

though it has been assumed that they could see color because of the relative numbers and arrangement of rods and cones in the retina of *Tursiops* (Perez et al. 1972). But since very little in the animals' open ocean experience involves much color, the painted marks may hold small significance for them.

Since our purpose was to test the feasibility of paint marking of porpoises, no attempt was made to create an ideal paint, though a paint formulated specifically for marking doubtless would have been better than those we used. Our experiments began with available paints, and those that were found to coat wet surfaces were modified for use in pressurized containers with high volume valves. Paint manufacturers generally are prepared to process only large volume orders, but we found that smaller specialty companies were able to prepare formulations to order and modify small quantities of pressurized paint containers.

#### Conclusions

Paint marking of porpoises provides a satisfactory short-term tag that can be applied at sea. The paint has not modified the animals' behavior and it seems not to be detrimental in any way. The high visibility of the colors we tried often made it possible to locate the marked animal when other porpoises of the school were obscured. The underwater paint marking technique would appear to be potentially useful in the study of other aquatic animals.

#### Acknowledgments

We appreciate the help and advice extended by G.V. Cass of Krylon Department, Borden, Inc., and Helene R. Johnson of Lenmar, Inc. We are grateful also to the Naval Undersea Center, San Diego, for their hospitality and good nature in allowing our paint experiment, especially J. C. Sweeney, Sam H. Ridgway, and William E. Evans. Teresa Bray participated in laboratory test and manuscript preparation. Support for this work was from the Oceanic Biology Program of the Office of Naval Research, contract N00014-74-C-0262.

#### Literature Cited

- EVANS, W. E.  
1974. Radio-telemetric studies of two species of small odontocete cetaceans. In W. E. Schevill (editor), *The whale problem*, p. 385-394. Harvard Univ. Press, Camb., Mass.
- EVANS, W. E., J. D. HALL, A. B. IRVINE, AND J. S. LEATHERWOOD.  
1972. Methods for tagging small cetaceans. *Fish. Bull., U.S.* 70:61-65.
- HARRISON, R. J., AND K. W. THURLEY.  
1972. Fine structural features of delphinid epidermis. (Abstr.) *J. Anat.* 111:498-500.
- NORRIS, K. S., W. E. EVANS, AND G. C. RAY.  
1974. New tagging and tracking methods for the study of marine mammal biology and migration. In W. E. Schevill (editor), *The whale problem*, p. 395-408. Harvard Univ. Press, Camb., Mass.
- NORRIS, K. S., AND R. L. GENTRY.  
1974. Capture and harnessing of young California gray whales, *Eschrichtius robustus*. *Mar. Fish. Rev.* 36(4): 58-64.
- NORRIS, K. S., AND K. W. PRYOR.  
1970. A tagging method for small cetaceans. *J. Mammal.* 51:609-610.
- PALMER, E., AND G. WEDDELL.  
1964. The relationship between structure, innervation and function of the skin of the bottle nose dolphin (*Tursiops truncatus*). *Proc. Zool. Soc. Lond.* 143:553-567.
- PEREZ, J. M., W. W. DAWSON, AND D. LANDAU.  
1972. Retinal anatomy of the bottlenosed dolphin (*Tursiops truncatus*). *Cetology* 11:1-11.
- SCHEVILL, W. E.  
1956. *Lagenorhynchus acutus* off Cape Cod. *J. Mammal.* 37:128-129.  
1966. Comments. In K. S. Norris (editor), *Whales, dolphins, and porpoises*, p. 487. Univ. Calif. Press, Berkeley and Los Ang.
- WATKINS, W. A., AND W. E. SCHEVILL.  
1975. Sperm whales (*Physeter catodon*) react to pingers. *Deep-Sea Res.* 22:123-129.

