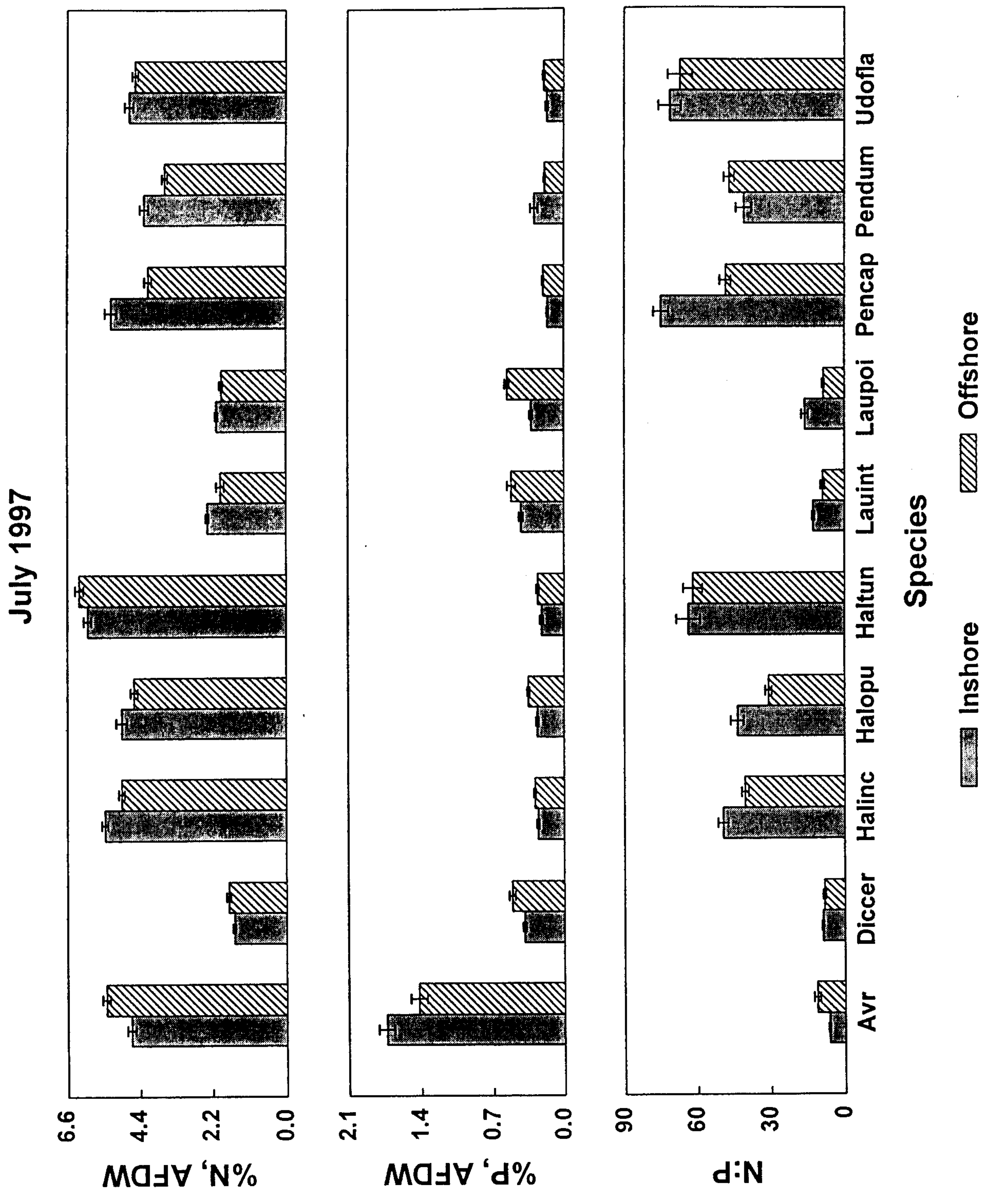

Fig. 196 Species means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for all inshore and offshore samples, July 1997. Codes for species are in Table 3.

