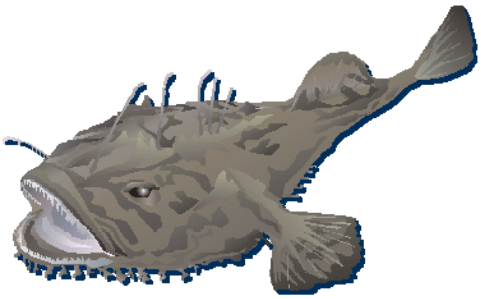

Final Report

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Critical diet and habitat shifts in New England monkfish (*Lophius americanus*): insights from stable isotopes and relation to biological condition

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A. EXECUTIVE SUMMARY

Despite their importance as one of New England's most valuable commercial fishery species, a great deal remains to be learned about monkfish life-history characteristics (e.g., habitat associations, diet preferences and relation of these to biological condition). This study was designed to fill some knowledge gaps in the basic biology of New England monkfish by examining diet and stable isotope signatures (tissue stable carbon and stable nitrogen ratios) of monkfish of various sizes (47-115 cm), from two different habitats (complex vs. mud) and two different management areas (NFMA vs. SFMA). The following major discoveries were made:

1) Large monkfish (primarily females > 80 cm) derive trophic and energetic benefits from living in complex habitats – Monkfish over 80 cm in complex habitats have higher trophic position and higher biological condition than similar sized monkfish in mud habitats. This preference may drive differences in length distributions among the two habitats, especially in the SFMA, where very few monkfish over 80 cm were found in mud habitats. This habitat preference should be considered when designing surveys.

2) Despite their assumed availability, herring were not found to be an important diet item for monkfish – Contrary to expectations, monkfish appear to prefer benthic prey over higher quality pelagic forage fish; biological condition (gutted k) was positively correlated with more benthic $\delta^{13}C$ values which correlate to higher $\delta^{15}N$ values and larger prey. For large monkfish, the bigger and more benthic the prey, the better.

3) Large diet differences exist among management areas (gadids in the north, skates in the south) – These differences likely reflect large scale differences in habitat with more complex habitat in the north (near Stellwagen) presumably favoring gadids. Regardless of these differences, monkfish primarily target fish prey over non-fish prey in both areas. The only notable non-fish prey in the diet was squid in the SFMA.

4) This study finds no evidence for an important role of cannibalism – In contrast to a recent study examining feeding in large monkfish which found a 5.6% incidence of cannibalism, only one out of 644 (0.16%) monkfish stomachs examined here was found to contain another monkfish.

B. BACKGROUND AND OBJECTIVES

Diet is a key factor in determining the productivity (growth and reproduction) and distribution of exploited fish species. While many fish species are considered generalists (e.g., cod which can "eat anything"), even these species have specific diet requirements which, when not met, either in terms of quantity or quality (e.g. prey type), may lead to reductions in growth, biological condition (e.g. weight-at-length or relative liver weight), and in extreme cases, failure to reproduce (Sherwood et al. 2007). It is therefore important to have up-to-date information on the feeding habits of commercially important fish species and how variations in these may contribute to variations in production and sustainability of managed fish species, as well as to variations in habitat associations and distribution. Such information is indeed one of the requirements for the implementation of an ecosystem-based approach to fisheries management, which has been strongly advocated for in recent years (Busch et al. 2003).

Monkfish (*Lophius americanus*) is a demersal (bottom) species which can be considered a generalist or opportunistic feeder (Link and Garrison, 2002). The diet of monkfish consists mostly of fish (Reid et al. 1999), but various invertebrates (e.g. crustaceans) are also of importance, particularly to younger smaller individuals (Smith et al. 2008). Recent results for the diet ontogeny (the sequence of diet shifts as fish get larger/older) of monkfish shows a progression from small crustaceans (e.g., mysids, *Neomysis Americana*, and northern shrimp, *Pandalus borealis*), to small fish (e.g., four bearded rockling, *Enchelyopus cimbrius*), and to larger fish (e.g., herring, *Clupea harengus*, and gadids) (Smith et al. 2008). Interestingly, diet results from this most recent study showed an importance of herring in the diet of larger monkfish, suggesting a link to pelagic production and that this importance varied on small spatial scales. Specifically, herring were more present in the diet of monkfish from more complex, edge bottom habitats than from uniform mud bottom habitats. This variation in feeding may reflect availability and may or may not have implications for condition and distribution of monkfish (i.e., via habitat choice). It is uncertain to what extent monkfish diet varies on larger spatial scales (e.g., the Northern Fishery Management Area, NFMA vs. the Southern Fishery Management Area, SFMA). Although monkfish diet does not seem to vary substantially on a seasonal level (Steimle et al. 1999), some results suggest that diet may vary on longer (e.g., decadal) time scales. The importance of fish in the diet of larger monkfish has been noted to vary among years with high importance in the 1970's to lower importance in the 1980's (Steimle et al.

1999). It is uncertain to what extent fish have regained importance in the diet of monkfish for the periods following 1990. Finally, there is some uncertainty regarding the importance of cannibalism in monkfish. Cannibalism is often assumed but very few incidences are actually observed with the possible exception of a study designed specifically to look at the diet of large monkfish (Johnson et al. 2008) which found a 5.6% frequency of cannibalism (699 stomachs). Laurenson (2005), on the other hand, found only one incident of cannibalism in 1056 stomachs for *Lophius piscatorius* (closely related) in Shetland. Overall, despite some advances, there is still scant and sometimes contradictory information on the diet requirements for monkfish.

Previous studies of feeding habits of monkfish, and virtually all other commercially exploited species for that matter, come from stomach content analyses (e.g., Link and Garrison 2002). While this approach can yield valuable results in terms of what prey *can* be present in the diet, there are always concerns regarding the validity of inferring diet from limited sampling. For instance, gut contents may only provide a "snap shot" in time of that day's feeding events which may or may not be representative of average feeding habits over an entire season for example. This problem can usually be overcome by very intensive sampling effort (i.e., by maximizing sampling dates and areas) but at great cost.

Another less expensive and less sampling-intensive method exists for inferring diet in fish. This technique, known as the stable isotope approach, exploits variations in the relative abundance of naturally occurring isotopes of carbon and nitrogen to infer what a particular fish consumed over an integrated (months) feeding period (Sherwood & Rose 2005). In essence, with the stable isotope approach, "*you are what you eat*". The tradeoff is that stable isotopes allow for the inference of feeding habits not on a prey-specific basis, but on a "trophic niche" specific or general basis; specifically, fish can have stable isotope values indicative of feeding on pelagic to benthic (bottom) prey, and from low to high trophic position (i.e., where they are in the food chain). Because stable isotopes measure the assimilated tissue that is derived from the diet, it is a more accurate measure of the importance of each prey source than traditional stomach content analyses. See figure A for a conceptual representation of this approach and how results are interpreted. In essence, stable isotopes allow us to "fingerprint" where fish are in their respective food webs with very low sampling effort and cost. Stable isotopes combined with more traditional gut content techniques represents a very powerful and state-of-the-art approach to modern diet and feeding studies.

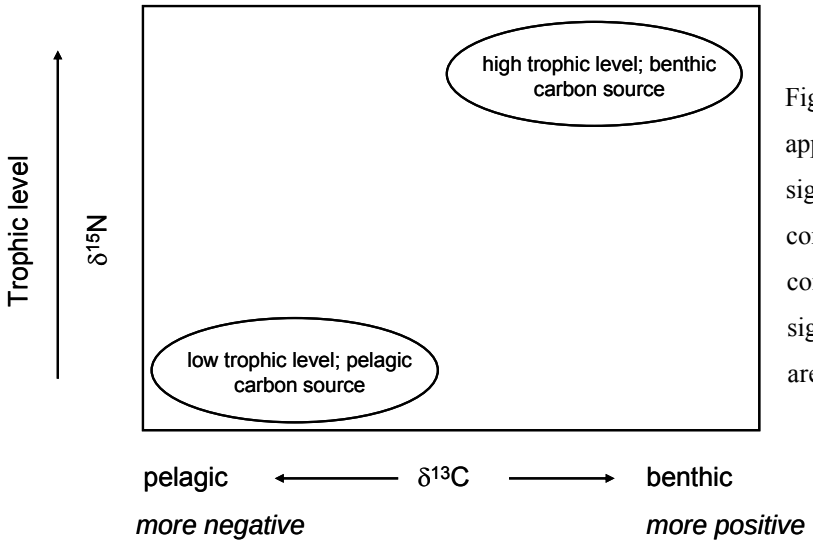

Figure A. Schematic of the dual isotope approach. Individual fish with isotope signatures falling in the top, right-hand corner are high trophic level, benthic consumers, and individual fish with signatures in the bottom, left-hand corner are low trophic level pelagic consumers.

The purpose of this study was to apply the stable isotope approach, in combination with stomach contents, to characterize diet variability (ontogenetic and spatial) in monkfish from US northeast waters. Stable isotopes have the added benefit of providing a continuous measure of diet that can be related to other biological parameters including growth and condition. An additional goal of this study was to explore relationships between diet parameters (i.e., stable isotopes primarily) and condition indices (as indicators of energetic fitness; see Sherwood et al. 2007 for comparative approach) to gain insights into what may constitute optimal feeding conditions for monkfish of various sizes. Specifically this study set out to explore:

1. Ontogenetic patterns in monkfish feeding – It was hypothesized that monkfish rely heavily on fish and potentially cannibalism as they get larger.
2. Large scale patterns in monkfish feeding (i.e., NFMA vs. SFMA) – No specific hypothesis.
3. Fine scale patterns in monkfish feeding (mud vs. complex bottom habitats) – It was hypothesized that monkfish would have access to a wider range of optimal piscine prey in complex habitats (e.g., energy rich herring as seen by Smith et al. 2008).
4. Relationships between monkfish diet and monkfish condition – It was hypothesized that monkfish condition would be positively related to pelagic diets (since pelagic forage fish represent a high energy prey source for many predator species).

C. METHODS

C.1. Sampling

Sampling was carried out at 4 sites (see Figure 1) over 8 sampling days in the summer of 2006 (July - September) and included 52 gillnet sets (12", ranging in soak time from 3 to 4 days) in 2 different habitats (rocky/ledge [complex] bottom vs. soft [mud] bottom) from two different management areas of the US northeast (the Southern Fishery Management Area, or SFMA, and the Northern Fishery Management Area, NFMA) selected by our fishing partners. A total of 644 monkfish ranging in size from 47 to 115 cm were captured. Total length (cm), total weight (g), liver weight (g), gonad weight (g), stomach weight (g), gutted weight (g) and sex were recorded for all monkfish captured; a small muscle sample (~ 1g, tail) from each monkfish was saved (frozen) for stable isotope analysis (SIA).

