Abstract—The community structure of fishes associated with pelagic Sargassum spp. and open water lacking Sargassum was examined during summer and fall cruises, 1999-2003, in the Gulf Stream off North Carolina. Significantly more individual fishes (n = 18,799), representing at least 80 species, were collected from samples containing Sargassum habitat, compared to 60 species (n=2706individuals) collected from openwater habitat. The majority (96%) of fishes collected in both habitats were juveniles, and planehead filefish (Stephanolepis hispidus) dominated both habitats. Regardless of sampling time (day or night), Sargassum habitat yielded significantly higher numbers of individuals and species compared with open-water collections. Overall, fishes collected by neuston net tows from Sargassum habitat were significantly larger in length than fishes collected from open-water habitat with neuston nets. A significant positive, linear relationship existed between numbers of fishes and the quantity of Sargassum collected by neuston net. Underwater video recordings indicated a layered structure of fishes among and below the algae and that smaller fishes were more closely associated with the algae than larger fishes. Observations of schooling behaviors of filefishes (Monacanthidae), dolphinfish (Coryphaena hippurus), and jacks (Carangidae), and fish-jellyfish associations were also recorded with an underwater video camera. Our data indicate that Sargassum provides a substantial nursery habitat for many juvenile fishes off the U.S. southeast coast.

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Fishes associated with pelagic Sargassum and open water lacking Sargassum in the Gulf Stream off North Carolina

Tara L. Casazza (contact author) Steve W. Ross

Email address for T.L. Casazza: tarac73@juno.com Center for Marine Science University of North Carolina Wilmington 5600 Marvin Moss Lane Wilmington, North Carolina 28409

In the western North Atlantic Ocean, pelagic brown algae of the genus Sargassum form a dynamic, floating habitat that supports a diverse assemblage of fishes, invertebrates, sea turtles, pelagic birds, and marine mammals. The pelagic species S. natans and S. fluitans provide resources in an otherwise nutrient-poor environment and serve as a nursery area for many juvenile fishes (Wells and Rooker, 2004), some of which are commercially or recreationally important, or both (e.g., Coryphaena hippurus [dolphinfish], Caranx spp. [jacks], Seriola spp. [amberjacks]). Sargassum habitat appears to be particularly important for early survival of some fishes because the majority of fishes collected from Sargassum habitat in the Gulf of Mexico (Bortone et al., 1977; Wells and Rooker, 2004) and off the southeastern United States (Dooley, 1972; Moser et al., 1998) are juveniles.

The spatial distribution and quantity of *Sargassum* are highly variable. Sargassum distribution along the U.S. east coast depends on the Florida Current and the Gulf Stream, which entrain pelagic Sargassum from the Sargasso Sea and move it northward. Aggregations of Sargassum range from small, widely dispersed clumps to rafts and large weedlines that continue for many kilometers, and the great variability in the structure of this habitat is due to variations in Gulf Stream flow, storms, tidal currents, and wind-generated waves and currents. Although estimates of Sargassum biomass in the western North Atlantic have varied (Howard and Menzies, 1969; Butler and Stoner, 1984), the majority of pelagic Sargassum has persisted and reproduced vegetatively in the western North Atlantic Ocean for at least decades and probably for hundreds to thousands of years (Parr, 1939).

Sargassum habitat is extremely difficult to sample consistently and quantitatively, and no single method of sampling provides a complete view of the Sargassum community. Even though Moser et al. (1998) recommended using multiple sampling methods, especially visual methods, to survey this ecosystem, most Sargassum community studies from the Gulf of Mexico (Bortone et al., 1977; Wells and Rooker, 2004) and the western North Atlantic (Dooley, 1972; Moser et al., 1998) have been based on limited sampling methods. Kingsford (1995) and Dempster and Kingsford (2004) suggested that a weakness in previous studies was a lack of open-water, unvegetated control samples, and to date, in only one study (Moser et al., 1998) in the western North Atlantic have fishes associated with Sargassum habitat been compared to fishes in open-water habitat. Additionally, most samples of *Sargassum* were collected during daytime only (Dooley, 1972; Moser et al., 1998; Wells and Rooker, 2004) or sampling times were not specified (Bortone et al., 1977; Stoner and Greening, 1984). In some cases, explicit association of samples with Sargassum was unclear because samples were not collected within the algae (e.g., Settle, 1993).

The relationships between the quantity of *Sargassum* and species richness and abundance or biomass of fishes are highly variable. Dooley (1972) and Fedoryako (1980) found no correlation between numbers of fishes and quantity of *Sargassum*, but significant positive correlations between fish abundances and quantity of algae have been found in other studies (Moser et al., 1998; Wells and Rooker, 2004). Sampling methods may substantially influence these results. Nevertheless, it is clear that objects floating in the ocean, like *Sargassum*, attract and concentrate fauna (Kingsford, 1992).

Despite several surveys and the widespread occurrence of Sargassum habitat, the fishes associated with this habitat have not been extensively documented along the U.S. east coast. Our objective was to describe fish community structure (species composition, day versus night species composition, sizes, and Sargassum abundance and fish distribution relationships) within Sargassum and open-water habitats off North Carolina. In addition, behaviors of fishes within and below Sargassum habitat were documented to better describe the close associations of fishes with the habitat, the different types of habitat usage, and to provide a three dimensional view of

the distribution of fishes within and beneath the Sargassum. Our approach was to use consistent methods (supplemented by further sampling) and extensive temporal (diel) and spatial sampling across ocean surface habitats with no Sargassum to those with high densities of Sargassum to examine the relative contribution of Sargassum to oceanic fish communities off the southeastern United States.

Materials and methods

Sampling

Surface waters were sampled during 2–7 August 1999, 20–27 July 2000, 22–28 August 2001, 20–26 September 2001, 6–15 August 2002, and 17–26 August 2003, in the Gulf Stream off Cape Hatteras, Cape Lookout, and Cape Fear, North Carolina (Fig. 1). The primary sampling device, a 1.1×2.4-m neuston net (6.4-mm mesh body, 3.2-mm tailbag), was towed in the upper meter of the water column at slow speeds (<3.7 km/h) for 30 minutes in 1999 and for 15 minutes during 2000–03. Sampling was conducted throughout the 24-h period to compare daylight (0700–2000 h eastern daylight time [EDT]) and nighttime (–0700 h EDT) collections. The neuston net was towed in both open water without *Sargassum* and in waters with varying amounts of *Sargassum*.