WILLIAM A. WATKINS  
WILLIAM E. SCHEVILL

Woods Hole Oceanographic Institution  
Woods Hole, MA 02543

#### GRAZING OF FRESHWATER AND ESTUARINE, BENTHIC DIATOMS BY ADULT ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*

The diet of the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe), varies with stages in metamorphosis and the availability of food resources, but it has been characterized consistently in the literature as derived from the particulate organic components of planktonic ecosystems (Reintjes 1969; June and Carlson 1971; Jeffries 1975; Peters and Kjelson 1975; Durbin and Durbin 1975). Menhaden larvae feed primarily by selective predation on the larger estuarine zooplankters. Their metamorphosis into prejuveniles brings about the

development of a functional branchial filtering apparatus which promotes a grazing of phytoplankton and suspended detritus. Late juveniles and adults are primarily herbivores also but retain the ability to eat zooplankton.

The stimulus for this investigation was a shoreline observation of adult menhaden grazing directly on the benthic microbial communities covering the rocks in the headwaters of a Massachusetts estuary. The fish were observed to bite or rip off chunks of the benthic community film and swallow them. This film was composed primarily of diatoms and detritus. Subsequent gut analyses of the fish and the epilithic diatom assemblage confirmed the field observations. Additionally, ingestion of these benthic primary producers and their associated detritus by juvenile menhaden is postulated from a reinterpretation of previous reports on their diet.

#### Methods

In the early afternoon of 19 September 1974, nine adult menhaden (25-34 cm fork length) were collected in the oligohaline region of the Slocum River estuary, Mass. (Hoff et al. 1969). The fish were sampled with a 10-m, 64-mm mesh haul seine from a school of about 150, which was observed feeding on the bottom within a 500-m<sup>2</sup> area about 1 m deep for the 15 min prior to collection. The pyloric stomachs were excised, opened, and their fullness visually estimated. The stomach contents of each fish were maintained and examined separately; they were preserved in 3% formaldehyde solution. A preliminary microscopic examination of the contents was made to determine the presence of diatoms and other components of the diet. Diatoms were prepared for detailed examination by a nitric acid-dichromate oxidation of an aliquot of the sample followed by washing of the cleaned frustules and mounting in Hyrax<sup>1</sup> (Hohn and Hellerman 1963). Diatom populations in each sample were identified and enumerated from a random sample of about 200 frustules, which were observed using oil-immersion phase-contrast optics at a magnification of 1000 $\times$ .

On 21 September 1974, a 20-cm diameter rock was removed from the same region of the estuary in which the menhaden had been observed feeding. The diatom assemblage on the rock was air-dried, then scraped off and subjected to the

same procedures of preparation and examination as those derived from the stomachs.

All samples and slides have been deposited in the Hellerman Diatom Herbarium at Southeastern Massachusetts University according to the following collection numbers: HH918-HH926 (stomach samples) and HH927 (epilithic sample).

The diatom populations were classified as freshwater, brackish, or marine based on the habitat in which they grow optimally. This classification was derived primarily from the works of Hustedt (1937-1938, 1939), Patrick and Reimer (1966), Foged (1947, 1954), and Cleve-Euler (1951-1955). Only those populations identified without reservation to the species level were classified ecologically. Additionally, in an ecological classification of diatoms, identification of populations to the level of variety is desirable among multivarietal species, because frequently different varieties of the same species have different optimal habitats.

The terms "common" and "rare," as employed in this paper, differentiate diatom populations having greater than 1% or less than 1% mean relative abundance, respectively, in the stomach samples.

#### Results

All fish stomachs were completely full or nearly so. Amorphous detritus and diatoms composed the bulk of the material with the detritus accounting for the greater portion, but as estimated microscopically, from 5 to 25% of the volume was diatomaceous. Most larger diatom cells were broken and without contents, but many smaller diatoms retained their chromatophores in structurally intact frustules. Other microorganisms, particularly filamentous blue-green algae and nematodes, were evident, and the remnants of some microcrustaceans were noted in a few stomachs.