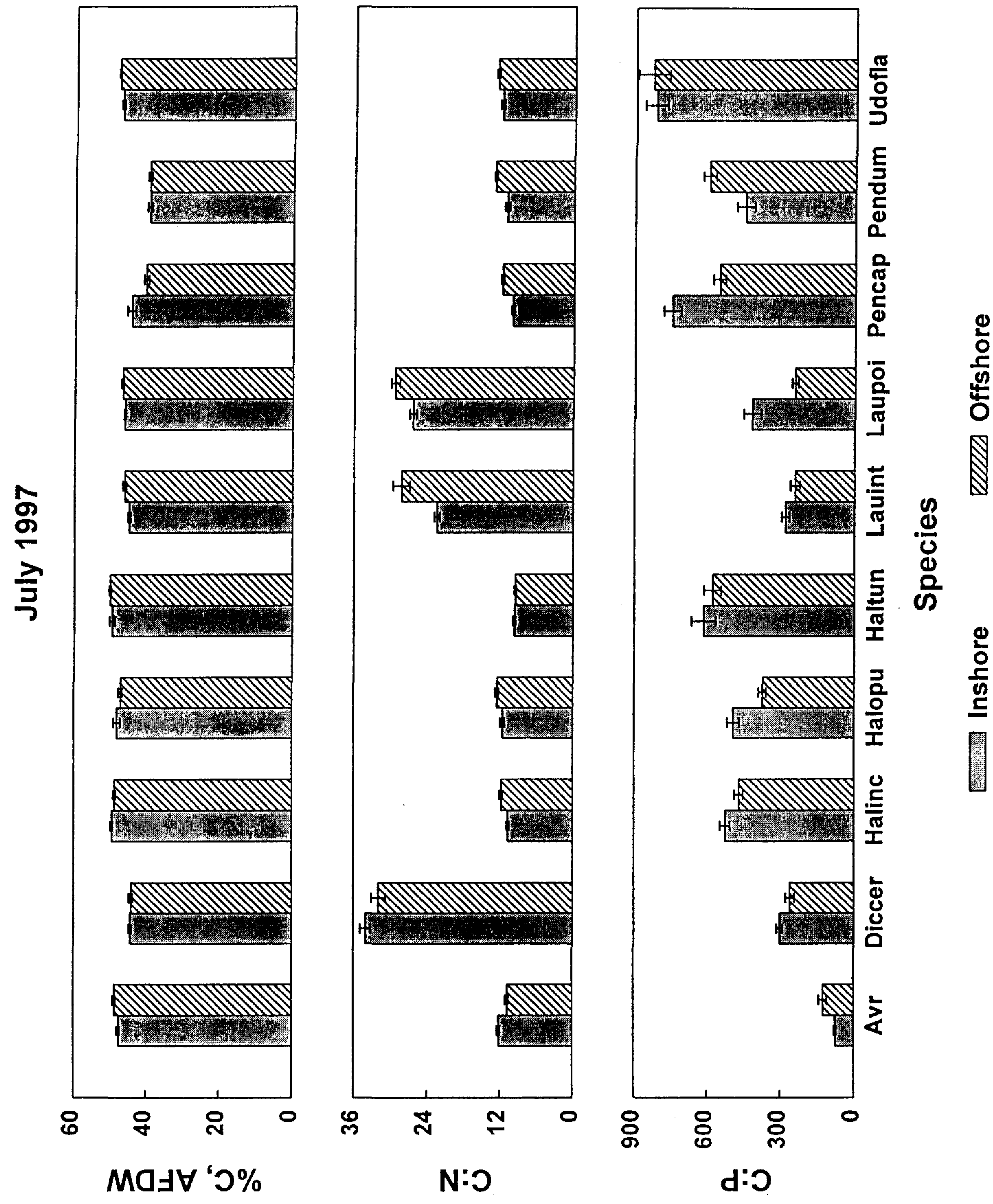

Fig. 197 Species means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for all inshore and offshore samples, July 1997. Codes for species are in Table 3.

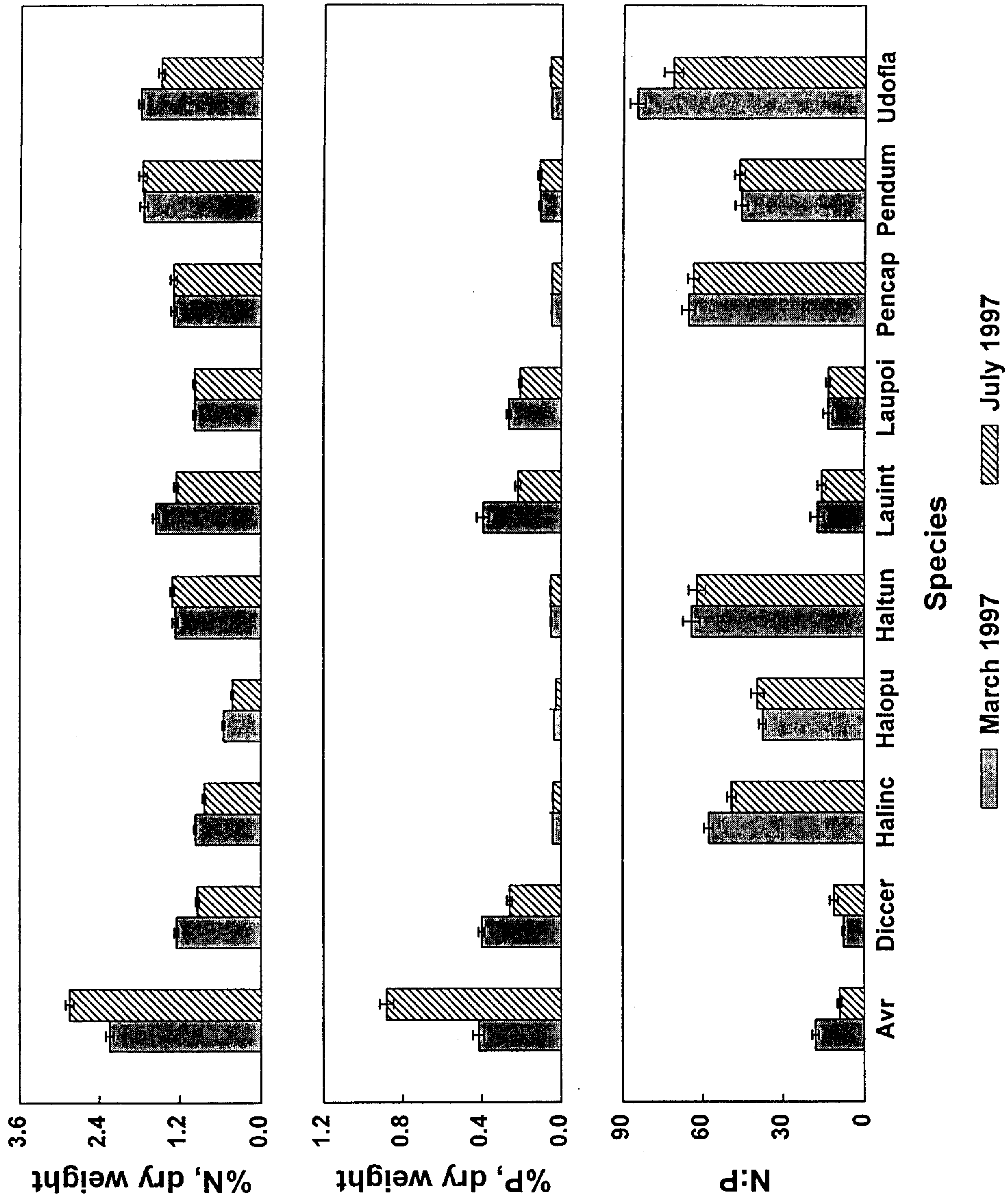

Fig. 198 Seasonal comparisons of species means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight basis, for all inshore and offshore samples, March and July 1997. Codes for species are in Table 3. Values for calcified species are omitted.