C.2. Stomach Content Analysis

Diet analysis was completed in the laboratory (on thawed stomachs) and included identification of prey items to family for fish, and prey size determinations (length to nearest mm, and weight to nearest g, where possible) were also made.

C.3. Stable Isotope Analysis

All samples (thawed muscle samples) were prepared in the laboratory for SIA (dried at 70ºC until constant weight, and ground to a fine powder) and sent to the Colorado Plateau Stable Isotope Laboratory for analysis (stable carbon and stable nitrogen isotope ratios, $\delta^{13}C$ and $\delta^{15}N$, respectively); SI results are presented in delta notation or parts per thousand (‰) deviation from a standard (Pee Dee belemnite limestone for $\delta^{13}C$ and nitrogen in air for $\delta^{15}N$).

C.4. Data Handling

Eleven variables have been included in the analyses and include two site variables (management area and habitat, both fixed effects with two treatment levels: 'NFMA' vs. 'SFMA' and 'complex' vs. 'mud', respectively), length (as either a continuous variable or a fixed effect [5 cm length interval]), four feeding variables (relative stomach weight [stomach k], $\delta^{13}C$, $\delta^{15}N$, and prey length), and four condition variables (liver somatic index [LSI], gonadal somatic index [GSI], gutted condition factor [gutted k], and CN ratio, from stable isotope analysis). Derived variables were calculated as follows:

(i) Stomach k = stomach weight (g) / length^3 × 1000

(ii) LSI = liver weight (g) / gutted weight (g) × 100

(iii) GSI = gonad weight (g) / gutted weight (g) × 100

(iv) Gutted k = gutted weight (g) / length^3 × 100

Prior to analyses, LSI and GSI were log (10) transformed to reduce heteroscedasticity. In addition to these 11 variables, 7 more diet related variables were calculated to address taxonomic variability (classified to family for fish) in the diet. Partial fullness index (PFI, a length-standardized volumetric measure for prey importance) values were calculated separately for cephalopods ('ceph', squids), clupeids ('clup', herring), cottids ('cott', sculpins), crustaceans ('crus', shrimp and lobster), gadids ('gadi', cod, haddock and hakes), pleuronectids ('pleu', plaice, halibut and unidentified flatfish), and rajids ('raji', unidentified skates), as:

(v) $\mathrm{PFI}_{ij} = W_{ij}/L_j \times 1000$

where W_{ij} is the weight (g) of prey taxa i in the stomach of monkfish j and L_j is the length of monkfish j.

C.5. Statistics

Length distributions were compared among management areas (region) and habitats using analysis of variance (ANOVA) and student's t-tests (each sex separately). Weight (total, log 10 transformed) versus length (log 10 transformed) relationships were generated for each management × habitat combination (by sex) using linear regression. Among region and habitat differences in overall diet and diet ontogeny were visualized using pie charts and stacked area graphs. Ontogenetic, regional and habitat patterns in each of the 4 feeding and 4 condition index variables were visualized by plotting mean ± 1 SE values by 5 cm length interval (each sex separately). The influence of management area, habitat, length interval, as well as interactions among all these terms, on all of the feeding and condition variables was explored by ANOVA. The influence of feeding variables on condition indices was assessed by multiple linear regression. Length versus δ^{15}N relationships by management area and habitat were explored by linear regression. Mean prey size was compared among management areas and habitats by ANOVA (females only). Finally, the influence of habitat on the δ^{13}C versus δ^{15}N relationship

was explored using Analysis of covariance (ANCOVA), with $\delta^{15}N$ as the dependent, $\delta^{13}C$ as the covariate and habitat as a fixed factor (the interaction was also tested).

D. RESULTS AND DISCUSSION

D.1. Length distributions and length – weight relationships

Monkfish length distributions for each management area, habitat and sex are shown in Fig. 2. There was a significant (ANOVA) effect of both management area ($F_{1,501} = 10.1$, $p < 0.01$) and habitat ($F_{1,501} = 11.2$, $p < 0.001$) on mean length for females; mean length was significantly larger in the NFMA and in complex habitats. There was also a borderline significant interaction effect ($F_{1,501} = 3.2$, $p = 0.07$) suggesting the difference among habitats is more pronounced in the SFMA. No such relationships were found for male monkfish. Length – weight relationships (LWR) are shown in Fig. 3. Scaling coefficient (*b*) values (from the LWR) were generally higher for females in the SFMA (significant only for complex habitats) but not for males. While not significant, *b* values were highest in complex habitats (both sexes) in the SFMA and highest (both sexes) in mud habitats in the NFMA.

D.2. Predator size – prey size relationships

Monkfish (predator) size versus prey size relationships are shown in Fig. 4. No significant relationships were found reinforcing the finding (Scharf et al. 2000) that monkfish have very broad trophic niches due to low gape limitation. Despite this, mean prey size did vary among management areas (ANOVA: $F_{1,89} = 20.7$, $p < 0.0001$) and habitats (ANOVA: $F_{1,89} = 6.3$, $p < 0.05$) such that mean prey size was larger in the NFMA and in mud habitats for female monkfish only (Fig. 5).

D.3. Diet trends

The overall diet of female and male monkfish in terms of broad taxonomic groups is shown in Fig. 6 (by management area and habitat). There were major differences in diet among monkfish from the NFMA and SFMA. NFMA monkfish diet (both sexes) was dominated by gadids (cod, haddock and hakes), while diet of monkfish in the SMFA was made up predominantly of rajids (skates and rays). Cephalopods (squid) made up a large part of the diet in the SFMA but were absent from the diet in the NFMA. With the possible exception of cottids (sculpins) which made up a significant portion of the diet in male monkfish, particularly from complex habitats, all

other taxa made up only minor portions of the overall diet. Interestingly, herring, despite their abundance in the GOM and Georges Bank (Overholtz & Friedland 2002), and contrary to the findings of Smith et al. (2008), were not very well represented in the diet of monkfish in any case. Finally, it is interesting also to note that monkfish (i.e., cannibalism) made up a very insignificant portion of the diet. Cannibalism has been found to be an important feeding mode for larger monkfish (Johnson et al. 2008), yet this study, similar to a study by Laurenson (2005), finds the incidence of cannibalism in monkfish to be extremely low (only 1 consumed monkfish was found throughout the whole study examining 644 stomachs: a 483 mm individual was found in a 610 mm monkfish). In terms of major habitat differences, gadids, although not very well represented in the diet of SFMA monkfish, were more prevalent in complex habitats in the SFMA (for males).

Ontogenetic patterns in diet for both sexes (by management area and habitat) are shown in Fig. 7. Cottids and cephalopods, neither of which made up large portions of the overall diet, were much more important for smaller monkfish (< 55 cm). Gadids were prevalent over all sizes larger than 55 cm in the NFMA and showed up in the diet in the SFMA (males in complex habitat) at 60 cm. The diet of monkfish in the SFMA was fairly uniformly made up of rajids over most size classes.

D.4. Stable isotope signatures

Mean stable isotope signatures ($\delta^{13}C$ and $\delta^{15}N$) are tabulated by management area, habitat, and 5 cm length interval in Tables 1 (females) and 2 (males) and shown in Figs. 8 (females) and 9 (males). $\delta^{15}N$ was significantly positively related to length in female monkfish from all areas and habitats (Tables 5 and 6). Interestingly, the coefficient (slope) for this relationship was much higher in complex habitats from both areas than from mud habitats. Note how mean $\delta^{15}N$ values spike sharply after 75 cm in complex habitats only (Fig. 8). These patterns suggests that monkfish use complex habitats to complete their diet ontogeny towards higher trophic levels ($\delta^{15}N$ is an indicator of trophic level). Similar to this result, plots of $\delta^{13}C$ versus $\delta^{15}N$ for female monkfish from both areas (Fig. 10) show steeper slopes for complex habitats than for mud habitats (interaction term from ANCOVA is significant for NFMA; see figure caption). In other words, as monkfish become more benthic (higher $\delta^{13}C$ values), they attain higher trophic positions in complex habitats than in open mud habitats. The fact that differences in $\delta^{15}N$ values exist among adjacent habitats separated by only small distances suggests that female monkfish

actively select habitats and remain (most of the time) in these habitats. If they moved regularly among the habitats, $\delta^{15}N$ difference would be averaged out and the results shown in Figs. 8 and 10 would not have been as apparent (stable isotope signatures represent time-averaged feeding habits on the order of months). No similar relationships between $\delta^{15}N$ and length and $\delta^{15}N$ and $\delta^{13}C$ were found for male monkfish likely due to a smaller size range.

Stable carbon isotope signatures ($\delta^{13}C$) were also positively related to length in all cases for females only (Table 5 and Fig. 8). In addition, $\delta^{13}C$ varied significantly among management areas (but not among habitats) for both sexes (Table 5). A significant Area × length interval interaction for females suggests that the area differences in $\delta^{13}C$ values are not due to baseline differences (i.e., differences in $\delta^{13}C$ at the base of the food web) in $\delta^{13}C$ but rather to differences in feeding preferences and/or prey availability. This interaction is also evident in Fig. 8 with the difference being most pronounced over medium size ranges (~ 60-80 cm); smaller (< 60 cm) and larger (> 80 cm) female monkfish from both areas had similar $\delta^{13}C$ values suggesting more similar feeding habits over these size ranges. The difference over medium sizes is likely due to SFMA monkfish feeding mostly on rajids (mostly benthic) and NFMA monkfish feeding mostly on gadids (which tend to have intermediate $\delta^{13}C$ values). Again, similar to fixed differences in $\delta^{15}N$ above (by habitat), area differences in $\delta^{13}C$ suggest that little within season movement is taking place between the SFMA and the NFMA for medium-sized female monkfish (otherwise, $\delta^{13}C$ differences would have been obscured).

