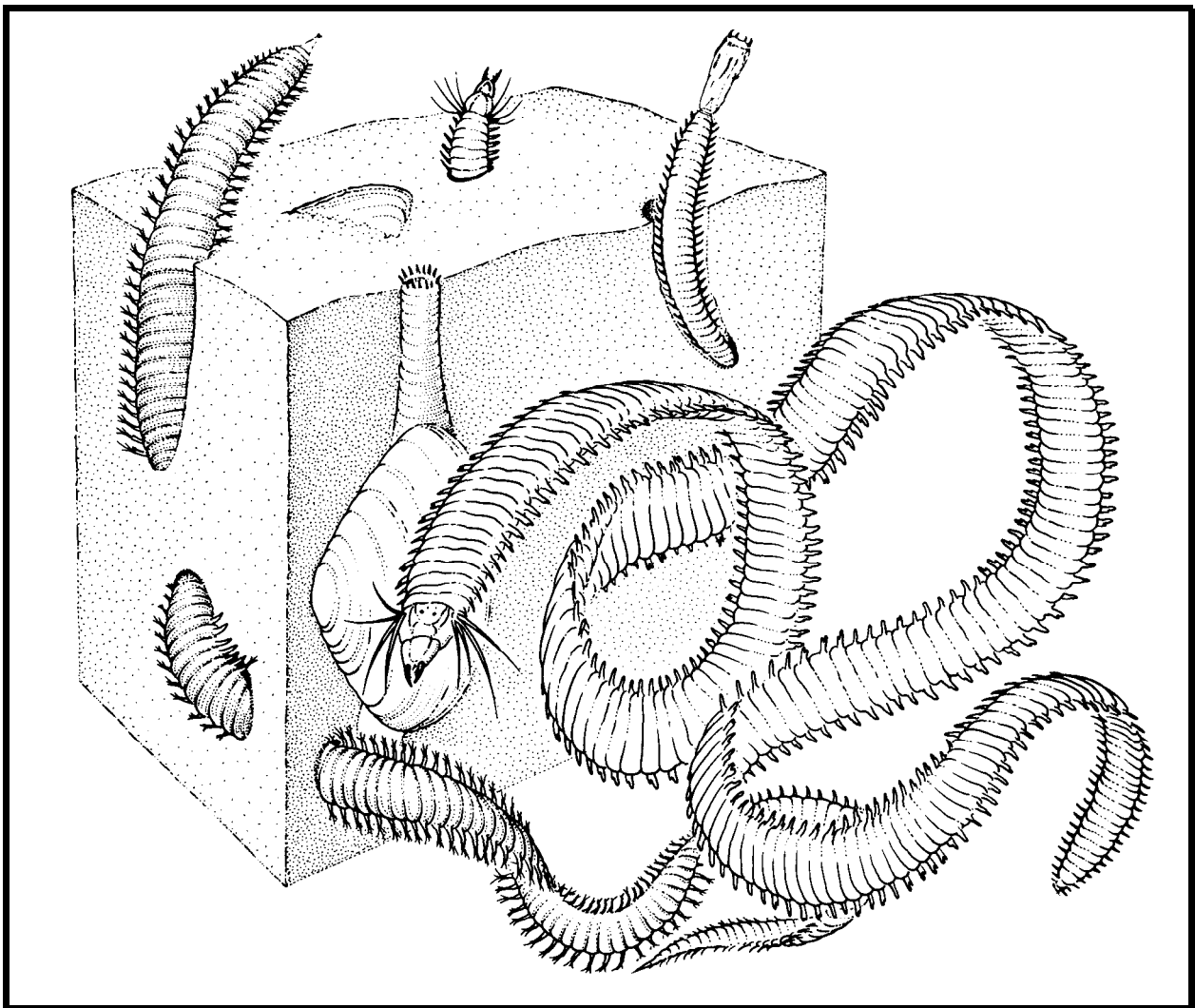


Species Profiles: Life Histories and
Environmental Requirements of Coastal Fishes
and Invertebrates (North Atlantic)

SANDWORM AND BLOODWORM



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**Species Profiles: Life Histories and Environmental Requirements
of Coastal Fishes and Invertebrates (North Atlantic)**

SANDWORM AND BLOODWORM

by

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and

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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CONVERSION TABLE

Metric to U.S. Customary

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m ²)	10.76	square feet
square kilometers (km ²)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m ³)	35.31	cubic feet
cubic meters (m ³)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft ²)	0.0929	square meters
square miles (mi ²)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft ³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F - 32)	Celsius degrees