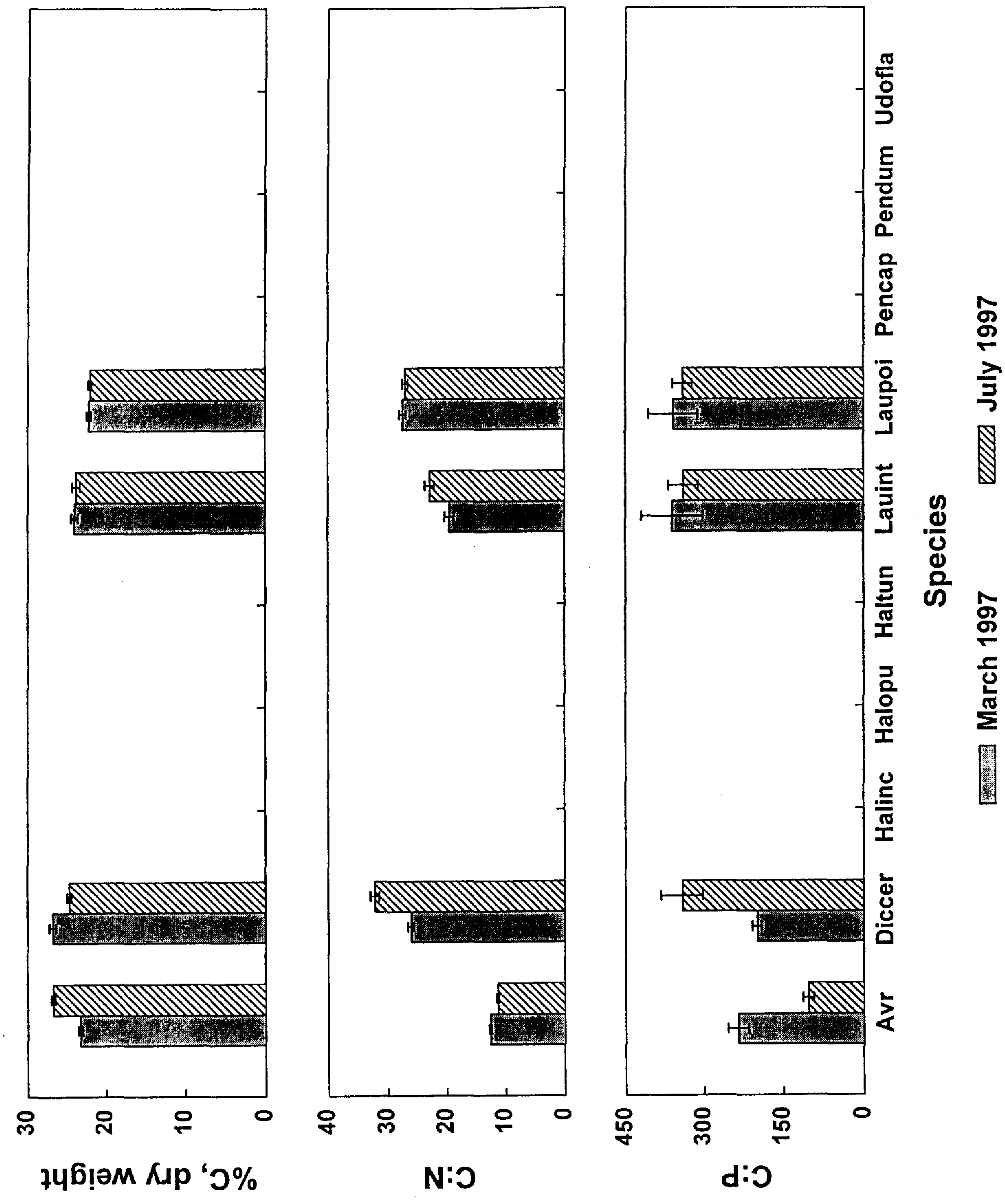

Fig. 199 Seasonal comparisons of species means (±SE) for %N, %P, and N:P ratio, on a carbonate-free dry weight basis (CFDW), for all inshore and offshore samples, March and July 1997. Codes for species are in Table 3.