D.5. Feeding – condition relationships

Significant linear relationships among the 4 condition variables and 4 feeding variables are shown in Table 7. When length was taken into account (all indices covaried with length), gutted k was significantly positively related to $\delta^{13}C$, $\delta^{15}N$ and stomach k, log LSI was significantly related to $\delta^{13}C$ (negatively) and $\delta^{15}N$, log GSI was significantly negatively related to $\delta^{13}C$, stomach k and prey size, and CN was significantly negatively related to $\delta^{13}C$ and positively related to $\delta^{15}N$. The condition endpoint most dependent on feeding parameters was gutted k (in terms of the most number of relationships and highest R^2 values). This matches with the visual representation shown in Fig. 8; e.g., when $\delta^{15}N$ was high for large monkfish in complex habitats, gutted k was also high for large monkfish in complex habitats. In fact, the sudden rise in trophic

position ($\delta^{15}N$) in monkfish from complex habitats corresponded to a sudden rise in gutted k and log LSI, leading to the speculation that this diet/habitat shift may have important (beneficial) energetic consequences similar to what has been described for diet shifts in other species (Sherwood et al. 2002, Sherwood & Rose 2007). In addition, an energetic advantage to foraging in complex habitats may be what drives differences in length distributions (particularly for the SFMA, Fig. 2). It is beyond the scope of this study to determine what may be causing this potential benefit, but it likely has to do with shelter seeking behavior of monkfish and/or their prey. For example, smaller monkfish may be more efficient at hiding in mud and larger monkfish may be more suited to sit-and-wait type tactics in complex habitats. Conversely, only large monkfish may be able to target larger fish which themselves may be foraging in complex habitats. The behavioral components of the trophic shift described here, one that seems to be determining the distribution of monkfish on the bottom, should be the topic of a future study.

E. CONCLUSIONS

This study has provided important new insights into monkfish feeding behaviors and habitat preferences. Industry members have known for some time that large monkfish tend to prefer hard (i.e., complex) bottom and that trawl surveys which do not sample these habitats may be underestimating the abundance of old/large females in the population. **This study supports the conclusion that large monkfish (primarily females) derive trophic and energetic benefits from living in complex habitats** thereby confirming the observations of fishermen. Medium-sized monkfish, on the other hand, appear to do better in mud habitats. This preference by large monkfish for complex bottom should be factored into future surveys and further studies may examine the behavioral and energetic reasons for habitat associations. This important finding would not have been possible without the help of stable isotope analysis which allows for time-integrated depictions of habitat and diet preferences; stomach contents alone would likely have missed this finding. Other important findings are as follows:

- **Despite their assumed availability, herring were not found to be an important diet item for monkfish.** Contrary to expectations, condition was positively correlated with benthic prey and not pelagic prey (i.e., herring). In many cases large prey size (1 large prey is less expensive to catch than 10 small prey) and the ability to capture prey (e.g., less evasive or in

the 'right place at the right time') override quality arguments (Sherwood et al. 2002) and this may be why monkfish appear to do better with demersal prey like cod and skates.

- **Monkfish currently rely heavily on fish prey.** This result suggests that fish prey have rebounded in importance since the 1980's (Steimle et al. 1999). The only non-fish prey of notable importance is squid in the SFMA.
- **This study finds no evidence for an important role of cannibalism.** Only 1 in 644 stomachs (0.16% frequency compared to 5.6% found by Johnson et al. 2008) was found to contain a monkfish. This doesn't rule out the possibility that cannibals may feed less frequently and therefore many instances of cannibalism may have been missed. $\delta^{15}N$ results (high values for large monkfish) are consistent with cannibalism, which would undoubtedly boost trophic position, however a number of alternative prey (e.g., large cod) may also drive this trophic shift.
- **This study reveals large feeding differences among the NFMA and SFMA.** NFMA monkfish rely heavily on gadids and SFMA monkfish rely heavily on rajids. Stable isotopes (more benthic in the SFMA and more pelagic in the NFMA) are consistent with these diet results.

F. ACKNOWLEDGEMENTS

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Table 1. Summary data (means, standard error and sample size) for various feeding and condition indices for female monkfish from two management areas (NFMA and SFMA), two habitats (complex and mud) and by 5 cm length interval.

			Feeding indices												Condition indices											
		Length interval	Stomach K			$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)			Prey length (mm)			log LSI			log GSI			FCF			CN		
Area	Habitat	(cm)	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N
												Females														
NFMA	Complex	55	0.52	0.07	3	-18.02	0.36	3	14.54	0.10	3	0	0	0	0.72	0.03	4	0.81	0.47	4	1.24	0.03	4	3.16	0.05	3
NFMA	Complex	60	1.07	0.29	9	-18.05	0.14	9	14.43	0.12	9	280	42	3	0.79	0.07	9	0.72	0.10	9	1.33	0.05	9	3.17	0.03	9
NFMA	Complex	65	0.59	0.08	31	-18.00	0.06	31	14.50	0.07	31	246	42	6	0.72	0.02	32	0.78	0.08	31	1.25	0.05	32	3.15	0.01	31
NFMA	Complex	70	0.50	0.03	41	-17.94	0.07	41	14.72	0.07	41	167	22	5	0.79	0.02	40	0.94	0.07	39	1.17	0.01	40	3.14	0.01	41
NFMA	Complex	75	0.50	0.07	30	-17.87	0.08	30	14.66	0.10	30	195	62	3	0.71	0.04	29	0.93	0.07	29	1.18	0.02	29	3.12	0.01	30
NFMA	Complex	80	0.54	0.06	11	-17.87	0.11	11	14.71	0.17	11	242	43	4	0.63	0.06	12	0.95	0.15	11	1.15	0.04	12	3.15	0.02	11
NFMA	Complex	85	0.61	0.18	8	-17.62	0.16	8	15.04	0.21	8	450	.	1	0.67	0.03	8	0.76	0.07	8	1.04	0.04	8	3.12	0.02	8
NFMA	Complex	90	0.59	0.08	4	-17.49	0.17	4	15.38	0.21	4	310	.	1	0.58	0.09	4	0.63	0.06	4	1.14	0.07	4	3.14	0.02	4
NFMA	Complex	95	0.51	0.04	4	-17.22	0.37	4	15.24	0.38	4	230	.	1	0.56	0.04	4	0.71	0.05	4	1.03	0.03	4	3.13	0.01	4
NFMA	Complex	100	0.33	0.07	3	-17.05	0.32	3	15.67	0.21	3	.	.	.	0.57	0.05	3	0.74	0.06	3	0.89	0.14	3	3.15	0.04	3
NFMA	Mud	50	0.60	0.04	2	-17.42	.	1	15.05	.	1	.	.	.	0.58	0.08	2	0.05	0.09	2	1.30	0.01	2	3.22	.	1
NFMA	Mud	55	0.52	0.07	3	-17.98	0.28	3	14.75	0.28	3	.	.	.	0.66	0.12	3	0.90	0.35	3	1.45	0.18	3	3.14	0.05	3
NFMA	Mud	60	1.02	0.36	14	-18.00	0.14	11	14.79	0.11	11	298	47	5	0.69	0.05	15	0.49	0.05	15	1.30	0.03	15	3.17	0.02	11
NFMA	Mud	65	0.64	0.09	24	-18.01	0.08	23	14.66	0.10	23	321	66	4	0.72	0.04	26	0.92	0.12	26	1.23	0.02	26	3.14	0.01	23
NFMA	Mud	70	0.70	0.12	30	-17.82	0.06	31	14.77	0.07	31	398	97	4	0.74	0.03	33	0.84	0.09	32	1.20	0.03	33	3.13	0.01	31
NFMA	Mud	75	0.66	0.15	19	-17.98	0.08	17	14.70	0.11	17	297	23	5	0.68	0.04	21	1.02	0.10	21	1.14	0.02	21	3.16	0.01	17
NFMA	Mud	80	0.51	0.06	13	-17.84	0.11	13	14.91	0.15	13	223	76	3	0.60	0.05	14	0.80	0.08	14	1.09	0.03	14	3.15	0.01	13
NFMA	Mud	85	0.51	0.10	3	-17.43	0.25	3	14.95	0.29	3	.	.	.	0.65	0.08	4	1.01	0.30	4	1.04	0.06	4	3.15	0.01	3
NFMA	Mud	90	0.46	0.03	7	-17.51	0.19	7	15.11	0.04	7	.	.	.	0.60	0.02	7	0.89	0.11	7	1.05	0.04	7	3.16	0.01	7
NFMA	Mud	95	0.37	0.03	2	-17.16	0.04	2	14.94	0.40	2	.	.	.	0.68	0.09	2	1.28	0.44	2	0.93	0.07	2	3.16	0.05	2
NFMA	Mud	100	0.52	.	1	-16.64	.	1	15.49	.	1	.	.	.	0.68	.	1	0.66	.	1	1.11	.	1	3.08	.	1
SFMA	Complex	55	0.96	0.22	5	-17.61	0.18	5	14.49	0.22	5	151	79	2	0.70	0.04	5	0.61	0.27	5	1.37	0.07	5	3.15	0.02	5
SFMA	Complex	60	0.53	0.02	12	-17.55	0.11	12	14.66	0.11	12	.	.	.	0.63	0.05	12	0.69	0.12	12	1.25	0.03	12	3.13	0.01	12
SFMA	Complex	65	0.63	0.10	30	-17.38	0.07	29	14.48	0.06	29	165	64	6	0.72	0.03	30	0.71	0.06	30	1.25	0.03	30	3.14	0.01	29
SFMA	Complex	70	0.54	0.03	34	-17.40	0.07	34	14.55	0.05	34	136	18	10	0.69	0.04	34	0.69	0.04	34	1.17	0.01	34	3.14	0.01	34
SFMA	Complex	75	0.49	0.03	22	-17.20	0.09	21	14.52	0.07	21	91	.	1	0.55	0.05	22	0.69	0.10	22	1.16	0.02	22	3.09	0.01	21
SFMA	Complex	80	0.59	0.05	14	-16.99	0.12	14	14.62	0.09	14	151	1	2	0.60	0.05	14	0.84	0.10	14	1.18	0.02	14	3.13	0.01	14
SFMA	Complex	85	0.54	0.07	8	-17.07	0.23	8	14.75	0.14	8	143	8	2	0.67	0.04	8	0.70	0.03	8	1.20	0.03	8	3.06	0.03	8
SFMA	Complex	90	0.26	0.12	3	-17.02	0.30	3	14.67	0.19	3	.	.	.	0.63	0.07	3	0.86	0.15	3	1.18	0.05	3	3.17	0.05	3
SFMA	Complex	95	0.49	0.12	2	-16.58	0.17	2	15.73	0.02	2	.	.	.	0.74	0.13	2	0.84	0.05	2	1.16	0.12	2	3.12	0.01	2
SFMA	Complex	100	0.54	0.06	2	-17.09	0.21	2	15.57	0.23	2	.	.	.	0.71	0.10	2	0.76	0.08	2	1.02	0.09	2	3.12	0.01	2
SFMA	Mud	50	1.05	0.19	4	-17.72	0.24	4	14.53	0.18	4	.	.	.	0.60	0.06	4	0.14	0.04	4	1.36	0.03	4	3.14	0.02	4
SFMA	Mud	55	0.69	0.11	7	-17.44	0.14	7	14.71	0.10	7	100	15	2	0.77	0.03	7	0.56	0.25	7	1.33	0.05	7	3.15	0.02	7
SFMA	Mud	60	0.89	0.22	16	-17.47	0.10	16	14.65	0.08	16	202	69	6	0.70	0.06	16	0.60	0.12	16	1.26	0.04	16	3.12	0.01	16
SFMA	Mud	65	0.75	0.16	17	-17.39	0.10	18	14.47	0.09	18	420	.	1	0.66	0.04	19	0.82	0.09	19	1.21	0.03	19	3.10	0.01	18
SFMA	Mud	70	0.69	0.08	33	-17.33	0.07	33	14.51	0.08	33	177	39	10	0.58	0.03	33	0.70	0.03	33	1.21	0.01	33	3.12	0.01	33
SFMA	Mud	75	0.42	0.06	5	-17.12	0.25	5	14.65	0.09	5	.	.	.	0.45	0.10	5	0.74	0.04	5	1.12	0.02	5	3.10	0.02	5
SFMA	Mud	80	0.54	0.09	7	-16.79	0.18	7	14.82	0.18	7	225	.	1	0.59	0.03	7	0.67	0.06	6	1.25	0.06	7	3.08	0.02	7
SFMA	Mud	90	0.43	.	1	-17.43	.	1	15.30	.	1	.	.	.	0.52	.	1	0.76	.	1	1.16	.	1	3.12	.	1
SFMA	Mud	95	0.51	0.05	2	-16.41	0.22	2	14.84	0.19	2	145	.	1	0.76	0.05	2	0.67	0.10	2	1.17	0.05	2	3.11	0.02	2