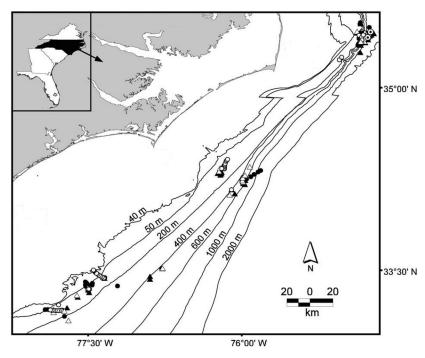


Figure 1

Surface sampling sites for fishes collected during summer and fall of 1999–2003 off North Carolina. Collections with neuston nets (triangles) and supplemental gears (circles) (i.e., nightlighting, dip net, hook-and line, longline) from Sargassum (closed symbols) and open-water (open symbols) habitats. The white circles with a black center off Cape Hatteras represent sites where underwater video recordings were taken.

Sargassum is in constant motion in the Gulf Stream, and without aerial surveillance its distribution and density are unpredictable, especially at night. Because we were unable to consistently target a particular habitat, and thus balance sampling effort, the nets were pulled through unknown habitat and the sample was classified later depending on whether Sargassum was present in the sample or not (see *Data analysis*). In most cases it was also not possible to determine the proximity of one habitat to another. When *Sargassum* was abundant, the neuston net was towed directly through the clumps. mats, or weedlines, but on some occasions, Sargassum was collected opportunistically. Fishes were sorted from the algae in the neuston tow catches, and the *Sargassum* was weighed (wet weight) to the nearest 0.1 kg and discarded. Because neuston net tows in 1999 were of longer duration and catches were not handled consistently, the catch data from the 1999 neuston net tows were not analyzed statistically (see *Data analysis*).

Additional collection methods supplemented the use of neuston nets, especially when *Sargassum* was too dense for use of the neuston net. When conditions were favorable (low wind and waves), stations with nightlighting were sampled by allowing the vessel to drift with the current or maintain its slowest speed into the current. The deck lights of the vessel, plus two 500-W and one 1000-W spotlights, were used to illuminate surface waters around the stern and both sides of the vessel,

and fishes that swam near the vessel were collected by five or six crew members using small mesh (6.4-mm mesh) dip nets. Each 30-minute segment of time during the drift represented a station. During the nightlighting sampling, the presence or absence of Sargassum within the field of view was recorded, and if present, whether the Sargassum was collected in dip nets was recorded. Fishes were also opportunistically collected with dip nets during daylight when dense aggregations of Sargassum were encountered. Limited hook-and-line sampling occurred in both Sargassum and open-water habitats during the day and at night, and each sampling period (station) lasted from 15 to 160 minutes. One longline set was made in the Cape Hatteras study area. The line was about 366-m long and contained 104 baited hooks that fished within 1-2 m of the surface. The set was made at night, lasted for 501 min, and drifted for 30 km through open-water habitat.

In 1999, underwater video was recorded under a large *Sargassum* weedline at two stations off Cape Hatteras, North Carolina (Fig. 1). Snorkelers using a handheld color camcorder (SONY model DCR-TRV900, New York, NY) in a waterproof case swam at and just below (<3 m) the surface along the edge of and under the weedline. A total of 62 minutes of video footage was recorded during the two stations. Analyses of the underwater video footage included identification of species, documentation of behaviors, and placement of fishes within or below the weedline.

Specimens were preserved at sea in 10% formalinseawater solution and later stored in 40% isopropanol. Larval fishes had been collected in previous Sargassum studies, and this fact implied an association with this habitat. However, because distributions of pelagic fish larvae are highly influenced by currents and they generally lack affinity for drift algae (Kingsford and Choat, 1985), their presence in Sargassum collections (Settle, 1993; Wells and Rooker, 2004) is probably coincidental. For this reason and because the neuston net mesh size was inappropriate for sampling larvae, larval fishes (classified according to Richards, 2006) were excluded from this study. Fishes were identified to the lowest possible taxon, counted, measured to the nearest mm for standard length (SL), and weighed (wet weight) to the nearest 0.1 g. Damage to some fishes precluded identification to species and SL measurements. When more than 500 individuals of the same species were collected in a tow, a subsample (approximately 10% of the catch) was measured for SL and wet weight.

Data analysis

Fish catches from neuston nets were analyzed statistically to assess differences in fish community structure between habitats, and diurnal differences in community structure. Neuston tows without Sargassum were designated as open-water (OW). Because clumps of algae as small as 0.005 kg could influence the distribution and abundance of fishes (Kingsford and Choat, 1985), samples were classified as Sargassum (S) if algae were

collected, regardless of the quantity. The number of individuals and number of species collected from Sargas*sum* and open-water habitats were $\log (x+1)$ transformed before analysis to correct for heterogeneity of variance, to reduce the influence of abundant species, and to enhance the contribution of rare species. If the assumptions of homogeneity of variance and normality were not satisfied after data transformation, a nonparametric Mann-Whitney test was applied to determine whether there were differences in the number of individuals and species in Sargassum versus open-water habitat. A Kruskal-Wallis test was used to compare day and night fish catches from neuston nets within and across station types (i.e., S versus OW), and a Dunn's multiple comparison test was used to determine where significant differences occurred. The relationship of fish abundance and species richness to the quantity of Sargassum collected by neuston nets was evaluated with regression analysis. Length-frequency distributions for dominant species collected from *Sargassum* habitat were compared to the size structures of the same species collected from open-water habitat by using a Kolmogorov-Smirnov test.

Habitat type sampled (S versus OW) was also designated for the supplemental methods. If *Sargassum* was collected by dip net, the station was designated as S; otherwise it was OW. Likewise, if the hook-and-line gear was placed in *Sargassum* (S), the catch was designated as S; if the gear was placed in unvegetated habitat, the catch was designated as OW.

Results

Catch composition

For all methods and cruises combined, most fishes were collected in samples containing Sargassum habitat. A total of 18,799 fishes, representing 80 species from 28 families, were collected in 162 Sargassum samples, and a total of 2706 fishes, representing 60 species from 23 families, were collected in 80 open-water samples (Fig. 1; Table 1). Both *Sargassum* and open-water collections were dominated by the families Monacanthidae (75% of S, 45% of OW), Carangidae (13%, 21%), and Exocoetidae (6%, 19%). Individuals of nine species represented 93% of the total Sargassum catch (in decreasing order of abundance): Stephanolepis hispidus (planehead filefish), Caranx crysos (blue runner), Cheilopogon melanurus (Atlantic flyingfish), Balistes capriscus (gray triggerfish), Seriola rivoliana (almaco jack), Parexocoetus brachypterus (sailfin flyingfish), Monacanthus ciliatus (fringed filefish), Decapterus punctatus (round scad), and Coryphaena hippurus (dolphinfish). Individuals of 10 species represented 92% of the total open-water catch (in decreasing order of abundance): S. hispidus, C. crysos, Clupea harengus (Atlantic herring) (all from a single station), C. melanurus, P. brachypterus, D. punctatus, Prognichthys occidentalis (bluntnose flyingfish), Oxyporhamphus micropterus (smallwing flyingfish), Istiophorus platypterus (sailfish), and C. hippurus. For all methods