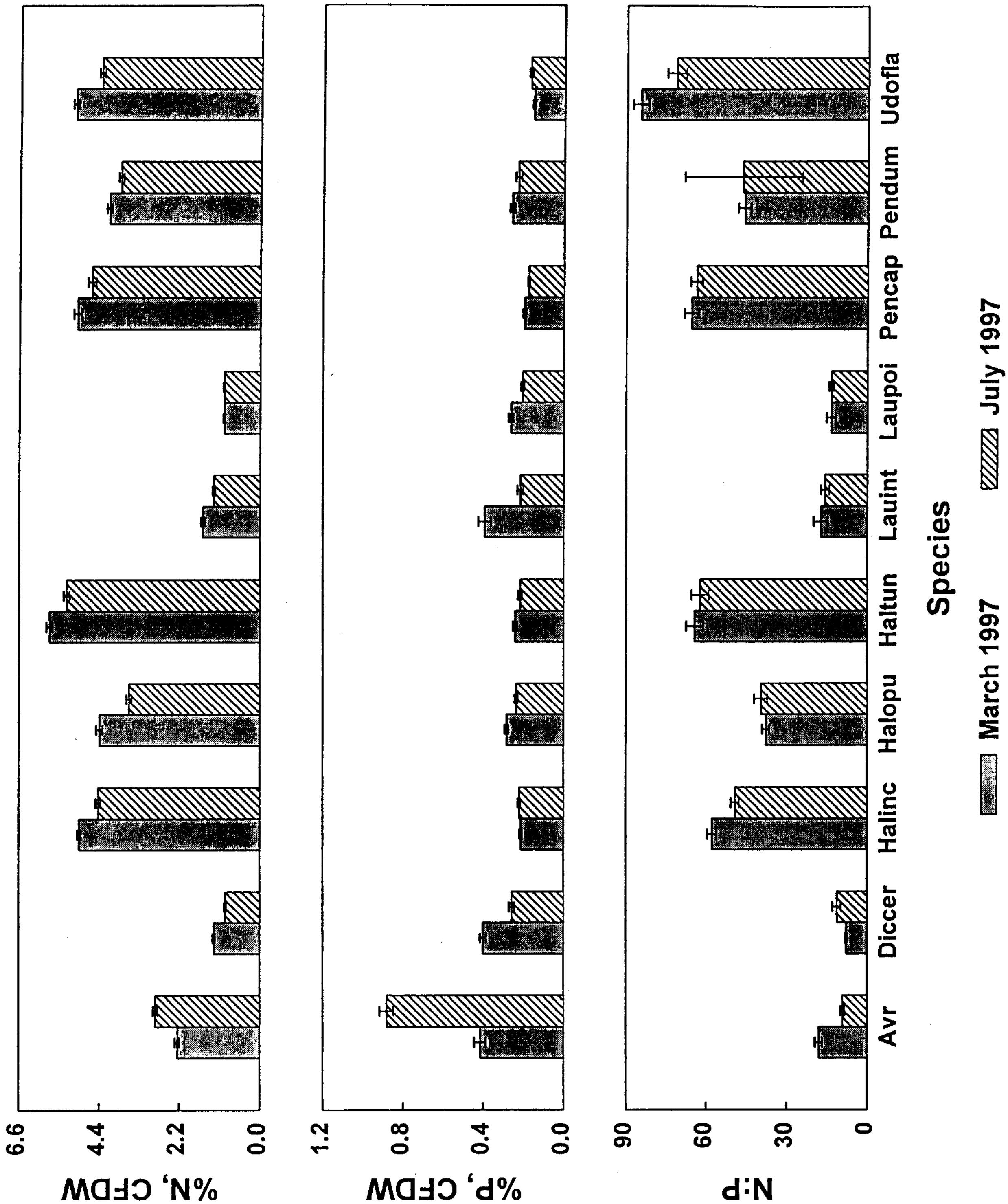

Fig. 200 Seasonal comparisons of species means (±SE) for %C, C:N ratio, and C:P ratio, on a carbonate-free dry weight basis (CFDW), for all inshore and offshore samples, March and July 1997. Codes for species are in Table 3.

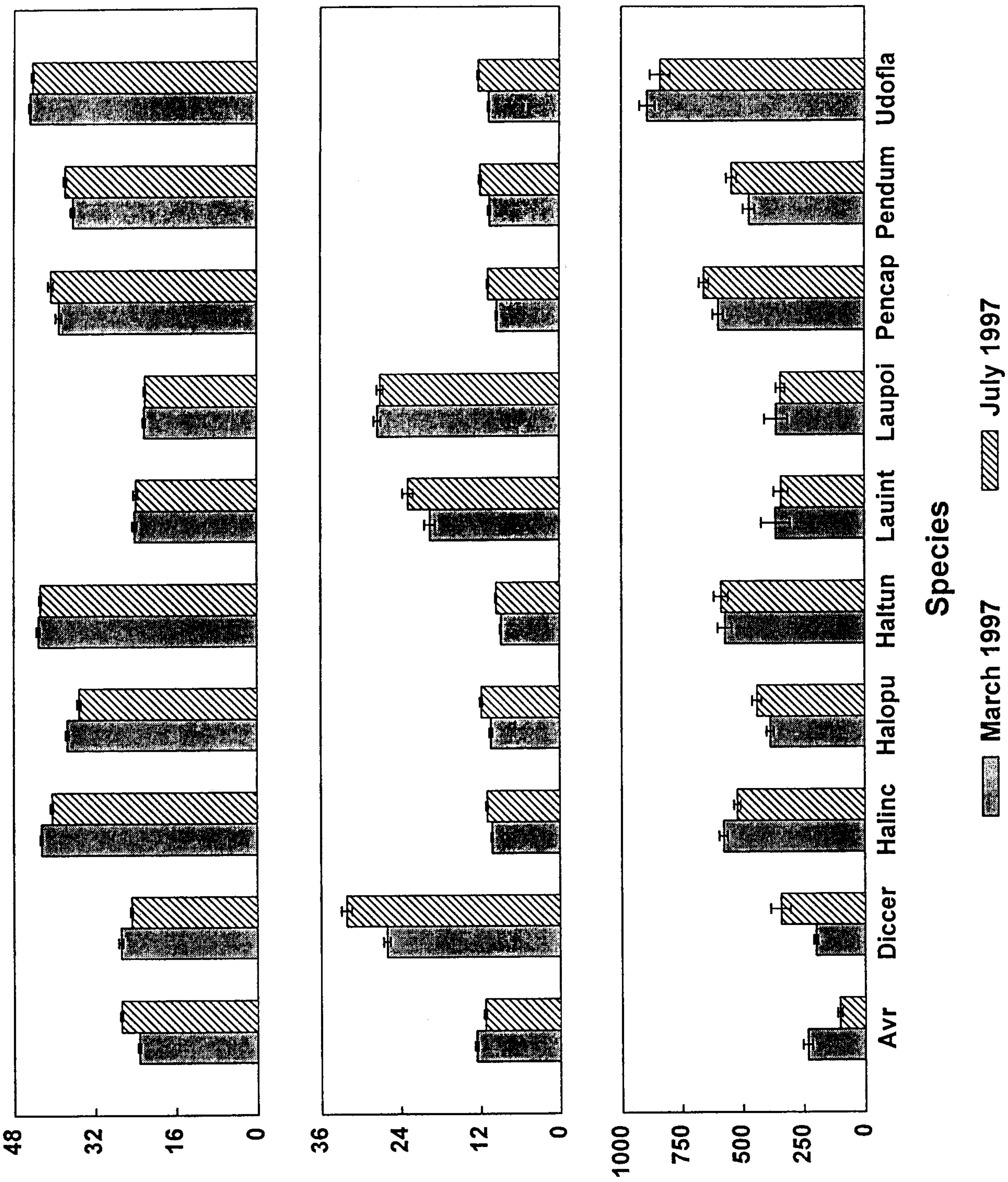

Fig. 201 Seasonal comparisons of species means (±SE) for %N, %P, and N:P ratio, on an ash-free dry weight basis (AFDW), for all inshore and offshore samples, March and July 1997. Codes for species are in Table 3.