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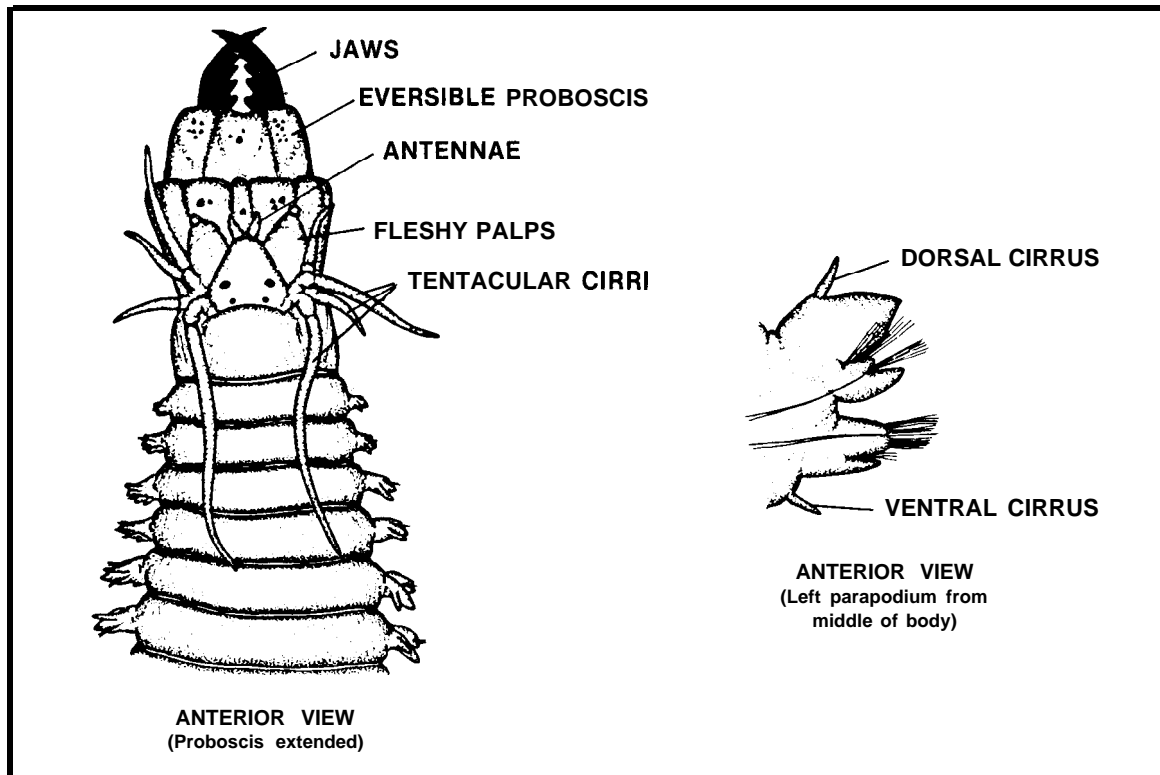


Figure 1. Sandworm (*Nereis virens*).

SANDWORM

NOMENCLATURE/TAXONOMY/RANGE

Scientific name....*Nereis (Neanthes) virens* Sars, 1835 (Figure 1)
Preferred common name.....Sandworm
Other common names.....Clamworm ragworm
Phylum.....Annelida
Class.....Polychaeta
Order.....Phyllodocta
Family.....Nereididae

Geographic range: Found on both sides of the North Atlantic as far south as France off Europe and south to Virginia off the east coast of the United States. Figure 2 shows the

distribution of the sandworm in the North Atlantic region of the United States. Also recorded in the north Pacific from Alaska to central California, in the Bering Sea, and off Japan. Ranges from the high water mark to about 150 m

MORPHOLOGY/IDENTIFICATION AIDS

Description

Body elongate, thickened anteriorly and somewhat flattened posteriorly, with more than 200 segments. Length up to 900 mm and width greater than