The examination of about 1,800 diatom individuals from the stomachs revealed 163 populations of which 134 were identified to species or variety. Twenty-three populations were common and only three of them were not assignable to a particular species (Table 1). The rare populations which were unidentified constituted less than 2% of all individuals. Practically all the populations are benthic. Eight of them, particularly *Skeletonema costatum* and *Thalassiosira* spp., are considered planktonic, but they contained less than 7% of all individuals and were found also on the rock. Freshwater populations composed 50% of the common and nearly 70% of all populations (Table

<sup>1</sup>Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—The relative abundance (%) and the optimal habitats of the common diatoms occurring both in the stomachs of Atlantic menhaden and on a rock from the Slocum River estuary, Mass. Only those populations having greater than 1% mean relative abundance in the stomachs are listed.

Diatoms	Fish stomachs		Rock	Optimal habitat <sup>1</sup>
	Mean	Range		
<i>Nitzschia frustulum</i> var. <i>perminuta</i> Grun.	8.0	4.1-13.3	2.3	F
<i>N. subtilis</i> var. <i>paleacea</i> Grun.	8.0	1.5-13.5	0.5	F
<i>Navicula cincta</i> (Ehr.) Ralfs	6.8	3.6- 9.6	5.0	B
<i>Melosira nummuloides</i> (Dillw.) Ag.	6.7	1.8-18.9	1.4	B
<i>Skelatonema costatum</i> (Grev.) Cl.	4.5	1.9- 6.3	0.5	B/M
<i>Cyclotella</i> sp. cf. <i>glomerata</i> Bachm.	4.2	1.5- 8.7	4.6	?
<i>Eunotia pectinalls</i> (Dillw.) Rabh. var. <i>pectinalls</i>	3.0	1.4- 4.5	2.7	F
<i>Achnanthes minutissima</i> Kütz.	2.9	0.5- 5.9	1.4	F
<i>Bacillaria paradoxa</i> Grmel.	2.8	0.9- 5.1	1.8	B
<i>Cyclotella</i> sp. cf. <i>atomus</i> Hust.	2.8	0.5- 5.8	5.5	?
<i>Melosira varians</i> Ag.	2.8	0.9- 5.0	0.5	F
<i>Navicula diserta</i> Hust.	2.3	0.0- 4.1	0.5	M
<i>Navicula capitata</i> var. <i>hungarica</i> (Grun.) Ross	2.2	0.5- 4.0	1.4	F
<i>Eunotia pectinalls</i> var. <i>minor</i> (Kütz.) Rabh.	2.1	0.9- 5.9	2.7	F
<i>Fragilaria construens</i> var. <i>venter</i> (Ehr.) Grun.	2.0	0.0- 5.0	2.7	F
<i>Navicula gregaria</i> Donk.	2.0	0.0- 4.0	1.4	B
<i>Rhoicosphenia curvata</i> (Kütz.) Grun.	1.9	1.4- 2.7	1.8	F/B
<i>Nitzschia sigma</i> W. Sm.	1.7	0.9- 4.4	1.4	M
<i>Thalassiosira</i> sp. cf. <i>nana</i> Hust.	1.7	0.5- 1.9	0.5	?
<i>Achnanthes wellsiae</i> Reim.	1.5	0.9- 2.8	0.9	F
<i>Nitzschia parvula</i> Lewis	1.5	0.0- 1.5	25.6	F
<i>Cyclotella striata</i> (Kütz.) Grun.	1.3	0.5- 3.0	4.1	B
<i>Fragilaria construens</i> var. <i>intercedens</i> (Grun.) Hust.	1.1	0.0- 2.7	1.8	F
Total	73.8		71.0	

<sup>1</sup>F = freshwater, B = brackish, M = marine.

2). They accounted also for more than 50% of all individuals. Brackish and marine populations were present in about equal numbers, but more common populations were brackish. Nearly 35% of all individuals belonged to brackish populations. All common populations in the stomachs were at least present on the rock, and 17 of the 23 also accounted for greater than 1% relative abundance in the epilithic assemblage (Table 1). Additionally, 24 rare populations were found in both the stomach and the epilithic samples. The greater number of rare populations found in the stomachs as compared to the rock is attributable to the greater sample size associated with the stomachs. These rare populations were primarily species of *Achnanthes*, *Amphora*, *Cocconeis*, *Cymbella*, *Eunotia*,

*Fragilaria*, *Gomphonema*, *Navicula*, *Nitzschia*, and *Synedra*.