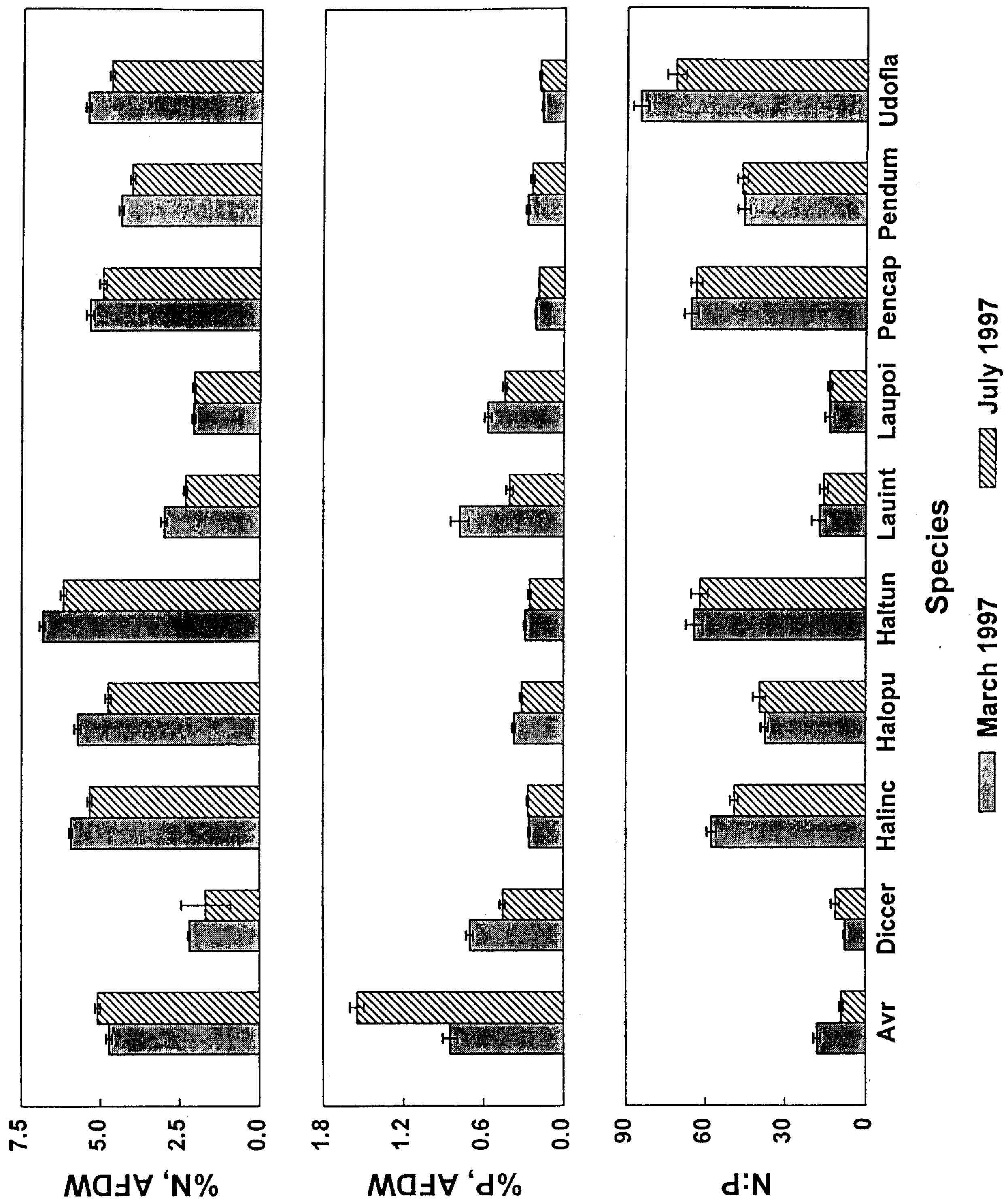

Fig. 202 Seasonal comparisons of species means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for all inshore and offshore samples, March and July 1997. Codes for species are in Table 3.