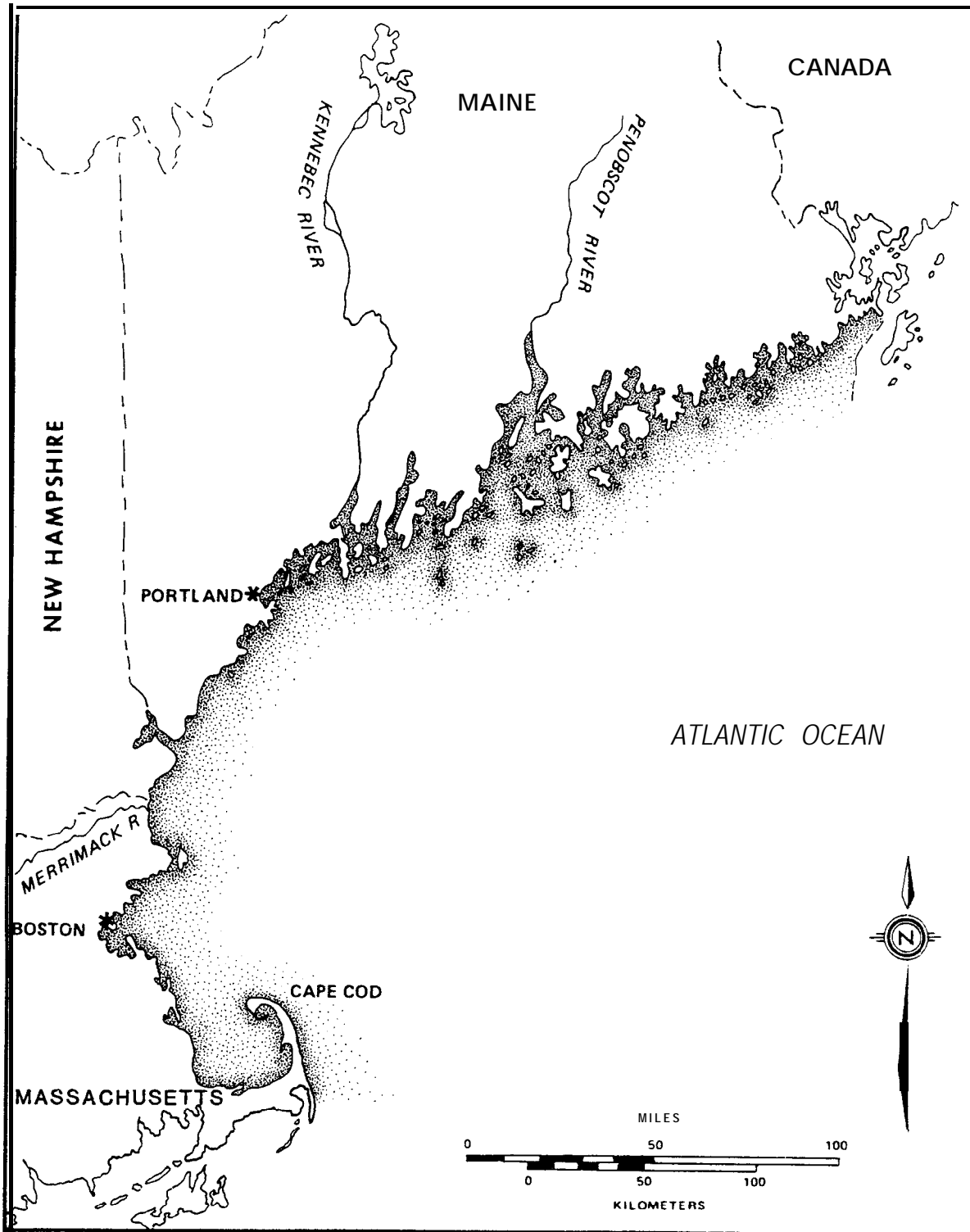


Figure 2. Distribution of sandworm in the North Atlantic region. Heavier stippling indicates regions of higher abundance.

40 mm Prostomium (head) small, pentagonal, with a distal pair of small antennae and two pairs of eyes in a trapezoidal arrangement (Figure 1). Head with a pair of stout, fleshy palps, each with a small, rounded palpostyle distally. Eversible proboscis with a pair of curved brownish or black jaws, each with 5 to 10 teeth. Dark, conical, chitinous paragnaths (teeth) embedded in the surface of the proboscis. Four pairs of slender tentacular cirri, the longest reaching as far as the ninth segment. The first segment lacking setae, twice the width of any following segment. Parapodia with dorsal and ventral lobes (biramous) with the same shape throughout the length of the body. Dorsal and ventral cirri digitiform. Setae from the dorsal rami (notopodia) consisting of long, jointed setae (homogonoph spinigers). Setae from the ventral rami of the parapodia (neuropodia) consisting of long, jointed setae (homogonoph and heterogonoph spinigers) and jointed setae with short, toothed blades (heterogonoph falcigers).