Based on the examination of about 200 individuals from the epilithic assemblage, 43 populations were identified to species or variety. Twenty identified and three unidentified populations were common in the fish stomachs (Table 1). Only four other populations were unidentified, and they represented less than 3% of all individuals in the sample. All populations are benthic. Given the means of collection of the epilithic assemblage, those populations usually considered planktonic were clearly benthic. They accounted for about 7% of the total number of individuals in the assemblage, as they did in the stomach samples. Nearly 90% of all populations found on the rock were recorded in the stomachs. Freshwater populations accounted for about 50% of both the common and all populations (Table 2). Brackish and marine populations occurred equally among all populations, but among the common ones, brackish populations were more frequent. A population of the freshwater diatom, *Nitzschia parvula*, constituted 25% of the whole assemblage.

#### Discussion

The benthic microbial communities of estuaries and the adjacent freshwater reaches of rivers, as

TABLE 2.—The distribution of numbers of common and rare diatom populations from the stomach and epilithic assemblages among their optimal habitats (F = freshwater, B = brackish, M = marine). Populations interpreted as growing equally well in two habitats are divided equally between them.

Diatom populations	Stomachs <sup>1</sup>				Rock <sup>2</sup>			
	F	B	M	Total	F	B	M	Total
Common	11.5	6.0	2.5	20.0	11.5	6.0	2.5	20.0
Rare	79.5	15.0	19.5	114.0	12.0	2.5	8.5	23.0
All	91.0	21.0	22.0	134.0	23.5	8.5	11.0	43.0

<sup>1</sup>Total sample size  $\approx$  1,800 individuals.

<sup>2</sup>Total sample size  $\approx$  200 individuals.

well as probably those of shallow marine coastal waters, are utilized directly as a food resource by adult and juvenile menhaden. Our field observations of their grazing habits, the preponderance of benthic diatoms in their stomachs, and the taxonomic and ecological similarity of the diatom assemblages in their stomachs with that of the benthos support this conclusion. The composition of the stomach and epilithic samples is commensurate with the expectations of random sampling of the benthos in this region of the estuary. The quantitative characteristics of estuarine benthic diatom assemblages can be extremely variable within a small space, even on similar substrates (McIntire and Overton 1971; Round 1971; Main and McIntire 1974), and so the expectation of quantitative identity among random samples is low. But, much greater qualitative similarity is expected of samples from similar substrates in the same area.

The data of other investigators, but not their conclusions, support our findings. In a study of the diet of juvenile menhaden collected between April and June 1961, in Delaware, June and Carlson (1971) found most frequently eight genera of diatoms present in their guts: "*Pleurosigma*, *Navicula*, *Nitzschia*, *Cyclotella*, *Melosira*, *Ampthora*, *Gyrosigma*, and *Surirella*." All these genera are characteristically benthic in marine and estuarine ecosystems. Compared to the list of diatom genera they reported from the phytoplankton, which they sampled between November 1960 and May 1961, in the same area, the eight genera accounted on the average for less than 10% of the total number of diatom phytoplankters. Furthermore, they reported that *Skeletonema*, *Coscinodiscus*, *Rhizosolenia*, *Thalassiosira*, and *Thalassiothrix* composed on the average 75% of the diatom phytoplankton, but all were unrecorded from their gut analyses of the fish. We conclude from their data that the juvenile menhaden they collected were not grazing primarily on the plankton but rather on the benthos. Likewise, Mulkana (1966) reported six diatom genera from the stomachs of juvenile menhaden collected in Rhode Island estuaries, and four of the six are usually benthic: *Gyrosigma*, *Grammatophora*, *Achnanthes*, and *Navicula*. Although the diatoms, whether planktonic or benthic, appear to constitute a less significant portion of the diet of juveniles and adults in estuaries than does detritus (Jeffries 1975; Peters and Kjelson 1975), they accurately reflect the immediate source of the

detritus, because they are good habitat labels (Round 1964, 1971).