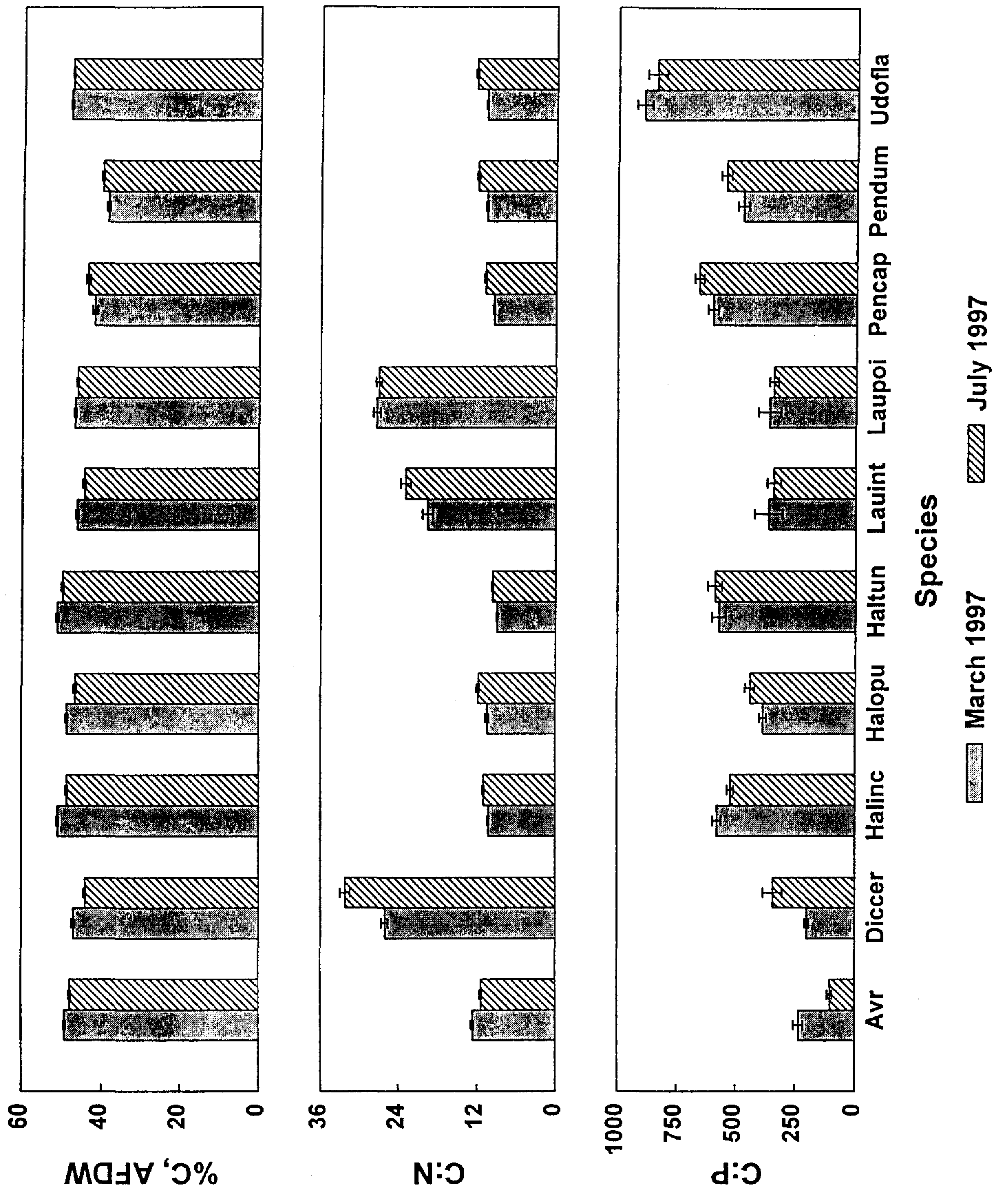

Fig. 203 Seasonal comparisons of species means (±SE) for %C, C:N ratio, and C:P ratio, on an ash-free dry weight basis (AFDW), for all inshore and offshore samples, March and July 1997. Codes for species are in Table 3.

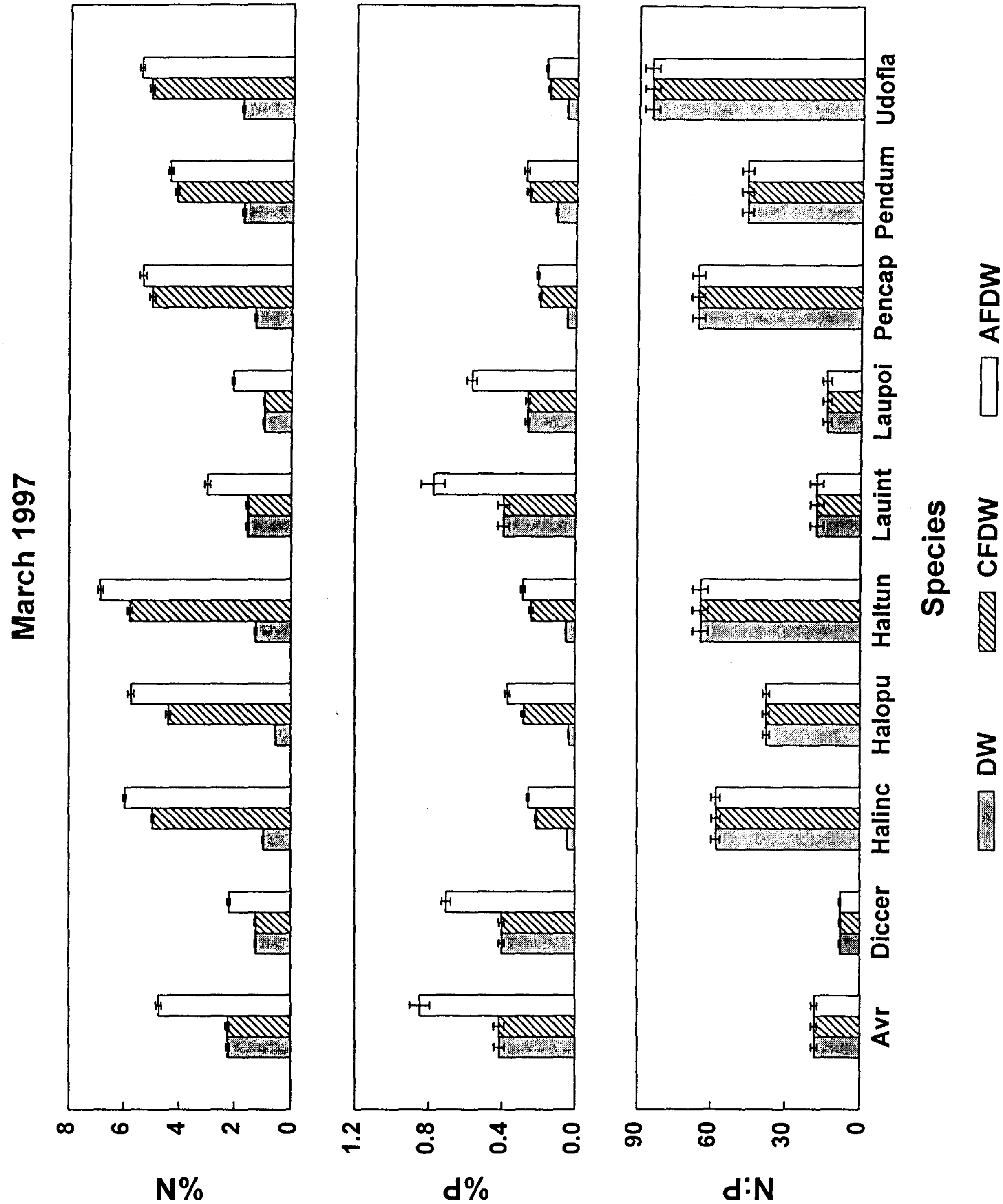

Fig. 204 Comparisons of species means (±SE) for %N, %P, and N:P ratio, on a dry weight, carbonate-free dry weight (CFDW), and ash-free dry weight basis (AFDW), for all inshore and offshore samples, March 1997. Codes for species are in Table 3.