Table 1

Number (and standard length [in mm] ranges in parentheses) of fishes collected by method from Sargassum and open-water habitats during summer and fall of 1999–2003 off North Carolina. NN=neuston net, NL=nightlighting, DN=dip net, HL=hook-and-line, LL=longline, number of stations is in parentheses under gear type. †=total length in mm, N/A=length not available due to specimen damage, *=species not previously collected in association with Sargassum. Identification to species was

		3 1	Sargassum				Орег	Open water		
Taxon	NN (95)	NL (42)	DN (18)	HL (7)	Total n	NN (39)	NL (33)	HL (7)	LL (1)	Total n
Carcharhinidae				1 (800)	-					
Carcharninas Jaicyornus Ophichthidae				1 (080)	7					0
$Ahlia\ egmontis*$		4(270-410)			4		1 (378)			1
Clupeidae										
Čľupea harengus					0		216 (22 - 42)			216
Gonostomatidae	, 4 ; h				,					(
Cyclothone sp.* Stemontwehidee	1 (N/A)				I					0
Argyropelecus aculeatus*	1 (41)				1					0
Phosichthyidae										
Vinciguerria poweriae					0		1(20)			1
Synodontidae										
$Synodus\ synodus$					0		1(31)			1
Myctophidae										
Diaphus dumerilii*	1 (61)				1					0
$Myctophum\ affine^*$	27 (13-27)				27					0
Myctophum obtusirostre*	10 (13-53)				10					0
$Myctophum\ punctatum^*$	5(39-51)				ಸಂ					0
$Myctophum\ selenops^*$	1(45)				П					0
Myctophum sp.	1 (18)				-					0
Antennariidae										
Histrio histrio	13 (9-45)	4 (7-36)	6(12-46)		23					0
Mugilidae	(·				•	(00	i d			C
Mugu curema	I (14)				T	4 (14–20)	4 (25–27)			×
Unidentified Relonidae	2(13-14)				27					0
A hlonnos hians*	14 (33–374)	8 (90–393)			66	3 (40–196)	4 (351–466)			7
Digtabolono angalue*	9 (149-155)	3 (149, 936)			1 1 п	(071-04) 0	(001-100) 1			
Tulyperone arguins	10 (E9 996)	14 (69 401)			· 6		(1000 000)			> =
1 ylosurus acus Tylosurus crocodilus*	18 (33–330)	14 (63–451) 1 (901)			32 1		4 (202–285)			4 0
Tylosurus sn	2 (44–57)	1 (201)			. 6					0 0
Exocoetidae					1					
Cheilopogon cyanopterus*	6 (24–112)	3(118-144)			6		8 (30–131)			œ
Cheilopogon exsiliens*		2(112-122)			4		6(20-108)			9
Cheilopogon furcatus	2(19-30)	6(35-120)			œ		4 (35-112)			4

		S	Sargassum				Ope	Open water		
Taxon	NN (95)	NL (42)	DN (18)	HL (7)	Total n	NN (39)	NL (33)	HL (7)	LL (1)	Total n
Exocoetidae (cont.) Cheilopogon melanurus	399 (13–205)	157 (21–253)	2 (17–32)		558	57 (12–56)	147 (28–257)			204
Cheilopogon sp. Cypselurus comatus*	6 (19-23) 1 (72)				1		1 (107)			0
Exocoetus obtusirostris Hirundichthys affinis	13 (17–95)	$\frac{1(137)}{18(56-164)}$			1 31	6 (17–47)	3 (18–71) 16 (49–105)			3 22
Oxyporhamphus					ì	,				,
micropterus** 2 (64–95 Parexocoetus brachypterus 160 (8–72)	2 (64-95) $160 (8-72)$	83 (33-183) $86 (15-113)$			85 246	46 (8–42)	43 (12-110) $112 (13-128)$			43 158
Prognichthys occidentalis* Hemiramphidae	36 (11–74)	45 (17–147)			81	7 (11–35)	62 (15–165)			69
$Euleptorhamphus\ velox*$	11 (45-216)	3 (180–318)			14	9 (44–75)	6 (56–388)			15
Hemiramphus balao		20 (32–198)			30		2(95-104)			7
Hemiramphus brasiliensis*	22 (33-84)	7 (45–114)			29	2(37-52)	3(58-111)		4 (236–242)	တ က
Hyporhamphus	09 (01–10)				oo		0 (24–110)			5
unifasciatus*	1 (30)				1					0
Holocentridae Holocentridae					c		1 (69)			-
Syngnathidae					0		1 (02)			-
$Bryx\ dunckeri^*$	4 (28–47)		4 (35-42)		œ	1(32)				1
Hippocampus erectus	$12 (17-143)^{\dagger}$				12	$2(25-67)^\dagger$				07 (
$Hippocampus\ reidi^*$	$2(72)^{\dagger}$				N -					0 0
Hippocampus sp. Syngnathus louisianae	$\frac{1}{24}$				- -					o
Syngnathus pelagicus	1 (117)		15 (78–158)		<u>-</u> 16	1 (110)				, ,
Fistularidae	(0)				•					c
Fistularia tabacariar Fistularia sp.	I (69)				1 0	1 (138)				1 0
Acropomatidae										
$Synagrops\ bellus^*$	1 (45)				1					0
$Echeneis\ naucrates^*$				2 (630–680)	2			1 (665)		1
Remora osteochir*	1(26)									0
Coryphaenidae Coryphaena eauiselis*	2 (26–32)	18 (28–68)			20	1 (30)	6 (37–91)			7
Coryphaena hippurus	99 (26–262)	22 (32–178)		41 (275–1020) 162) 162	7 (26–112)	7 (27–188)	23 (370 - 623)	1(286)	38
Carangidae <i>Alectis ciliaris</i>					0	4 (12–15)				4