Table 2. Summary data (means, standard error and sample size) for various feeding and condition indices for male monkfish from two management areas (NFMA and SFMA), two habitats (complex and mud) and by 5 cm length interval.

			Feeding indices												Condition indices											
		Length interval	Stomach K			$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)			Prey length (mm)			log LSI			log GSI			FCF			CN		
Area	Habitat	(cm)	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N	Mean	SE	N
												Males														
NFMA	Complex	45	1.43	.	1	-18.01	.	1	14.14	.	1	220	.	1	0.95	.	1	0.33	.	1	1.80	.	1	3.12	.	1
NFMA	Complex	50	1.03	0.32	6	-17.64	0.05	6	14.86	0.15	6	252	39	3	0.65	0.11	6	0.35	0.07	6	1.31	0.07	6	3.13	0.04	6
NFMA	Complex	55	1.00	0.28	7	-17.72	0.13	7	14.86	0.18	7	287	41	3	0.65	0.08	7	0.33	0.03	7	1.28	0.03	7	3.15	0.02	7
NFMA	Complex	60	0.64	0.19	7	-18.03	0.20	7	14.46	0.12	7	145	.	1	0.50	0.11	8	0.35	0.07	7	1.31	0.23	8	3.16	0.02	7
NFMA	Complex	70	0.35	.	1	-17.86	.	1	14.97	.	1	.	.	.	0.75	.	1	0.74	.	1	1.19	.	1	3.13	.	1
NFMA	Complex	80	0.34	.	1	-17.59	.	1	14.76	.	1	.	.	.	0.60	.	1	0.57	.	1	1.06	.	1	3.10	.	1
NFMA	Mud	50	0.46	.	1	-17.77	.	1	15.25	.	1	.	.	.	0.45	.	1	0.26	.	1	1.12	.	1	3.14	.	1
NFMA	Mud	55	0.63	0.17	5	-17.54	0.29	5	14.78	0.25	5	110	.	1	0.55	0.03	5	0.31	0.09	5	1.11	0.03	5	3.14	0.02	5
NFMA	Mud	60	0.85	.	1	-17.78	.	1	14.29	.	1	.	.	.	0.79	.	1	0.15	.	1	1.15	.	1	3.15	.	1
NFMA	Mud	65	0.64	.	1	-17.66	.	1	14.52	.	1	.	.	.	0.67	.	1	0.04	.	1	1.13	.	1	3.15	.	1
SFMA	Complex	50	0.61	0.10	5	-17.53	0.11	5	14.59	0.17	5	148	51	4	0.75	0.07	5	0.43	0.04	5	1.32	0.08	5	3.15	0.02	5
SFMA	Complex	55	0.63	0.13	18	-17.52	0.10	17	14.58	0.10	17	171	54	3	0.69	0.03	18	0.43	0.05	18	1.22	0.03	18	3.14	0.01	17
SFMA	Complex	60	1.32	0.33	10	-17.10	0.11	11	14.49	0.08	11	250	68	6	0.67	0.03	11	0.54	0.08	11	1.18	0.03	11	3.13	0.01	11
SFMA	Complex	65	0.49	0.05	2	-17.55	0.15	2	14.54	0.06	2	.	.	.	0.63	0.13	2	0.44	0.18	2	1.16	0.08	2	3.18	0.02	2
SFMA	Mud	50	0.73	0.11	19	-17.61	0.06	18	14.47	0.07	18	120	17	5	0.64	0.02	19	0.42	0.04	19	1.30	0.03	19	3.15	0.01	18
SFMA	Mud	55	0.92	0.22	23	-17.29	0.10	23	14.59	0.09	23	256	64	6	0.67	0.04	23	0.42	0.03	23	1.22	0.03	23	3.13	0.01	23
SFMA	Mud	60	0.82	0.19	22	-17.16	0.12	21	14.41	0.05	21	139	43	6	0.60	0.04	23	0.46	0.05	23	1.15	0.02	23	3.12	0.01	21
SFMA	Mud	65	0.75	0.34	5	-17.14	0.15	5	14.63	0.17	5	370	.	1	0.51	0.06	6	0.32	0.05	6	1.04	0.02	6	3.17	0.01	5

Table 3. Mean partial fullness index values for various prey items by 5 cm length interval for female monkfish from two management areas and two habitats.

Area	Habitat	Length interval (cm)	N	PFI_{ceph}	PFI_{clup}	PFI_{cott}	PFI_{crus}	PFI_{gad}	PFI_{pleu}	PFI_{raji}
						Females				
NFMA	Complex	55	3	.	.	.	.	.	.	.
NFMA	Complex	60	9	.	.	.	.	1.92	.	.
NFMA	Complex	65	31	.	.	0.19	.	0.98	.	.
NFMA	Complex	70	41	.	.	0.06	.	0.17	.	.
NFMA	Complex	75	30	.	0.03	.	.	0.71	.	.
NFMA	Complex	80	11	.	0.08	.	.	3.46	.	.
NFMA	Complex	85	8	.	.	.	.	.	.	.
NFMA	Complex	90	4	.	.	.	.	0.62	.	.
NFMA	Complex	95	3	.	.	.	.	.	.	.
NFMA	Complex	100	3	.	.	.	.	.	.	.
NFMA	Mud	50	2	.	.	.	.	.	.	.
NFMA	Mud	55	3	.	.	.	.	.	.	.
NFMA	Mud	60	14	0.02	.	.	0.07	0.47	.	.
NFMA	Mud	65	24	.	0.07	.	.	0.10	.	0.68
NFMA	Mud	70	32	.	.	.	.	3.19	.	.
NFMA	Mud	75	19	.	.	.	.	0.42	.	.
NFMA	Mud	80	13	.	0.01	.	.	0.27	.	.
NFMA	Mud	85	3	.	.	.	.	0.93	.	.
NFMA	Mud	90	7	0.07	.	.	.	.	.	.
NFMA	Mud	95	2	.	.	.	.	.	.	.
NFMA	Mud	100	1	.	.	.	.	.	.	.
SFMA	Complex	55	5	0.65	.	.	.	.	.	.
SFMA	Complex	60	12	.	.	.	.	.	.	.
SFMA	Complex	65	29	0.17	.	0.05	.	.	.	0.91
SFMA	Complex	70	33	0.01	.	0.06	.	0.04	0.01	0.15
SFMA	Complex	75	22	0.23	.	.	.	.	.	.
SFMA	Complex	80	14	.	.	.	.	.	.	0.04
SFMA	Complex	85	8	.	.	.	.	.	.	0.57
SFMA	Complex	90	3	.	.	.	.	.	.	.
SFMA	Complex	95	2	.	.	.	.	.	.	.
SFMA	Complex	100	2	.	.	.	.	.	.	.
SFMA	Mud	50	4	1.19	.	0.61	0.02	.	.	.
SFMA	Mud	55	7	0.44	.	.	.	.	.	.
SFMA	Mud	60	16	.	.	.	.	0.11	.	3.24
SFMA	Mud	65	18	0.20	.	.	.	.	.	1.64
SFMA	Mud	70	33	0.11	.	.	.	.	.	0.13
SFMA	Mud	75	5	.	.	.	.	.	.	.
SFMA	Mud	80	7	.	.	.	.	.	.	1.26
SFMA	Mud	90	1	.	.	.	.	.	.	.
SFMA	Mud	95	2	.	.	.	.	.	.	0.12

Table 4. Mean partial fullness index values for various prey items by 5 cm length interval for male monkfish from two management areas and two habitats.

Area	Habitat	Length interval (cm)	N	PFI_{ceph}	PFI_{clup}	PFI_{cott}	PFI_{crus}	PFI_{gad}	PFI_{pleu}	PFI_{raji}
						Males				
NFMA	Complex	45	1	.	.	8.33	.	.	.	.
NFMA	Complex	50	6	.	.	2.15	.	2.66	.	.
NFMA	Complex	55	7	.	.	.	.	4.37	.	.
NFMA	Complex	60	7	.	.	.	.	1.59	.	.
NFMA	Complex	70	1	.	.	.	.	.	.	.
NFMA	Complex	80	1	.	.	.	.	.	.	.
NFMA	Mud	50	5	.	.	.	0.01	.	0.80	.
NFMA	Mud	55	18	.	.	.	.	.	.	0.36
NFMA	Mud	60	11	.	.	.	.	1.76	.	2.65
NFMA	Mud	65	2	.	.	.	.	.	.	.
SFMA	Complex	50	1	.	.	.	.	.	.	.
SFMA	Complex	55	5	.	.	.	.	0.16	.	.
SFMA	Complex	60	1	.	.	.	.	5.18	.	.
SFMA	Complex	65	1	.	.	.	.	.	.	.
SFMA	Mud	50	18	0.25	.	.	.	.	0.17	0.33
SFMA	Mud	55	23	0.15	.	.	.	.	.	1.38
SFMA	Mud	60	22	0.15	.	.	.	.	.	2.34
SFMA	Mud	65	5	.	.	.	.	.	.	2.69

Table 5. Summary of ANOVA results for effect of management area, habitat, and length interval (including interactions; although only area × length interaction was found to be significant in some cases) on feeding and condition variables for female and male monkfish

	Effect									
	Area (*df* = 1)		Habitat (*df* = 1)		Length interval (*df* = 6)		Area x L (*df* = 3)			
Dependent	F	*p*	F	*p*	F	*p*	F	*p*	Model R^2	Total N
					Females					
Stomach K					2.0	*< 0.05*			0.09	486
$\delta^{13}C$	49.1	*< 0.0001*			7.9	*< 0.0001*	2.0	*< 0.5*	0.43	479
$\delta^{15}N$					5.9	*< 0.0001*			0.22	479
Prey size	7.4	*<0.01*	4.8	*< 0.5*					0.40	89
Log LSI					2.7	*<0.01*	2.0	*< 0.5*	0.15	499
Log GSI					2.6	*< 0.01*			0.13	494
Gutted K	6.1	*< 0.5*			8.2	*< 0.0001*	1.8	*< 0.5*	0.25	499
C/N	12.7	*< 0.0001*			1.8	*< 0.5*			0.15	479
					Males					
Stomach K						ns				
$\delta^{13}C$	9.9	*<0.01*							0.29	133
$\delta^{15}N$						ns				
Prey size						ns				
Log LSI						ns				
Log GSI	8.7	*<0.01*							0.15	139
Gutted K			6.0	*< 0.5*					0.19	140
C/N						ns				

Table 6. Linear regression results for relationship between $\delta^{15}N$ and length for female monkfish from two management areas and two habitats.