Both juvenile and adult menhaden tolerate salinities of less than 1‰ (Reintjes 1969), but we know of no records other than our own of their feeding on primarily freshwater or oligohaline resources.

The Atlantic menhaden is among the commercially most important species in the United States fishery, and consequently, the factors which regulate its population size are of considerable interest. Assuming that human and other predators are prudent, trophic energy availability is likely to be limiting. McHugh (1967) has postulated that "the rate of plankton production will limit the numbers of menhaden . . . that a particular body of water can support." If we interpret the concept of the plankton liberally, including the living organisms plus the suspended detritus, the idea is certainly tenable; however, it is conditional upon the menhaden's grazing being restricted to the plankton. Also, adult menhaden's minimum-size threshold for filtration of particles appears to be around 15  $\mu\text{m}$  with the consequence that a substantial portion of the phytoplankton will be unavailable to them (Durbin and Durbin 1975). But, considering the productivity of benthic primary producers and the quantities of sedimented detritus in shallow estuaries (Darnell 1967; Odum 1971; Smayda 1973), the menhaden's exploitation of the benthos, potentially, at least, doubles the energy available to it. Unfortunately, the quantitative significance of their benthic grazing habits and their ability to assimilate the ingested materials during the estuarine portions of their life cycle are unassessed.

Jeffries (1975) has characterized the menhaden as an adaptable species capable of switching from one food resource to another, and thus compensating for the variability in the availability of estuarine food resources. In general, this apparent switching in juveniles and adults is more the product of a fine-grain feeding in resource-different habitats than of coarse-grain feeding on the plankton. Our observations extend this mode of feeding in menhaden to include benthic habitats.

#### Literature Cited

- CLEVE-EULER, A.  
1951-55. Die Diatomeen von Schweden und Finnland. K. Sven. Vetenskaps akad. Handl., Ser. 4, 1,2(1):1-163, (1951);