			Sargassum				Op	Open water		
Taxon	NN (96)	NL (42)	DN (18)	HL (7)	Total n	NN (39)	NL (33)	HL (7)	LL (1)	Total n
Carangidae (cont.) Caranx bartholomaei	3 (20–61)	1 (34)			4					0
Caranx crysos	1646 (11–82)	91 (12–65)	96 (11–61)		1833	271 (11-72)	73 (12-99)			344
$Caranx\ lugubris^*$	57 (16_89)	3(21-29)			လ ဂိ					0 0
Caranx sp.	20 (11-21)	3(15-21)	18 (11–22)		g. 14	12 (11–18)	2 (11–17)			5 4
Decapterus punctatus	144 (10-44)	19 (10-32)	3(24-35)		166	150 (10–44)	$\frac{1}{1}(18)$			151
Decapterus sp.	11 (16–30)		1(20)		12		1(28)			-
Elagatis bipinnulata	18 (17-81)	5(24-43)			73	4 (18 91)	1(19)			— ч
Selene setaninnis st	(67–11) ‡		1 (19)		+ -	$\frac{4}{1}(13)$	1 (20)			- c
Selene vomer					0	$\frac{3}{3}(11-13)$				က
Selene sp.	1	1	,		0	1 (14)				1
Seriola dumerili	7(11-70)	3(37-47)	1(48)		11	(00,00)				0 1
Seriola fasciata Seriola rinoliana	59 (12–107) 260 (12–95)	1 (26) $4 (16-57)$	2 (29–32) 4 (20–36)		268 268	4(23-30) $13(21-47)$	3 (14–34)			4 4
Seriola zonata	4 (23–37)				4	$\frac{1}{1}(16)$				7
Seriola sp.	21(12-66)	4 (13–71)	8 (11–22)		33	4 (11–16)	1(12)	1 (N/A)		9
Trachinotus carolinus Trachinotus falcatus					0 0	1 (14)	2(21-23)			- 7
Lobotidae					>	(11) 1				4
Lobotes surinamensis	11(11-52)	2(29-30)	1 (33)		14					0
Mullidae										
Mulloidichthys martinicus*		1 (87)			- с		60			0 -
<i>Pseudupeneus macutatus</i> Kyphosidae		3 (31–43)			n		1 (26)			-
Kyphosus incisor	2(29-91)	4 (19–39)	1 (14)		7					0
Kyphosus sectatrix Kyphosus sp.	30 (15-89) $1 (15)$	2 (25–33)			32		2 (19–21)			0 8
Formacentrique $Abudefduf$ saxatilis	45 (16–29)	2 (18–19)	4 (16–20)		51					0
Sphyraenidae										
Sphyraena barracuda					0			1(1219)		1
Sphyraena borealis*	1(31)				1					0
Gempylus serpens					0		3 (64–81)			က
Scombridae										
$Auxis\ thazard^*$		2(62-86)			21 C			0 (439 495)		0 0
Scomber colias					0					27
C L L L					<				(000 010)	٥

			Tab	Table 1 (continued)	tinued)					
		37	Sargassum				Open	Open water		
Taxon	NN (96)	NL (42)	DN (18)	HL (7)	$\begin{array}{c} \text{Total} \\ n \end{array}$	NN (39)	NL (33)	HL (7)	LL (1)	$\begin{array}{c} \text{Total} \\ n \end{array}$
${\rm Istiophoridae} \\ Istiophorus \ platypterus^*$	4 (22–41)	4 (32–118)			∞	2 (17–24)	38 (20–204)			40
Makaira nigricans Nomeidae					0		1(205)			1
Psenes cyanophrys Balistidae	5 (35–52)				ŭ					0
Balistes capriscus	345 (10–74)	19 (12–113)	37 (11–63)		401	17 (10–35)	2(19-25)			19
Canthidermis maculata Canthidermis suffamen	17(11-24) $26(11-18)$		2(14-22) $1(45)$		19 27	1 (13)				0 -
Xanthichthys ringens	$\frac{1}{1}(21)$	1 (65)			; ²⁷					0
Unidentified Monacanthidae	2 (N/A)				73					0
Aluterus heudelotii	69 (25–70)	1(50)	4 (31–44)		74	1(24)	2 (36–39)			က
Aluterus monoceros	34 (33-151)	6(53-95)			40	1(52)	1 (103)			2
$Aluterus\ schoepfii$	21 (18-69)				21	9(16-38)	1 (46)			10
Aluterus scriptus	42(20-113)	5(36-122)			47		1(32)			Н (
Aluterus sp.	3(15-26)	(90) 1			1 cc					0 0
Cantherhines macrocerus Cantherhines pullus	0(30-67)	$\frac{1}{1}(90)$			- 25	2 (42–60)				0 8
Monacanthus ciliatus	176 (10–26)		6(16-27)		182	7 (12–17)	1 (21)			∞
Monacanthus tuckeri	14 (16-24)		4(17-25)		18					0
Monacanthus sp. $1 (14)$	1(14)	0) 000	1064 (0.60)		10 770	1(13)	(90 (10) 36)			1177
Stephanolepis nispiaus 12 Stephanolepis setifer	$\frac{2,420(8-09)}{1(40)}$	(16-8) 887	1004 (8-08)		10,772	(64-0) 1011	10 (10–10)			0
Stephanolepis sp.					0	2(10-11)				2
Tetraodontidae										
Lagocephalus		1 (197)			-					C
Diodontidae		(171)			4					Þ
Chilomycterus sp.	1(22)				1					0
Diodon holocanthus	6(15-55)	3(46-75)			6		1 (51)			П
don hystrix	2(37-219)	1(85)			က		2(160-212)			2
Total 16	16,482	886	1285	44	18,799	1820	820	55	11	2706

combined, 33 species were collected only in association with *Sargassum* habitat, and 13 species were unique to open-water habitat (Table 1).

There was a large discrepancy between *Sargassum* and open-water catches from the 2000-03 neuston net samples. A total of 14,123 fishes, representing 65 species, were collected in 91 neuston tows in *Sargassum* habitat. Thirteen open-water tows produced no catch, whereas 14 open-water tows yielded 1393 fishes,

representing 27 species (Table 2). Dominant families collected by neuston net in both Sargassum and openwater habitats were Monacanthidae (83% of S, 79% of OW), Carangidae (9%, 13%), and Exocoetidae (4%, 6%). Individuals of eight species represented 95% of the total Sargassum catch with neuston nets (in decreasing order of abundance): $S.\ hispidus,\ C.\ crysos,\ C.\ melanurus,\ B.\ capriscus,\ M.\ ciliatus,\ S.\ rivoliana,\ P.\ brachypterus,\ and\ C.\ hippurus.$ Individuals of four species represented 93%

 $\textbf{Table 2} \\ \text{Number of fishes collected in neuston net tows from } Sargassum \text{ and open-water habitat off North Carolina during 2000-03, separated by day and night. Number of samples is in parentheses. Species are listed in phylogenetic order.}$