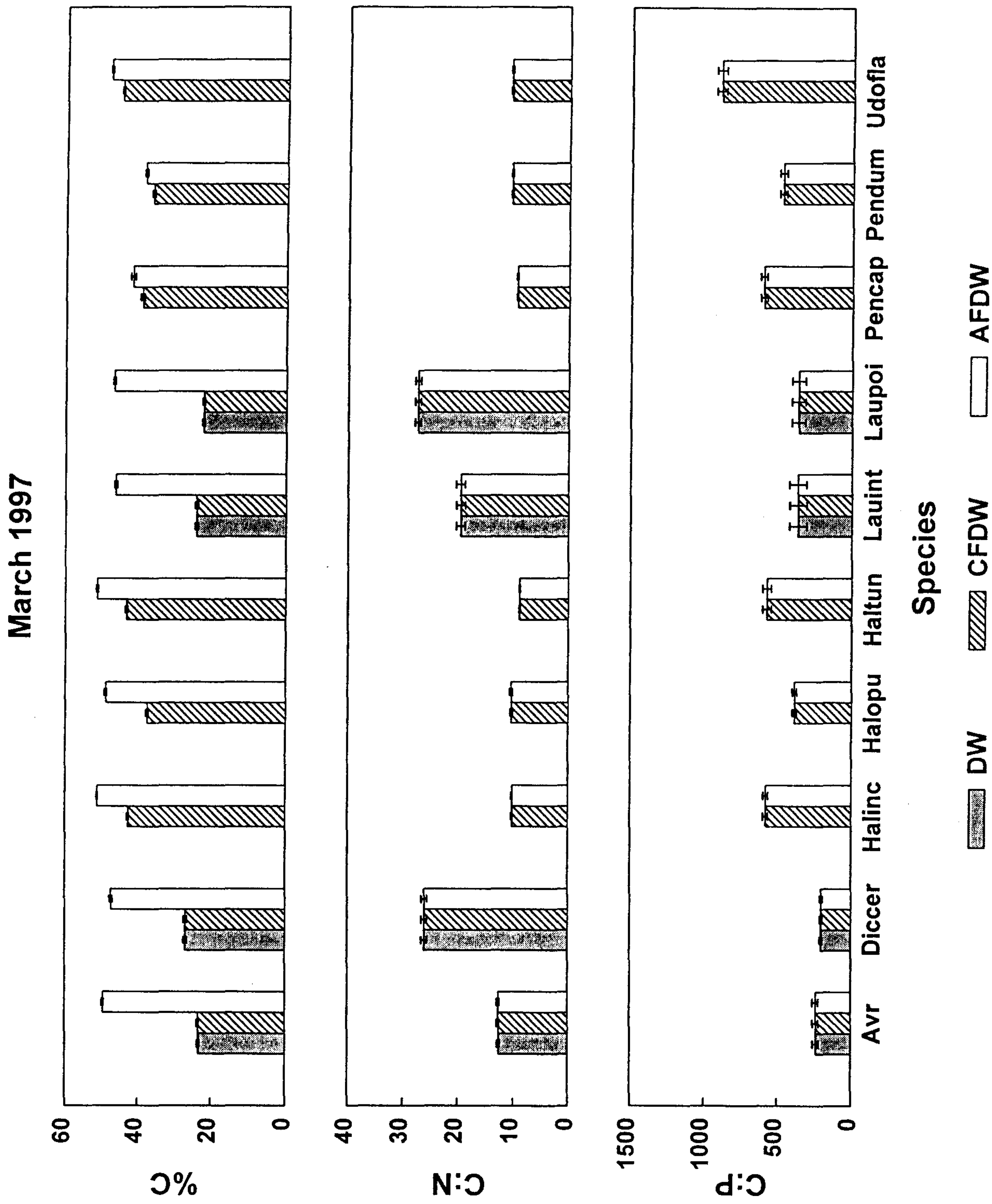

Fig. 205 Comparisons of species means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight, carbonate-free dry weight (CFDW), and ash-free dry weight basis (AFDW), for all inshore and offshore samples, March 1997. Codes for species are in Table 3. Dry weight values for calcified species are omitted.