Identification Aids

The surface of the skin is iridescent, reflecting bright hues in the light. The body of the male is a dark blue, blending into green at the base of the parapodia. The females are a dull, greenish color. In both sexes, the parapodia appear orange to bright red due to the numerous capillaries in these appendages.

Taxonomic References

Refer to Sars 1835; Verrill 1873, 1881; Webster and Benedict 1884, 1887; Fauvel 1923; Treadwell 1939, 1941; Pettibone 1963; Imajima 1972.

REASON FOR INCLUSION IN SERIES

The harvesting of sandworms and bloodworms (Glycera dibranchiata) is a

multi-million dollar industry in Maine (Dow and Creaser 1970; Dow 1978; Schroeder 1978). Over 1,200 people are licensed to dig baitworms in Maine (Schroeder 1978). Since the early 1970's, the bloodworm populations in Maine have been declining, leading to increased harvesting of sandworms. Nevertheless, there seems to be no major concern that sandworms are being overharvested. Creaser et al. (1983) calculated the Maximum Sustainable Yield and Optimal Sustainable Yield for Maine populations. Blake (1979) suggested that bait-diggers are not altering the population structure of a heavily dug mudflat.

LIFE HISTORY

Gametogenesis

Like most polychaetes, the sexes in N. virens are separate (Bumpus 1898). In females from Maine populations, oocytes begin rapid growth in October or November with oocyte maturation occurring in the following April or May, when the oocytes' diameters reach 185-195 μ m (Creaser and Clifford 1982). The oogenic cycle requires 12-20 months, depending on when the oocytes are released into the coelom. The oocytes synthesize their own yolk (Fischer and Schmitz 1981). Snow and Marsden (1974) reported a similar temporal pattern of oogenesis for a N. virens population in the Bay of Fundy, with maturation occurring in May. Brafield and Chapman (1967) reported that oogenesis requires 12-14 months in a British population and that ripe oocytes appear in May. Spermatogenesis follows a similar chronology (Brafield and Chapman 1967; Snow and Marsden 1974; Creaser and Clifford 1982).

Spawning

Nereis virens is a semelparous species; reproduction results in death (Bass and Brafield 1972). Mature males become structurally modified for

swimming (epitokous) and swarm in the water column during times of the new moon (Brafield and Chapman 1967; Bass and Brafield 1972; Snow and Marsden 1974; Creaser and Clifford 1982). Temperatures in excess of 7-8 °C seem to be a precondition for spawning (Creaser and Clifford 1982; Goerke 1984a; Yokouchi 1985). Premature spawning can be induced by increasing temperature in the laboratory (Bass and Brafield 1972). Swarming of males is known to be under hormonal control as well (Marsden 1971, 1978; Marsden and Jost 1975; Bell and Marsden 1980). Females do not become swimming epitokes and do not swarm; fertilization is presumed to occur in the burrows of females (Creaser and Clifford 1982). Fecundity varies between 50,000 and 1,300,000 eggs, depending on the size of the female (Creaser and Clifford 1982).

Larval Development

Females of *N. virens* extrude fertilized eggs onto the surface of the mud (Snow and Marsden 1974). Development apparently occurs on or near the sediment surface. Snow and Marsden (1974) believed that planktonic embryos or larvae are not found in New Brunswick populations, although weak spontaneous swimming of larvae was observed in laboratory cultures. Bass and Brafield (1972) reported that trochophore larvae do enter the plankton, but never for more than 15 h. Sveshnikov (1960) and Yokouchi (1985) reported larvae with four segments in the plankton. Juveniles are benthic 12 days after fertilization and crawl into the intertidal zone after 16 weeks (Bass and Brafield 1972).

Population Structure

The demography of the sandworm is controversial. Brafield and Chapman (1967) concluded from their size-frequency data that sandworms mature in 2 or, occasionally, 3 years. Snow and Marsden (1974) claimed that Bay of

Fundy worms do not mature until 5 or 6 years of age. They re-analyzed the data of Brafield and Chapman (1967) and claimed that British worms mature after 6 or 7 years. Creaser and Clifford (1982) reported 5 distinct nodes in a Maine population which probably correspond to year-classes. Worms in a Norwegian population reproduce after 3 years (Kristensen 1984a). As with all other populations, reproduction results in death.