	Model Coefficients				Model Summary		
	Var	B	SE	Sig.	R^2	F	N
NFMA Complex	Constant	12.8126	0.3181	1.4E-79			
	Length	0.0025	0.0004	1.6E-08	0.202	35.98	143
NFMA Mud	Constant	14.0606	0.3308	4.3E-70			
	Length	0.0010	0.0004	2.8E-02	0.043	4.98	111
SFMA Complex	Constant	13.4706	0.2555	1.1E-88			
	Length	0.0015	0.0003	1.1E-88	0.133	19.6	129
SFMA Mud	Constant	14.1518	0.3383	3.2E-61			
	Length	0.0006	0.0005	2.0E-01	0.018	1.69	92

Table 7. Linear regression results for relationship between condition and feeding variables for female monkfish (no significant results were found for male monkfish). Most variables covaried with length, and length was therefore included as a variable in most cases.

	Model Coefficients				Model Summary			
Dependent	Var	B	SE	Sig.	R^2	F	Sig.	N
Gutted K	Constant	2.5491	0.2272	0.000	0.203	60.4	0.000	475
	Length	-0.0007	0.0001	0.000				
	$\delta^{13}C$	0.0455	0.0119	0.000				
	Constant	0.8835	0.2005	0.000	0.208	62.1	0.000	475
	Length	-0.0008	0.0001	0.000				
	$\delta^{15}N$	0.0603	0.0144	0.000				
	Constant	1.6464	0.0503	0.000	0.201	60.4	0.000	482
	Length	-0.0006	0.0001	0.000				
	Stomach K	0.0387	0.0124	0.002				
Log LSI	Constant	0.1360	0.3040	0.655	0.039	9.62	0.000	475
	Length	-0.0002	0.0000	0.007				
	$\delta^{13}C$	-0.0414	0.0159	0.009				
	Constant	0.0574	0.2677	0.830	0.047	11.66	0.000	475
	Length	-0.0004	0.0001	0.000				
	$\delta^{15}N$	0.0632	0.0192	0.001				
Log GSI	Constant	-1.2142	0.6906	0.079	0.027	6.58	0.002	470
	Length	0.0007	0.0002	0.001				
	$\delta^{13}C$	-0.0852	0.0361	0.019				
	Constant	0.4908	0.1531	0.001	0.041	10.25	0.000	477
	Length	0.0005	0.0002	0.013				
	Stomach K	-0.1239	0.0376	0.001				
	Constant	0.8568	0.0729	0.000	0.048	4.32	0.041	87
	Prey Length	-0.0006	0.0003	0.041				
CN	Constant	2.6546	0.0842	0.000	0.064	32.4	0.000	478
	$\delta^{13}C$	-0.0272	0.0048	0.000				
	Constant	2.9381	0.0852	0.000	0.031	7.59	0.001	478
	Length	-0.0001	0.0000	0.001				
	$\delta^{15}N$	0.0183	0.0061	0.003				

Figure 1. Chart showing location of sampling sites in the northern and southern fishery management areas (NFMA and SFMA, respectively).

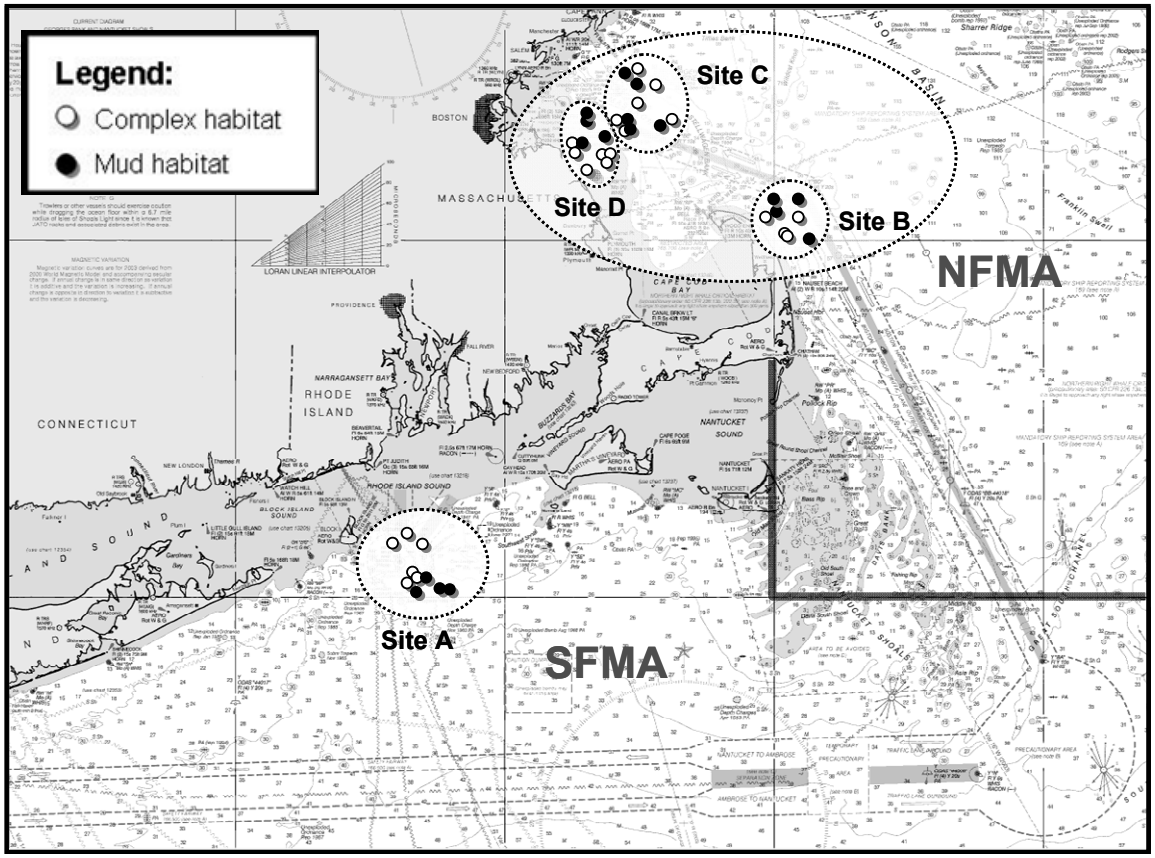

Figure 2. Length frequency distributions for female and male monkfish from two management areas and two habitats.

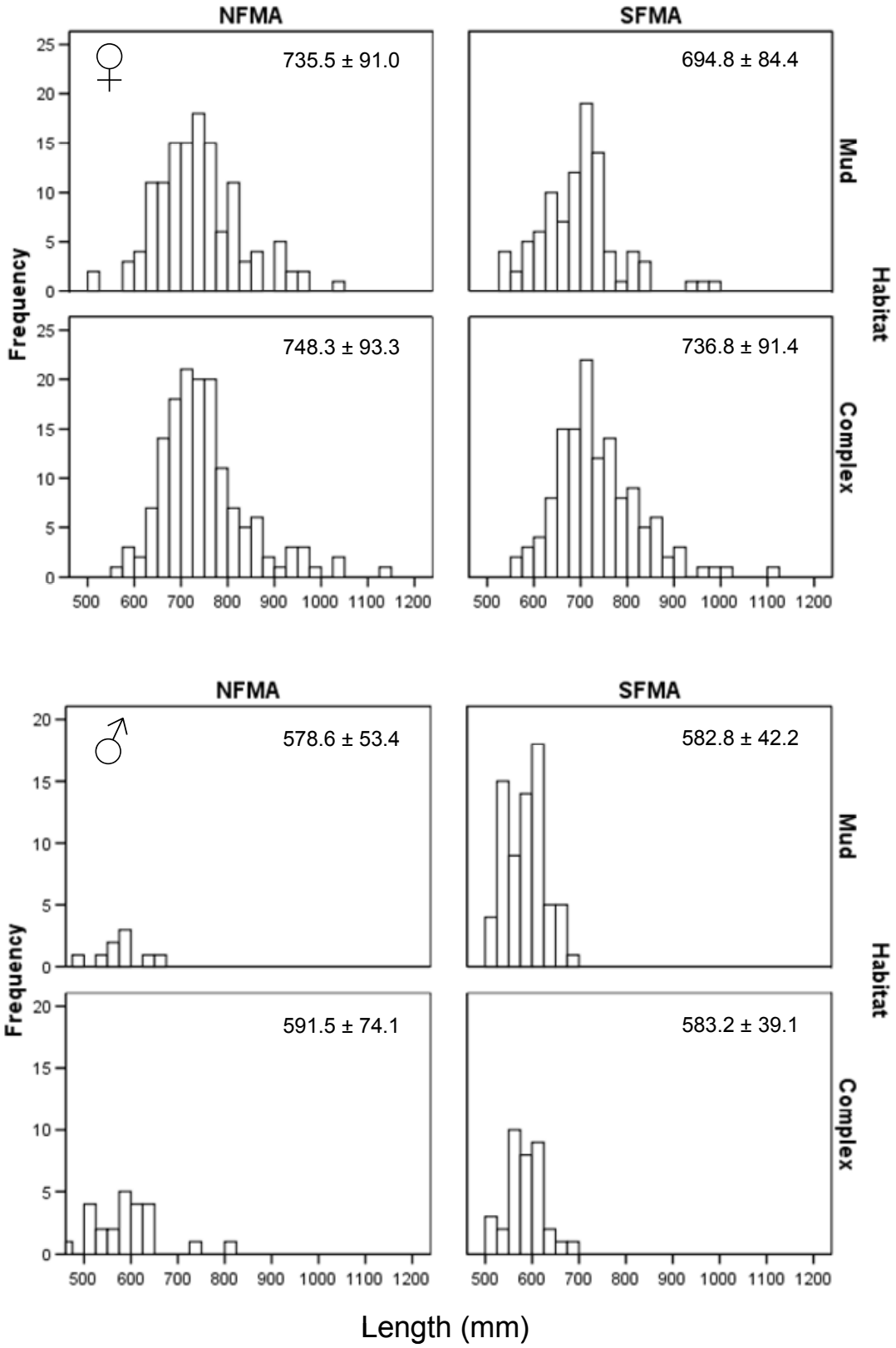

Figure 3. Length – weight relationships for female and male monkfish from two management areas and two habitats. Scaling coefficients (b from $W = a{\cdot}L^b$), ± 95% confidence intervals, are shown at bottom. Asterisks indicate only 2 values that are significantly different from one another.