	Sarg	gassum	Open	water		Sarga	ssum	Open w	ater
Species	Day (47)	Night (44)	Day (19)	Night (8)	Species	Day (47)	Night (44)	Day (19)	Night (8)
$Cyclothone \; { m sp.}$	1	0	0	0	Caranx bartholomaei	2	1	0	0
Argyropelecus aculeatus	1	0	0	0	Caranx crysos	342	468	31	43
Diaphus dumerilii	1	0	0	0	Caranx ruber	23	33	0	0
Myctophum affine	0	27	0	0	Caranx spp.	2	18	1	1
Myctophum obtusirostre	0	10	0	0	Decapterus punctatus	9	44	78	1
Myctophum punctatum	1	4	0	0	Decapterus spp.	4	7	0	0
Myctophum selenops	0	1	0	0	Elagatis bipinnulata	5	5	0	0
Myctophum sp.	0	1	0	0	Selar crumenophthalmus	2	0	0	0
Histrio histrio	7	2	0	0	Selene setapinnis	0	0	1	0
Mugilidae	0	2	0	0	Seriola dumerili	3	4	0	0
Ablennes hians	6	8	1	2	Seriola fasciata	30	21	4	0
Platybelone argalus	0	$\overset{\circ}{2}$	0	0	Seriola rivoliana	125	35	13	0
Tylosurus acus	1	2	0	0	Seriola spp.	12	9	3	1
Tylosurus spp.	0	2	0	0	Seriola zonata	0	4	1	0
Cheilopogon cyanopterus	0	6	0	0	Lobotes surinamensis	9	1	0	0
Cheilopogon exsiliens	0	2	0	0	Kyphosus incisor	0	2	0	0
Cheilopogon furcatus	0	2	0	0	Kyphosus sectatrix	11	1	0	0
Cheilopogon melanurus	31	365	5	49	Kyphosus sp.	1	0	0	0
Cheilopogon spp.	0	6	0	0	Abudefduf saxatilis	5	5	0	0
Cvpselurus comatus	0	1	0	0	Istiophorus platypterus	1	3	1	1
Cypseturus comatus Hirundichthys affinis	0	13	0	6	Psenes cyanophrys	0	5	0	0
	U	15	U	O	Balistes capriscus	120	109	9	5
Oxyporhamphus	0	2	0	0	Canthidermis maculata	9	109	0	0
micropterus	0	2	0	0		23	3	0	1
Parexocoetus	10	140	0	177	Canthidermis sufflamen		0	0	0
brachypterus	19	140	2	17	Xanthichthys ringens Balistidae	1 0	2	0	0
Prognichthys occidentalis	9	26	1	6					
Euleptorhamphus velox	1	10	0	2	Aluterus heudelotii	48	17	0	0
Hemiramphus balao	3	7	0	0	Aluterus monoceros	1	3	0	1
Hemiramphus brasiliensis	0	21	1	0	Aluterus schoepfii	10	7	0	1
Hemiramphus spp.	2	31	0	0	Aluterus scriptus	31	8	0	0
Hyporhamphus	_			_	Aluterus sp.	0	1	0	0
unifasciatus	0	1	0	0	Cantherhines macrocerus	2	3	0	0
Bryx dunckeri	2	1	1	0	Cantherhines pullus	3	9	2	0
Hippocampus erectus	3	8	0	1	Monacanthus ciliatus	75	97	1	6
Hippocampus reidi	1	1	0	0	Monacanthus tuckeri	9	4	0	0
Hippocampus sp.	1	0	0	0	Monacanthus sp.	1	0	0	0
Syngnathus louisianae	1	0	0	0	Stephanolepis hispidus	7840	3541	681	408
Syngnathus pelagicus	1	0	1	0	Stephanolepis setifer	1	0	0	0
Fistularia sp.	0	0	1	0	Chilomycterus sp.	0	1	0	0
Synagrops bellus	0	1	0	0	Diodon holocanthus	1	5	0	0
Coryphaena equiselis	2	0	0	1	Diodon hystrix	1	1	0	0
Coryphaena hippurus	13	71	1	0	Total	8869	5254	840	553

of the total open-water catches with neuston nets (in decreasing order of abundance): *S. hispidus, D. punctatus, C. crysos,* and *C. melanurus.* There were significantly more individuals (Mann-Whitney test: df=117, P<0.001) and numbers of species (Mann-Whitney test: df=117, P<0.001) in Sargassum habitat compared with open-water habitat. The three most abundant species in neuston net collections containing Sargassum habitat also exhibited the highest frequencies of occurrence: S. hispidus (70% of samples), C. crysos (64%), and C. melanurus (46%), whereas in open-water habitat these species occurred in 41%, 19%, and 22% of samples, respectively. Forty of the total 65 species collected in 2000–03 neuston net tows in Sargassum were unique

to this habitat, whereas only two (*Fistularia* sp., *Selene* setapinnis) of the total 27 species collected in open-water habitat were unique (Table 2).

Day versus night catch composition

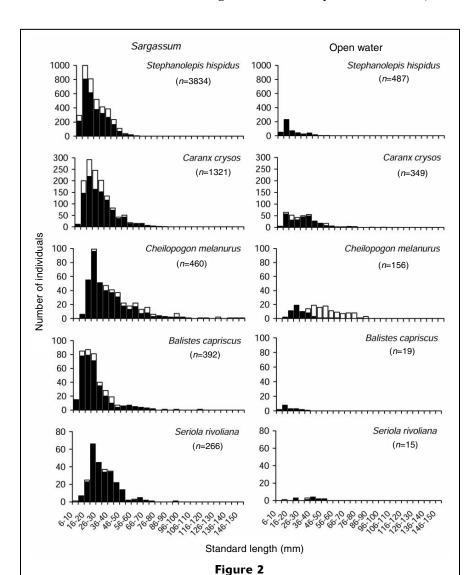
Regardless of sampling time (day or night), Sargassum habitat yielded significantly (Kruskal-Wallis test: df=3, P<0.05) higher numbers of individuals and species than open-water habitat. Daytime neuston net samples from Sargassum habitat (n=47) yielded 8869 fishes from 48 species, and nighttime neuston net samples from Sargassum habitat (n=44) yielded 5254 fishes from 56 species (Table 2); however, these differences were not statisti-

cally significant (Kruskal-Wallis test: df=3, P=0.924). Supplemental methods used in Sargassum habitat (dip nets, hook-and-line, 1999 neuston net) yielded different results; slightly more fishes (350 individuals) were collected at night than during the day. This finding was likely due to the slightly higher effort at night and the attraction of fish by the nightlighting.

As above, most fishes from neuston net samples in open-water habitat were collected during the day. Ten of the total 19 daytime neuston net tows in open-water habitat yielded 840 fishes, representing 20 species, and four of the total eight nighttime neuston net samples in open water yielded 553 fishes, representing 18 species (Table 2); however, these differences were not statistically significant (Kruskal-Wallis test: df=3, P=0.843). Supplemental methods used in open-water habitat (dip nets, hook-and-line, 1999 neuston net, long line), as above, produced more fishes at night (213 more individuals), probably for the same reasons.