- II,4(1):1-158, (1953); III,4(5):1-255, (1953); IV,5(4):1-232, (1955); V,3(3):1-153, (1952).
- DARNELL, R. M.  
1967. Organic detritus in relation to the estuarine ecosystem. In G. H. Lauff (editor), *Estuaries*, p. 376-382. Am. Assoc. Adv. Sci. Publ. 83.
- DURBIN, A. G., AND E. G. DURBIN.  
1975. Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. *Mar. Biol. (Berl.)* 33: 265-277.
- FOGED, N.  
1947. Diatoms in water-courses in Funen. II. Lindved AA (The Lindved Brook). III. Odense AA (The Odense Brook). *Dan. Bot. Ark* 12(6):1-69. 1954. On the diatom flora of some Funen lakes. *Folia Limnol. Scand.* 6, 75 p.
- HOFF, J. G., P. BARROW, AND D. A. MCGILL.  
1969. Some aspects of the hydrography of a relatively unpolluted estuary in southeastern Massachusetts. *Proc. 24th Ind. Waste Conf., Purdue Univ. Eng. Exten. Ser.* 135:87-98.
- HOHN, M. H., AND J. HELLERMAN.  
1963. The taxonomy and structure of diatom populations from three eastern North American rivers using three sampling methods. *Trans. Am. Microsc. Soc.* 82:250-329.
- HUSTEDT, F.  
1937-1938. Systematische und ökologische Untersuchungen über die Diatomeen-Flora von Java, Bali und Sumatra. *Arkiv Hydrobiol. Suppl.-Bd. XV: "Tropische Binnengewässer,"* 506 p.  
1939. Die Diatomeenflora des Küstengebietes der Nordsee vom Dollart bis zur Elbe-mündung. *Abh. Naturwiss. Ver. Bremen* 31:572-677.
- JEFFRIES, H. P.  
1975. Diets of juvenile Atlantic menhaden (*Brevoortia tyrannus*) in three estuarine habitats as determined from fatty acid composition of gut contents. *J. Fish. Res. Board Can.* 32:587-592.
- JUNE, F. C., AND F. T. CARLSON.  
1971. Food of young Atlantic menhaden, *Brevoortia tyrannus*, in relation to metamorphosis. *Fish. Bull., U.S.* 68:493-512.
- MAIN, S. P., AND C. D. MCINTIRE.  
1974. The distribution of epiphytic diatoms in Yaquina Estuary, Oregon (U.S.A.). *Bot. Mar.* 17:88-99.
- MCHUGH, J. L.  
1967. Estuarine nekton. In G. H. Lauff (editor), *Estuaries*, p. 581-620. Am. Assoc. Adv. Sci. Publ. 83.
- MCINTIRE, C. D., AND W. S. OVERTON.  
1971. Distributional patterns in assemblages of attached diatoms from Yaquina Estuary, Oregon. *Ecology* 52: 758-777.
- MULKANA, M. S.  
1966. The growth and feeding habits of juvenile fishes in two Rhode Island estuaries. *Gulf Res. Rep.* 2:97-167.
- ODUM, E. P.  
1971. *Fundamentals of ecology.* 3rd ed. W. B. Saunders, Phila., 574 p.
- PATRICK, R., AND C. W. REIMER.  
1966. The diatoms of the United States exclusive of Alaska and Hawaii. Vol. 1: Fragilariaceae, Eunotiaceae, Achnantheaceae, Naviculaceae. *Monogr. Acad. Nat. Sci. Phila.* 13, 688 p.
- PETERS, D. S., AND M. A. KJELSON.  
1975. Composition and utilization of food by postlarval and juvenile fishes of North Carolina estuaries. In L. E. Cronin (editor), *Estuarine Research*. Vol. 1, p. 448-472. Academic Press, N.Y.
- REINTJES, J. W.  
1969. Synopsis of biological data on the Atlantic menhaden, *Brevoortia tyrannus*. U.S. Fish Wildl. Serv., Circ. 320, 30 p.
- ROUND, F. E.  
1964. The ecology of benthic algae. In D. F. Jackson (editor), *Algae and man*, p. 138-184. Plenum Press, N.Y.  
1971. Benthic marine diatoms. *Oceanogr. Mar. Biol., Annu. Rev.* 9:83-139.
- SMAYDA, T. J.  
1973. Phytoplankton. In *Coastal and offshore environmental inventory: Cape Hatteras to Nantucket Shoals*, Sec. 3, 100 p. Mar. Publ. Ser. 2, Univ. Rhode Island, Kingston.

ROBERT K. EDGAR  
JAMES G. HOFF

*Hellerman Diatom Herbarium*  
*Southeastern Massachusetts University*  
*North Dartmouth, MA 02747*

#### ELECTROPHORETIC EVIDENCE OF HYBRID SNOW CRAB, *CHIONOECETES BAIRDI* × *OPILIO*

Karinen and Hoopes (1971) and Hoopes et al. (1972) reported finding snow (Tanner) crabs in the southeastern Bering Sea which possessed morphological characteristics that were atypical for either *Chionoecetes bairdi* or *C. opilio* and, instead, were intermediate. The females of this form appeared to have reduced reproductivity, as many were nongravid at maturity, and those that were gravid possessed abnormally small egg clutches containing large numbers of dead eggs. These conditions were presented as evidence of hybridization. Hybrid-type males constituted 1.0% of all male snow crabs captured, while hybrid-type females made up 0.4% of the females captured.

Karinen (1974) confirmed the above reports and found that hybrids made up 4.6% of the snow crabs collected in the Bering Sea and were most abundant west of lat. 166°W. The carapace width frequency of the hybrids was intermediate between *C. bairdi* and *C. opilio*—providing additional evidence of hybridization.

The purpose of the present study was to determine if electrophoretic differences between the parent species and the hybrid could be detected.

The samples used were collected from the southeastern Bering Sea in July 1974, identified, and frozen by National Marine Fisheries Service (NMFS) personnel. The general proteins of leg