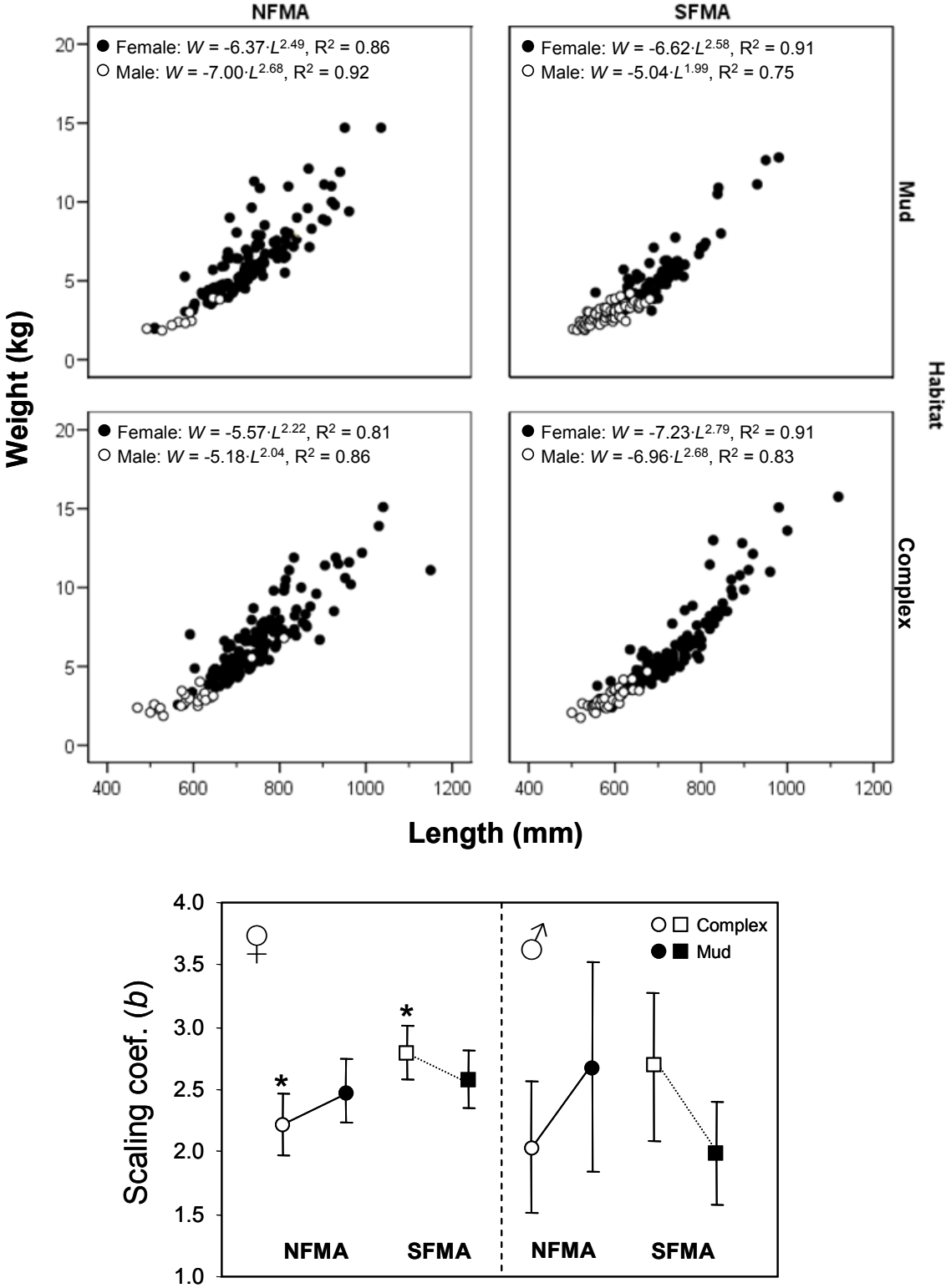

Figure 4. Predator length (monkfish length) versus prey length relationships for female and male monkfish from two management areas and two habitats.

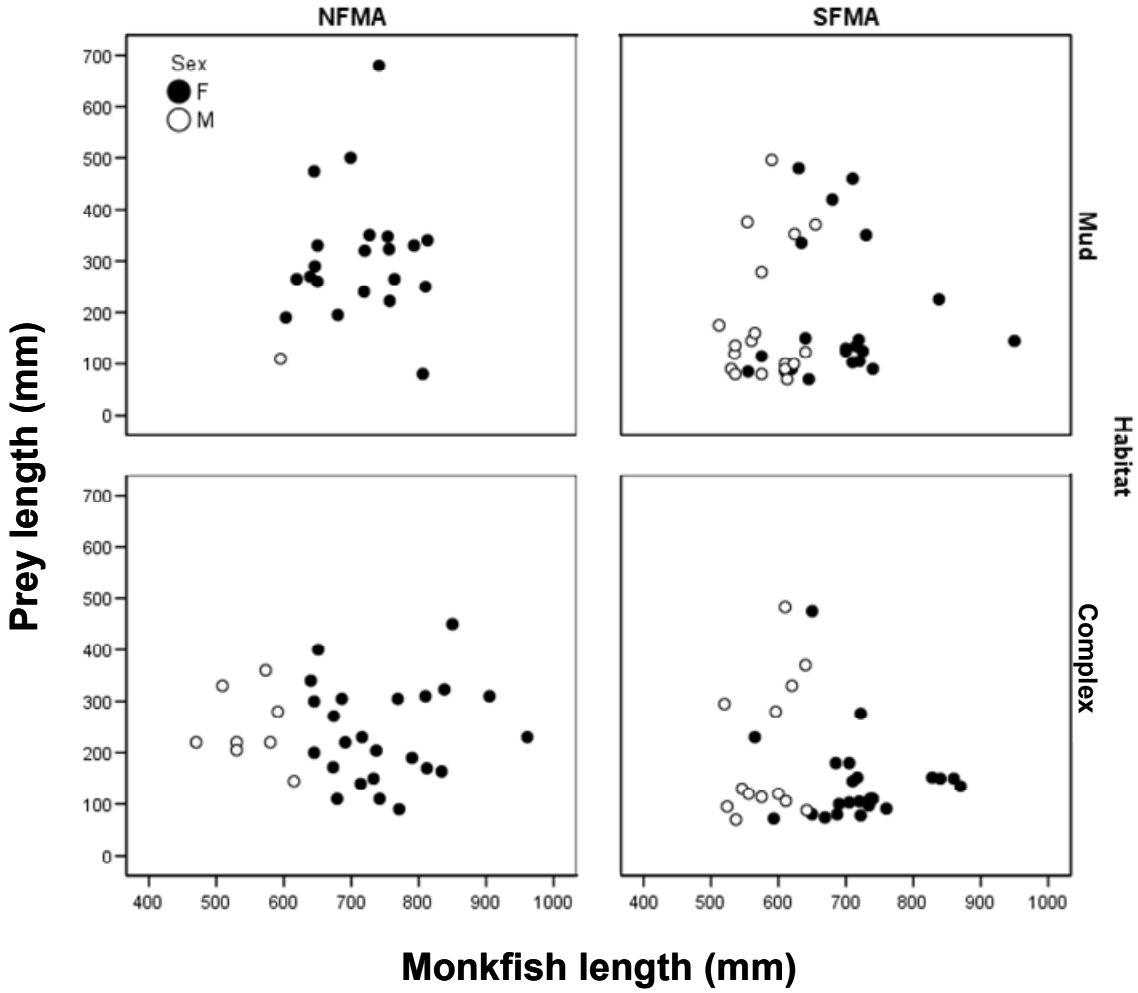

Figure 5. Mean (± 95% CI) prey size for female monkfish from two management areas and two habitats. Bars with different letters are significantly different (ANOVA, $p < 0.05$).

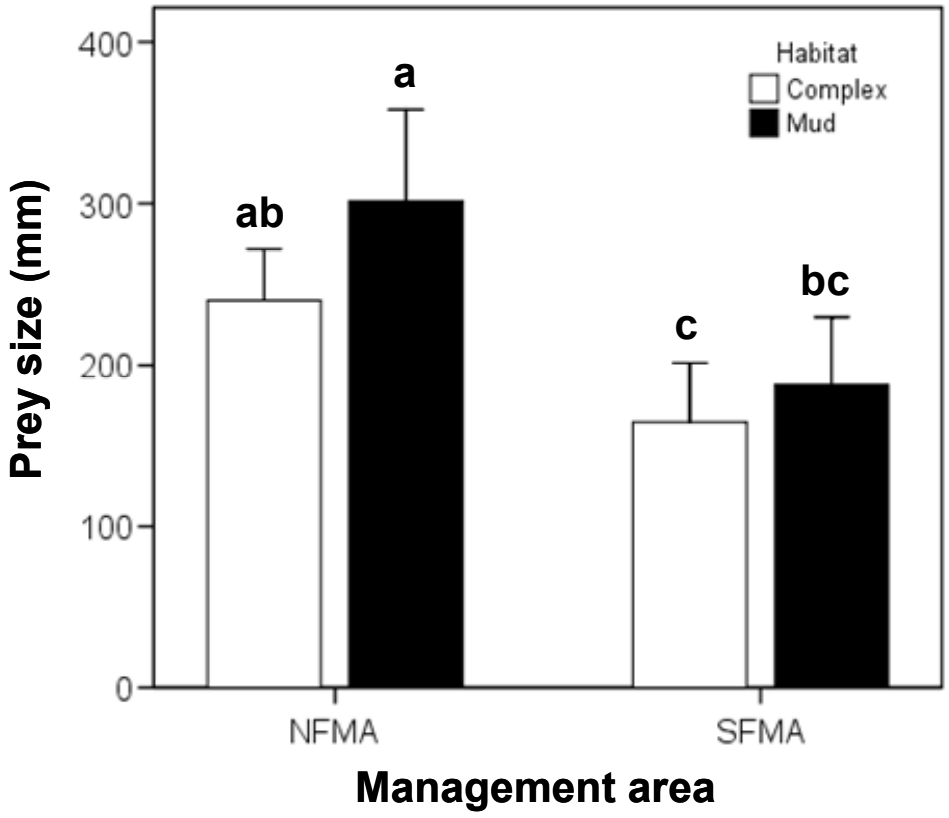

Figure 6. Pie charts showing percent (volumetric) contribution of various prey items to the diet of female and male monkfish from two management areas and two habitats.