Size distributions

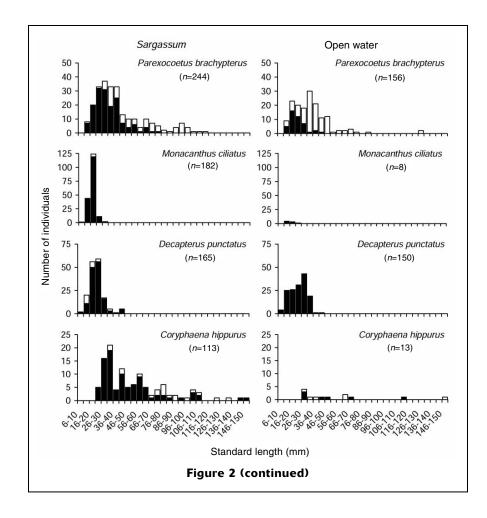
Ninety-six percent of all fishes collected in surface waters during these summer and fall cruises were juveniles and most (88%) were \leq 50 mm SL. The majority of S. hispidus (79% S, 87% OW), C. crysos (72%, 61%), B. capriscus (79%, 95%), M. ciliatus (100%, 100%), and D. punctatus (93%, 86%) collected in both Sargassum and open-water habitats were \leq 30 mm SL (Fig. 2). Cheilopogon melanurus collected



Length-frequency distributions of the nine most abundant fishes collected from Sargassum and open-water habitats during summer and fall of 1999–2003 off North Carolina. Neuston net collections = black bars and supplemental gears = white bars. Only juvenile specimens were graphed for *Cheilopogon melanurus* (Atlantic flyingfish) and $Coryphaena\ hippurus$ (dolphinfish). Note differences in y-axis scale.

in Sargassum habitat ranged from 13 to 253 mm SL, but the majority (84%) were juveniles <150 mm SL. Cheilopogon melanurus collected in open-water habitat ranged from 12 to 257 mm SL, and the majority (77%) were also juveniles <150 mm SL (Fig. 2). Coryphaena hippurus collected in Sargassum habitat ranged from 25 to 1020 mm SL, the majority (80%) of which were at the juvenile stage (<300 mm SL), and C. hippurus collected in open-water habitat ranged from 26 to 623 mm SL, 45% of which were juveniles (<300 mm SL) (Fig. 2).

Overall, fishes collected from neuston net tows containing Sargassum habitat (8-374 mm SL, $mean=26 mm [\pm 0.2 mm])$ were significantly larger (Kolmogorov-Smirnov test: df=7464, *P*<0.001) than fishes collected from openwater habitat (8-138 mm SL, mean=23 mm $[\pm 0.4]$) by the same method. Individuals collected in neuston net tows with Sargassum were significantly larger (Kolmogorov-Smirnov test, P < 0.05) than individuals of the same species collected in neuston tows in open water for seven of the nine most abundant species (Table 3).



Sargassum abundance and fish distribution

Despite variability, the quantity of Sargassum habitat was correlated with fish species richness and density. A significant positive linear relationship existed between the overall numbers of fishes and Sargassum wet weight

from neuston net samples (Fig. 3A). For five (S. hispidus, C. melanurus, B. capriscus, S. rivoliana, P. brachypterus) of the eight most abundant Sargassum-associated fish species collected by neuston net during 2000–03, a significant positive relationship existed between numbers of individuals and Sargassum wet weight (Fig. 4).

Table 3

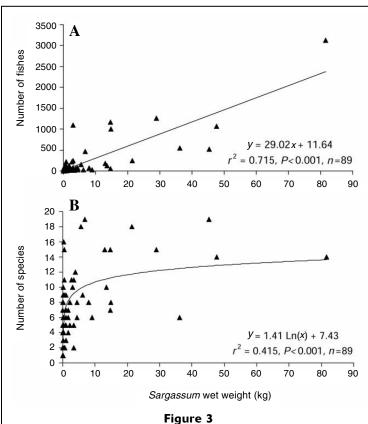
Mean standard length (SL) (\pm standard error [SE] in mm) of abundant fish species collected with neuston nets from Sargassum (S) and open-water (OW) habitats off North Carolina during 1999–2003. n=number of fishes, * = statistically significant (Kolmogorov-Smirnov test, P<0.05).

		Mean Sl	$L \pm SE (mm)$	
Species	S	n	OW	n
Stephanolepis hispidus	22* (±0.2)	2872	18 (±0.4)	470
Caranx crysos	$28*(\pm 0.4)$	1007	$27 (\pm 0.7)$	276
Cheilopogon melanurus	$35*(\pm 0.8)$	392	$27 (\pm 1.2)$	57
Balistes capriscus	$23*(\pm 0.7)$	336	17 (±1.7)	17
Seriola rivoliana	$32 (\pm 0.7)$	257	$35 \ (\pm 2.6)$	12
Monacanthus ciliatus	$17*(\pm 0.2)$	176	14 (± 0.8)	7
Parexocoetus brachypterus	$31*(\pm 1.0)$	158	22 (±1.0)	44
Decapturus punctatus	$21 \ (\pm 0.5)$	143	$23*(\pm 0.6)$	149
Coryphaena hippurus	$40*(\pm 2.6)$	142	29 (±5.1)	21

Although a significant positive logarithmic relationship was observed between numbers of species and Sargassum wet weight (Fig. 3B), similar numbers of species were often collected regardless of Sargassum quantities. For example, the maximum number of species (n=19) collected in one neuston tow coincided with a relatively low quantity of Sargassum habitat (6.8 kg) (Fig. 3B).

Behavioral observations

Underwater video recordings clarified the close association of juvenile fishes to structure compared with open water. Many juvenile fishes rapidly explored and associated with any new substrata introduced near the *Sargassum* mats (e.g., snorklers, vessel). As in our other collections, the two most abundant families of fishes observed in the video recordings were Monacanthidae (mostly *S. hispidus*) and Carangidae (*Caranx* spp. and *Seriola* spp.). Fishes exhibited a size-related layering among and below the *Sargassum* (Fig. 5, A–C). Smaller juvenile fishes were usually very close to or within the *Sargassum* and were rarely observed more than one meter below the algae (Fig. 5A), whereas larger, more mobile juvenile fishes (e.g., carangids and kyphosids)



Relationships between number of individuals (**A**) and number of species (**B**) and *Sargassum* wet weight (kg) for all fishes collected with neuston nets in *Sargassum* habitat during summer and fall of 2000–2003 off North Carolina. Note differences in *y*-axis scale.

were further below the *Sargassum* (Fig. 5B). Even deeper below the *Sargassum* (up to 3 m), larger predators (e.g., adult dolphinfish and jacks) were observed, usually in schools (Fig. 5C). When large predators swam below the *Sargassum*, smaller fishes moved upward into the algae (Fig. 5A).