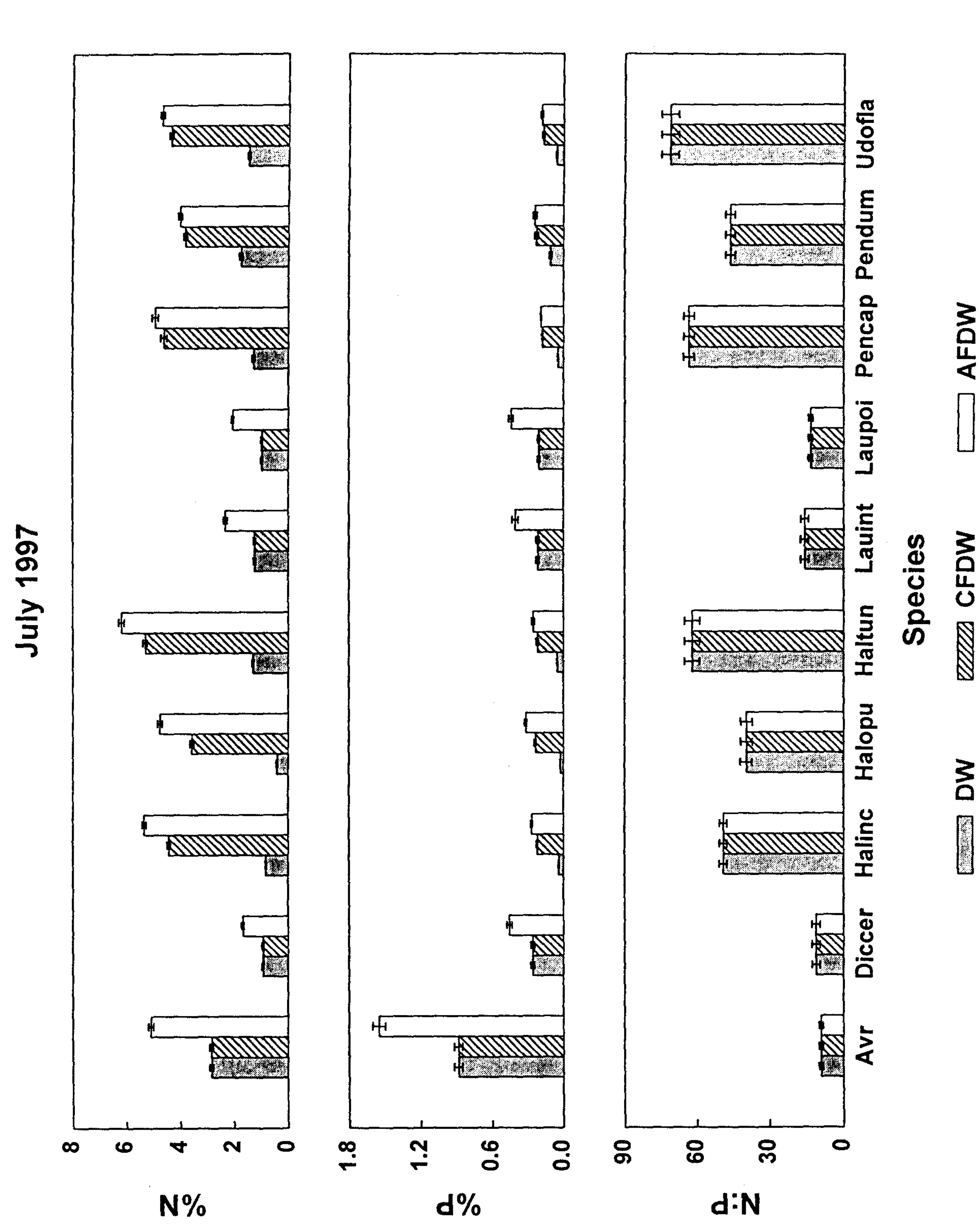

Fig. 206 Comparisons of species means (±SE) for %N, %P, and N:P ratio, on a dry weight, carbonate-free dry weight (CFDW), and ash-free dry weight basis (AFDW), for all inshore and offshore samples, July 1997. Codes for species are in Table 3.

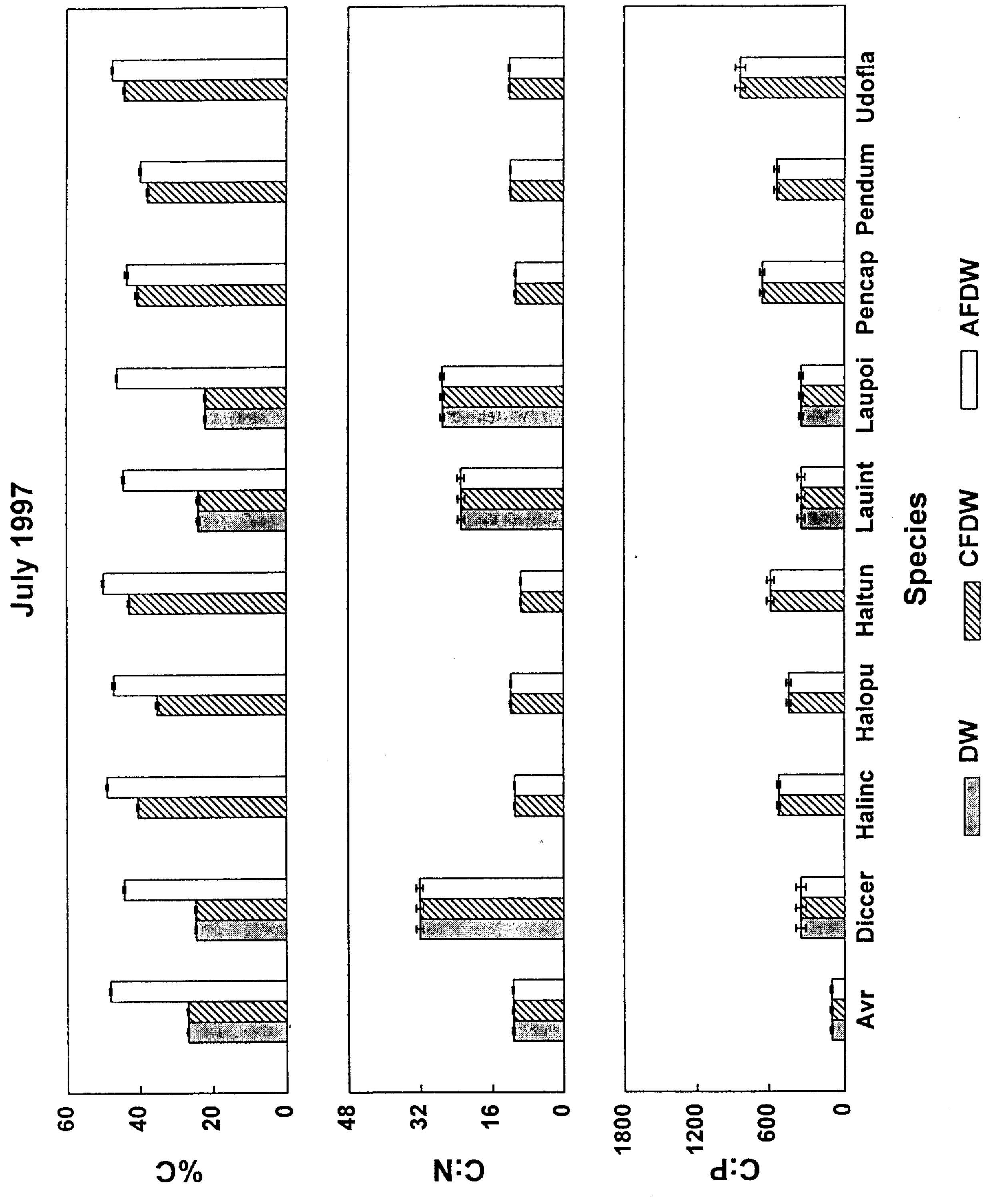

Fig. 207 Comparisons of species means (±SE) for %C, C:N ratio, and C:P ratio, on a dry weight, carbonate-free dry weight (CFDW), and ash-free dry weight basis (AFDW), for all inshore and offshore samples, July 1997. Codes for species are in Table 3. Dry weight values for calcified species are omitted.