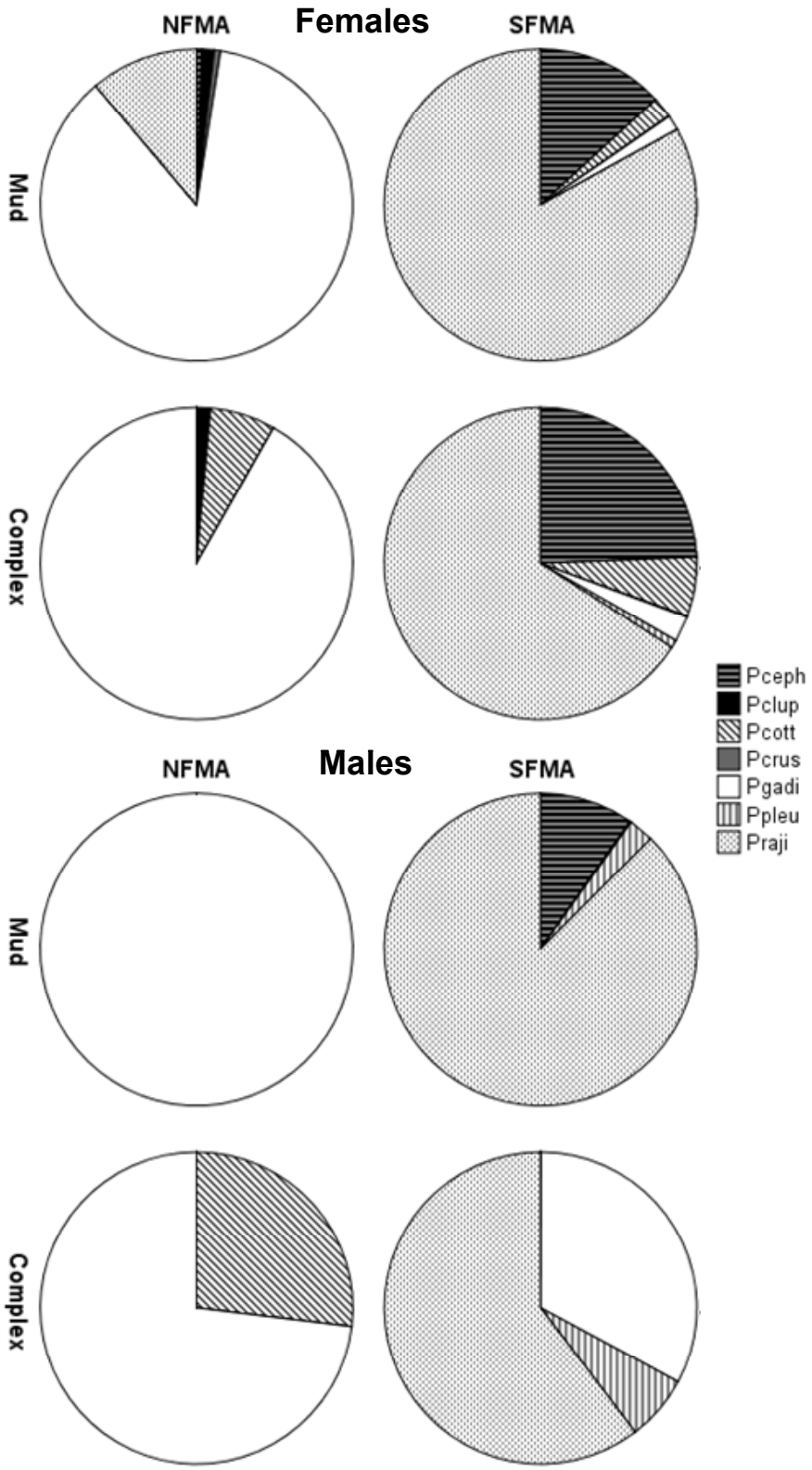

Figure 7. Area graphs showing ontogenetic trends in mean partial fullness index of various prey items by 5 cm length interval for female and male monkfish from two management areas and two habitats.

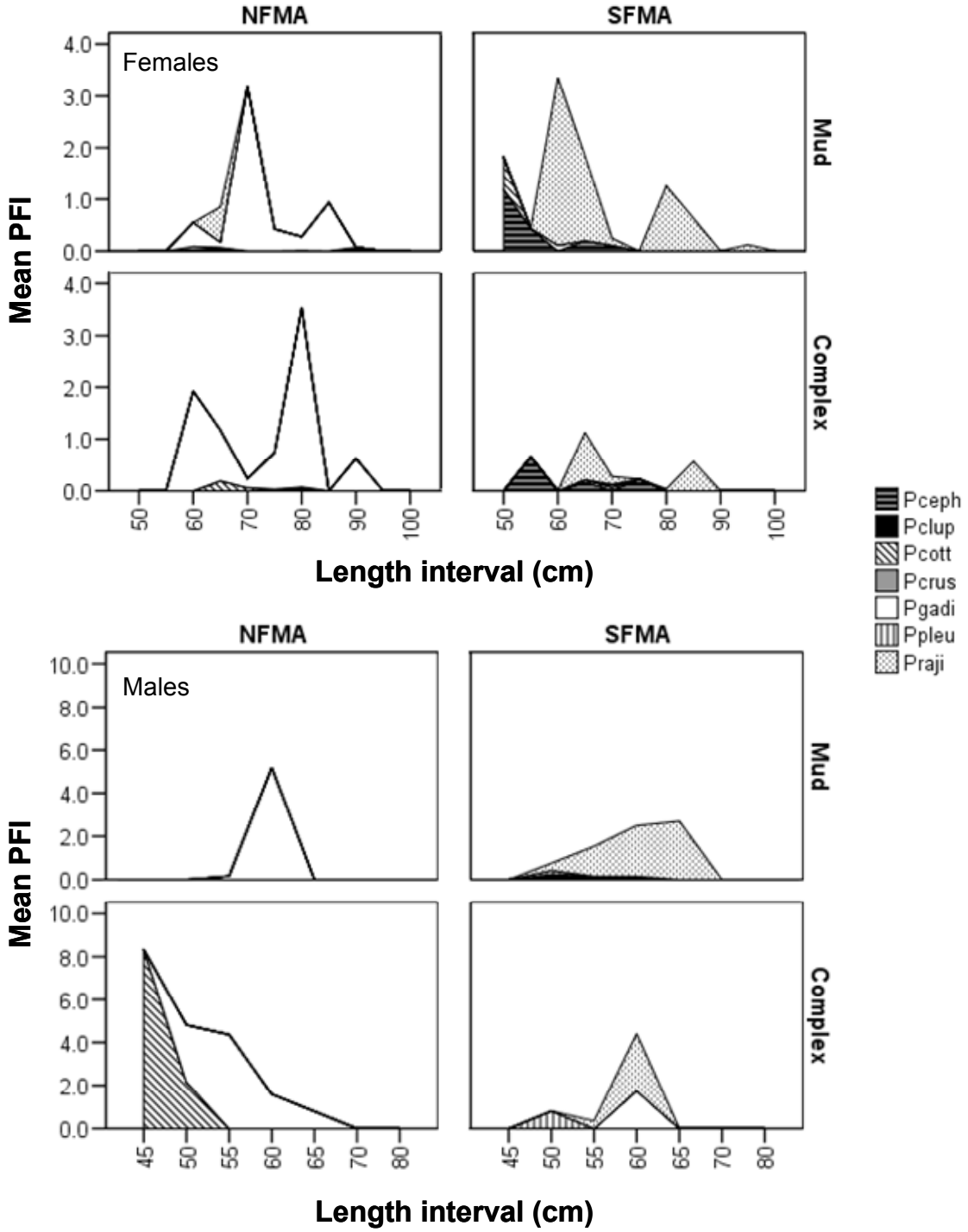

Figure 8. Mean (± 1 SE) values for various feeding and condition indices by 5 cm length interval for female monkfish from two management areas and two habitats. Shaded areas highlight differences (not necessarily significant) among habitats.