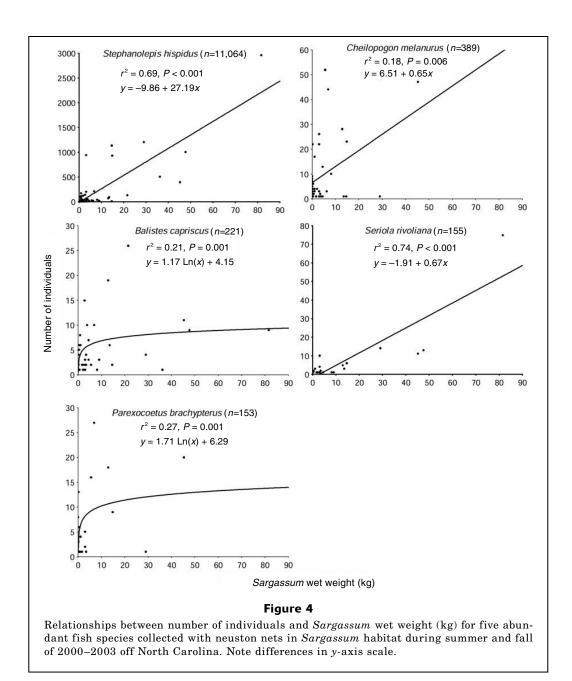
Other behaviors were also observed from the underwater video recordings. Individuals and groups (7–10 individuals) of juvenile Aluterus monoceros (with a light to dark brown mottled pattern, Fig. 5D) were observed hovering just below the Sargassum with heads down at a 45° angle, tails near the surface (Fig. 5D). A school (about 65 individuals) of adult A. monoceros (silver body color) exhibited the same behavior under the hull of the vessel, which was adjacent to the weedline. On 15 occasions, small groups (2-15 individuals) of juvenile S. hispidus were observed pursuing and nipping at lobate ctenophores, Mnemiopsis leidyi (Fig. 5E). These interactions took place about 1.5 m below the Sargassum, and S. hispidus was the only species observed displaying this behavior. A distinct boundary was observed between open-water and Sargassum habitats; the open water adjacent to the edge of the weedline was unpopulated, whereas a high density of juvenile

fishes were observed underneath and within the *Sargassum* (Fig. 5F).

Schools of adult dolphinfish (approximately 10-50 individuals) were observed swimming under the weedline on seven occasions. Most of these appeared to be females based on head shape and estimated sizes, but some may have been immature males. A female (295 mm SL), ripe with eggs, was collected from the vessel by hook-and-line during video recording operations. On five of the seven occasions, adult Caranx bartholomaei and C. crysos were mixed with the school of dolphinfish or swam closely behind them. On one occasion, a single large juvenile dolphinfish (approximately 300 mm SL) swam rapidly upward into the Sargassum with its mouth open, turned away at the weedline, and swam away; however, no small fishes were observed under the Sargassum in the vicinity of the strike, and it was not possible to determine the success of this apparent feeding attempt.

Discussion

Pelagic *Sargassum* habitat supports an abundant and diverse assemblage of juvenile fishes, providing structure and protection in relatively barren oceanic surface waters. Juvenile fishes dominate the *Sargassum* community, and the majority of fishes collected in this study from *Sargassum* habitat were comparable in size (<50 mm SL) to those reported from other *Sargassum* studies (Dooley, 1972; Wells and Rooker, 2004). As with seagrass ecosystems



(Stoner, 1983), the strong association of small fishes with *Sargassum* and their behaviors around the algae indicates that this habitat provides shelter from predation. Schooling of *A. monoceros* to mimic floating seaweed (Crawford and Powers, 1953) and the camouflage coloration of juvenile monacanthids, balistids, and other taxa within *Sargassum* fronds help conceal them from predators (Fig. 5, A and D). The increasingly close association of fishes to the floating algae with decreasing fish size further indicates a strong role of the habitat in mitigating predation. Larger fishes, like adult dolphinfishes and jacks, aggregating below the weedlines, appeared to use *Sargassum* primarily during feeding (Dooley, 1972; Moser et al., 1998; this study). *Sargassum* habitat seems

to provide an ecological advantage as illustrated by the trend of several species exhibiting larger sizes in *Sargassum* habitat compared to open-water habitat, but it is not clear if this advantage results from better food resources or lack of predation within the algal habitat.

As a result of intensive sampling, the number of fish species known to associate with *Sargassum* habitat in U.S. waters was substantially increased. Eighty fish species were collected in association with *Sargassum* in this study, forty-one percent of which had not been previously reported in association with pelagic *Sargassum*. Mesopelagic fishes spend most of their lives in a habitat lacking structure and have not been reported to seek structured habitats. Thus, the seven species of



Figure 5

Fishes under a Sargassum weedline observed during underwater video recordings, August 1999, off Cape Hatteras, North Carolina. (A) Small planehead filefish ($Stephanolepis\ hispidus$) amongst the Sargassum, (B) larger, more mobile jacks (carangids) below the Sargassum, (C) large predators ($Coryphaena\ hippurus\ [dolphinfish]$) using $Sargassum\ habitat$, (D) schooling of $Aluterus\ monoceros\ (unicorn\ filefish)$ at a 45° angle, (E) $Stephanolepis\ hispidus\ pursuing\ and\ picking\ at\ a\ lobate\ ctenophore\ (<math>Mnemiopsis\ leidyi$), and (F) edge of a $Sargassum\ weedline$.

mesopelagic fishes representing three families (Gonostomatidae, Sternoptychidae, Myctophidae) collected with Sargassum likely resulted from combinations of their upward diel migrations, upwelling (reported from the Cape Hatteras study area: Lohrenz et al., 2002; Thomas et al., 2002), or convergent currents bringing them into contact with Sargassum, rather than the result of attraction to the algae. The associations of many fish species with Sargassum appears to be facultative (Dooley, 1972; Wells and Rooker, 2004), and all studies to date have recorded fishes incidentally associated with Sargassum that are normally not considered to be structure-associated species. It remains difficult to determine exactly why or how some species use this habitat and the degree to which it influences their life histories.

Despite methodological differences between the studies, patterns of abundance for dominant species collected from Sargassum habitat were comparable to those from previous collections off North Carolina, Florida, and in the Gulf of Mexico. Stephanolepis hispidus dominated all Sargassum collections in all areas, followed closely by C. crysos and B. capriscus (Dooley, 1972; Wells and Rooker, 2004). Histrio histrio was abundant in Gulf of Mexico (Bortone et al., 1977; Wells and Rooker, 2004) and Florida east coast (Dooley, 1972) collections with Sargassum but was not abundant in collections off North Carolina (Dooley, 1972; Moser et al., 1998; this study). Because the majority of *H. histrio* are found in the Sargasso Sea and Caribbean Basin (Adams, 1960), their lower abundance off North Carolina may represent a winnowing of the population with northward or westward drift. Dooley (1972) suggested a progressive decrease in fish species richness from Florida to North Carolina and across the Atlantic to the Azores. This decrease in species richness may be an artifact of limited collections off North Carolina and the Azores because our more extensive sampling produced Sargassum-related species richness exceeding that reported in other areas. Although based on limited sampling, data indicate that fewer fish species are associated with Sargassum habitat in the Sargasso Sea compared with Sargassum habitat in the Gulf of Mexico or the Gulf Stream (Fine, 1970; Stoner and Greening, 1984). The great difference between the Sargasso Sea and U.S. continental shelf collections indicates that the majority of the fish fauna recruits to Sargassum habitat after the algae are entrained into the Loop Current (Gulf of Mexico) and the Florida and Gulf Stream currents.

The structural complexity of habitats strongly affects fish assemblages. Our open-water samples contained fewer fishes compared with samples containing Sargassum habitat. Clearly, fishes that use Sargassum habitat also are found in open water without Sargassum, but abundance is heavily skewed toward floating structured habitat (Kingsford, 1993). Stephanopelis hispidus dominated both habitats but was two orders of magnitude more abundant in Sargassum collections. Considering this, and that S. hispidus usually occupies structured habitat, it seems likely that the S. hispi

dus collected from open-water habitat may have been displaced by physical disturbance to Sargassum mats, or they may have been caught in open water because they had strayed away from the preferred habitat. If so, an even larger difference exists between open-water and Sargassum fish communities. The strong fidelity of fishes to floating Sargassum habitat is also illustrated by the distinct boundary observed between open-water and Sargassum habitats (Fig. 5F). The open water adjacent to the edge of the weedline was unpopulated, compared with the area immediately underneath and within the *Sargassum* where a high density of juvenile fishes was evident. Higher abundances and diversity of fishes in vegetated (versus unvegetated) habitats is a common theme (Weinstein et al., 1977; Orth and Heck, 1980) that results from increased structural complexity (Stoner, 1983). Although fundamental differences exist between Sargassum and seagrass ecosystems, fish communities use the two habitats in similar ways. Both habitats are nursery areas for juvenile fishes and support diverse and abundant fish communities. Additionally, the abundance of fishes increases with increasing seagrass density (Orth and Heck, 1980; Thayer and Chester, 1989) and Sargassum abundance (Moser et al., 1998; Wells and Rooker, 2004).

Juvenile fishes may seek drifting objects to improve future benthic settlement opportunities (Dempster and Kingsford, 2004), thus facilitating early survival and eventual recruitment to adult populations. Most of the juvenile fishes using Sargassum are species that ultimately occupy either inshore benthic reef or complex, structured habitats (demersal) or the open ocean (pelagic). However, the length of time juvenile fishes reside in Sargassum and the fates of juvenile fishes after leaving this habitat are unknown. Some fishes remain in the Sargassum longer than expected, perhaps because they missed a settlement opportunity. This appears to be the case for some unusually large juveniles (e.g., Hippocampus spp., Mulloidichthys martinicus, Kyphosus spp., A. saxatilis, balistids, monacanthids) collected in the present study. Caribbean damselfishes, including A. saxatilis, settle between 10 and 12 mm SL (Robertson et al., 1993), yet A. saxatilis collected in our study from Sargassum habitat were 16–29 mm SL. The dominant Sargassum-associated fish, S. hispidus, may settle into North Carolina estuarine seagrass beds at 11-40 mm (Adams, 1976; Ross and Epperly, 1985), well below the sizes of some individuals collected offshore in this study. The movement of large quantities of Sargassum habitat across the continental shelf as far as the estuaries transports vast numbers of associated juvenile fishes toward other habitats (e.g., seagrass beds, reefs) and probably facilitates recruitment to adult populations.

Young fishes entrained in the Gulf Stream that ultimately have demersal populations, including species using *Sargassum*, have a more uncertain future once they drift north of Cape Hatteras where the Gulf Stream moves offshore (McBride and Able, 1998; Ross et al., 2007). Juveniles of demersal species that do not move from *Sargassum* before reaching the Cape Hatteras area

may 1) exit the Gulf Stream and settle north of North Carolina, 2) continue across the North Atlantic in the Gulf Stream and possibly settle in the eastern Atlantic, 3) complete a circuit of the North Atlantic until they return to the western North Atlantic, or 4) ultimately not contribute to their respective populations (McBride and Able, 1998; Ross et al., 2007). Even though Sargassum and associated fishes can be transported into the Middle Atlantic Bight or farther north (Dooley, 1972), the first alternative is unlikely given that most demersal fish species using Sargassum are of tropical or warm temperate origins and are not established as adults north of North Carolina (Winge, 1923; McBride and Able, 1998). The second alternative, also suggested by Dooley (1972), seems possible because fifty-three (66%) of the 80 total species collected off North Carolina are established in the eastern Atlantic (Hureau and Monod, 1973a, 1973b), but the link (if any) between these fishes and those in the western Atlantic remains unclear. The third alternative seems least likely because most of the fishes collected in the surface waters do not have larval or juvenile periods long enough to complete a circuit of the Atlantic basin (Ross et al., 2007). It seems likely that many of the fishes remaining in the Sargassum north of Cape Hatteras eventually perish. Pelagic species (e.g., carangids, exocoetids, Coryphaena spp.) are probably not as restricted and can emigrate from Sargassum habitat to open-water habitat over a broader geographic area. Despite the fact that huge numbers of fishes use Sargassum habitat in the early life stages, data are lacking regarding its role in transporting juveniles to inshore habitats, in settlement processes, and to what extent Sargassum-associated fishes contribute to their respective populations.

Sargassum is an unusual and difficult habitat to sample, and no ideal sampling method has yet been applied. The algae and their medium (water) are in constant motion, and the density and structure of the habitat are constantly changing. One cannot predict exactly when or where Sargassum will occur and, unlike static habitats, it cannot be mapped. Thus, it is generally difficult to collect a known number or type of samples from this habitat. Sampling in this study was balanced between day and night, but for the above reasons was not balanced between the two habitats. Sampling the Sargassum fauna includes collecting the habitat as well, and the density of the habitat coupled with the three dimensional layering of associated nekton reduce the efficiencies of most sampling gear (especially dip nets). The approach in this study of using a large neuston net to consistently encompass a substantial volume of surface water allowed for large enough samples over a wide range of algal densities.

There is little doubt that *Sargassum* habitat constitutes an important and unique marine ecosystem. It provides a feeding area for many large pelagic fishes, marine mammals, seabirds, and sea turtles. *Sargassum* may enhance early survival of many fishes by protecting them from predation and by concentrating prey, thus providing a unique nursery habitat in an otherwise

relatively barren area of the western North Atlantic Ocean. For these reasons, Sargassum was designated as essential fish habitat by the South Atlantic Fisheries Management Council. The role of Sargassum in transporting juveniles to inshore habitats and subsequent impacts on population recruitment should be investigated.

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