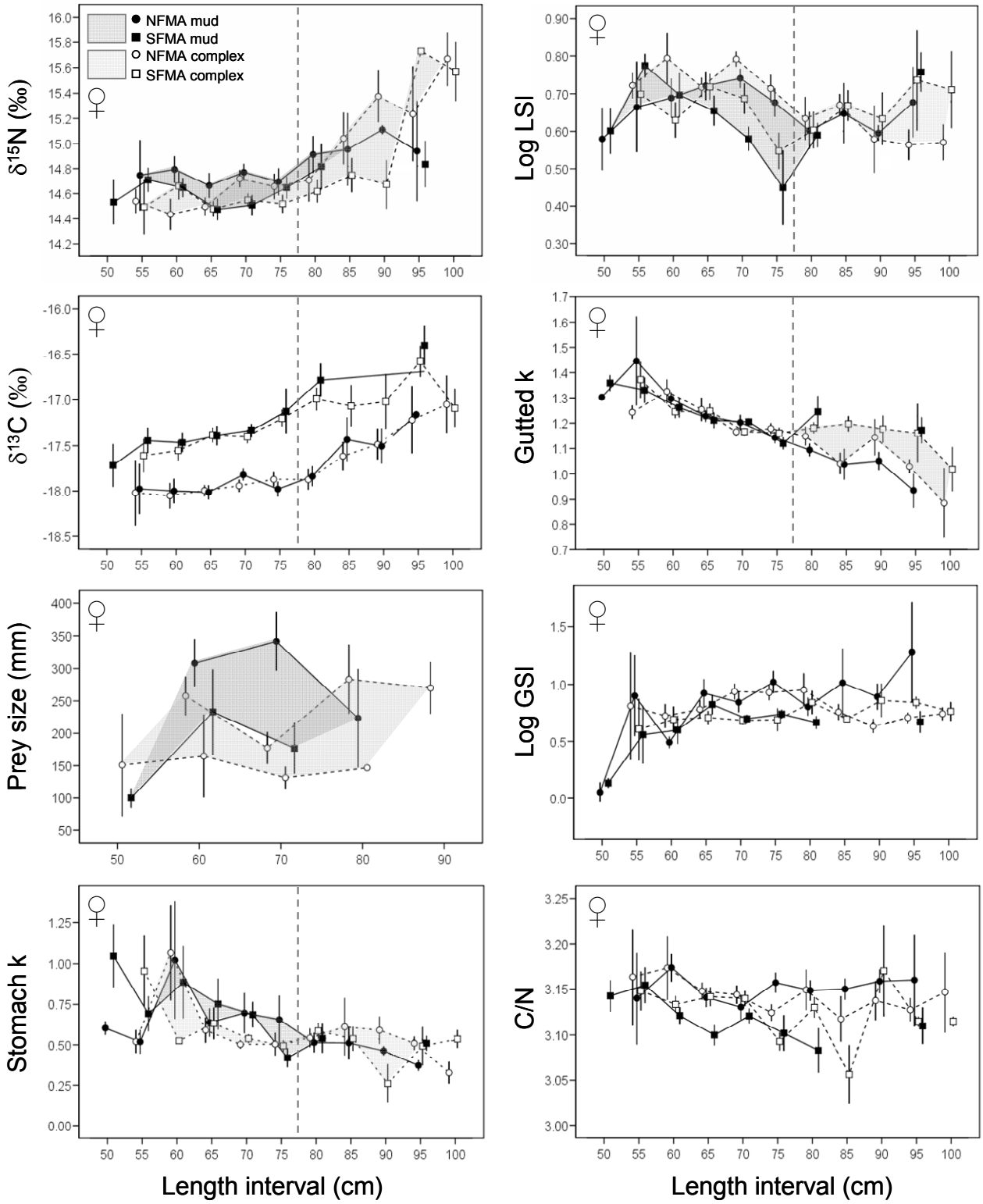

Figure 9. Mean (± 1 SE) values for various feeding and condition indices by 5 cm length interval for male monkfish from two management areas and two habitats.

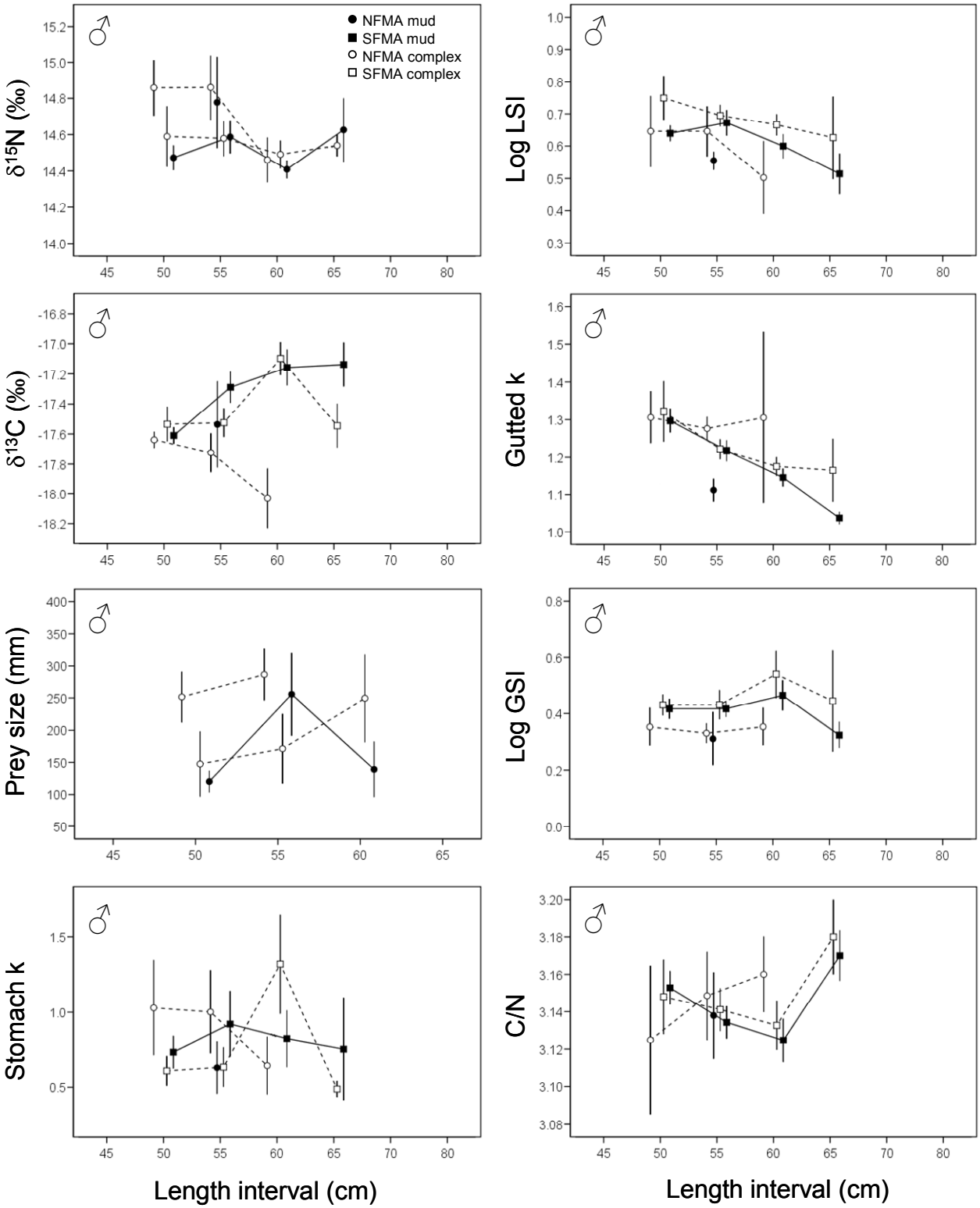
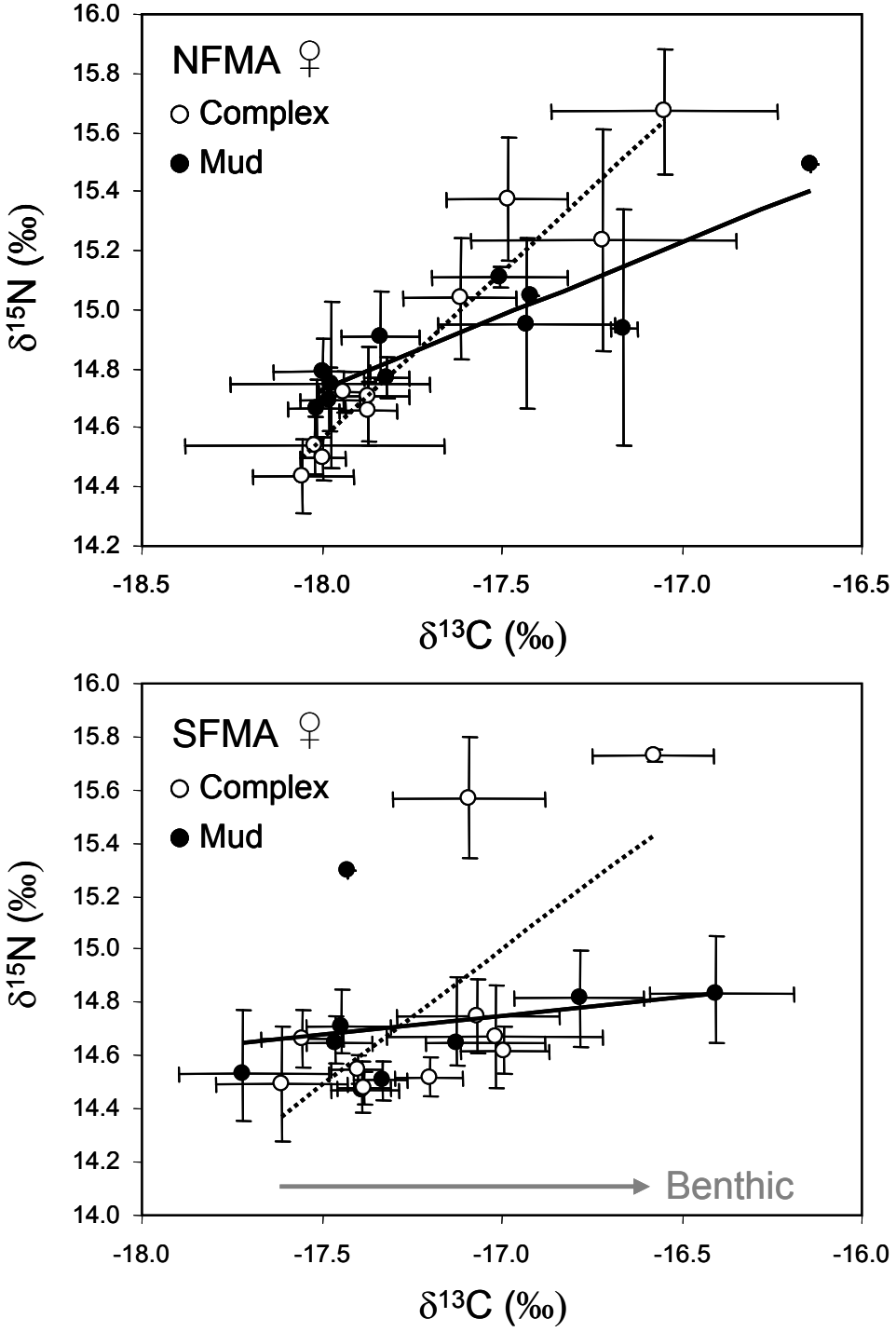
Figure 10. Mean (± 1 SE) $\delta^{15}N$ versus mean $\delta^{13}C$ by 5 cm length interval (not shown but values in top right quadrant represent larger intervals) for monkfish from complex and mud habitats in the NFMA and SFMA. Benthic (larger) monkfish achieve the highest trophic positions in complex habitats: NFMA: $R^2 = 0.42$, $p < 0.0001$, N = 255; $\delta^{15}N = 28.8(1.2) + 0.79(0.07)\times\delta^{13}C - 4.45(1.92)\times HAB - 0.25(0.11)\times interaction$; SFMA: $R^2 = 0.08$, $p < 0.01$, N = 222; $\delta^{15}N = 18.5(0.9) + 0.23(0.05)\times\delta^{13}C$.