ECOLOGICAL ROLE

Feeding

Sandworms feed by extending a portion of their bodies from an opening of their mucus-lined burrows. The burrows consist of a series of interconnected U-shaped sections, generally in the upper 10 cm of mudflats (Reise 1981). Disagreements over the trophic status of sandworms span a century. *Nereis virens* was regarded as a predatory-ill (1873) and Maxwell (1897), and as an omnivore by Turnbull (1876). Gross (1921) concluded that sandworms are herbivorous and that they locate their food by chance encounter. His conclusion was challenged by Copeland and Wieman (1924) who showed that sandworms captured and ate animals in the laboratory; sandworms also demonstrated a well-developed chemoreceptive sense (see also Retzius 1895; Hamaker 1898; Case 1962). The thorough work by Goerke (1971a, b) showed that sandworms fed on both plant and animal material and that they should be considered omnivores. Recent field experiments have shown that sandworms feed on amphipods and polychaetes (Commito 1982; Ambrose 1984a, b; Commito and Schrader 1985).

Nereis virens feeds by capturing a food item with its eversible proboscis which is armed with two jaws. The jaws, especially the distal biting portions, are hardened with zinc, which accounts for up to 2.4% of the total jaw weight (Bryan and Gibbs

1979, 1980). The jaws are powerful enough to crush small bivalves (Lewis and Whitney 1968). Food items are passed into the esophagus, where a trypsin-like proteolytic enzyme is produced (Michel and DeVillez 1979), as well as other enzymes (Kay 1974). Lewis and Whitney (1968) have identified a cellulase which is induced by the presence of algae in the gut. Michel and DeVillez (1980) described striated spines in the esophagus which apparently triturate food items.

Several workers have estimated assimilation efficiency and production of sandworms. Kay and Brafield (1973) calculated an assimilation efficiency of 85.2% and annual production of 8.4 g ash-free dry weight/m². Kristensen (1984a) calculated the annual production of a Norwegian population as 23.7 g ash-free dry weight/m². Neuhoff (1979) demonstrated that *Nereis virens* has faster growth and higher efficiency than two congeners, *N. diversicolor* and *N. succinea*. Sandworm growth and efficiency is greater when worms are fed clam tissue than when fed oyster biodeposits (feces and pseudofeces) (Tenore and Gopalan 1974; Tenore et al. 1978).

Sandworms are also capable of taking up dissolved organic matter. Compounds shown to be absorbed include glutamic acid and aspartic acid (Chapman and Taylor 1968; Taylor 1969; Jorgensen and Kristensen 1980a, b), leucine (Bass et al. 1969), glycine (Jorgensen 1980), valine (Jorgensen 1979), and alanine and guanine (Jorgensen and Kristensen 1980a, b). All of these studies demonstrate that net influx occurs when worms are exposed to natural concentrations of free amino acids (varying from 40 to 2,011 mol). Jorgensen and Christiansen (1980a) showed that sandworms can obtain their total respiratory energy requirements by absorption of interstitial amino acids. The larvae can take up to 200 times the amount of leucine that adult worms take up, yielding final tissue concentrations

700 times that of the incubation medium (Bass et al. 1969).

Predator-Prey Relations

Predation by sandworms can have significant effects in marine soft-sediment communities. *Nereis virens* has been shown to reduce significantly the abundance of the amphipod *Corophium volutator*, permitting associated infauna to increase in abundance (Commito 1982; Ambrose 1984a, b). Commito and Schrader (1985) suggested that *N. virens* consumes the predatory polychaete *Nephtys incisa* when *C. volutator* is not present.

Sandworms are potential prey in marine food webs. A number of gull and tern species take spent sandworms (Spaans 1971; Shklyarevich 1979). Ambrose (1986) showed that gulls may take large, nonreproductive individuals. Cantin et al. (1974) showed that 16%-40% of the diet of Common Eiders, *Somateria mollissima*, in late May and mid-July is composed of *N. virens*. Significant numbers of sandworms are preyed upon by the polychaete *Glycera dibranchiata* (Ambrose 1984a, b).

Biogeochemical Effects

The exchange of solutes, such as nitrate, between the sediment and the overlying water is strongly affected by burrow-dwelling infauna like *Nereis virens* (Kristensen 1984b, 1985; Kristensen et al. 1985). The burrows of *N. virens* have been shown to increase the flux of ammonia into the water column and to be responsible for 35% of the nitrification and 38% of the denitrification in an estuarine habitat (Henriksen et al. 1980). Nitrification rates are higher in the burrow walls than on the sediment surface (Kristensen 1984b, 1985; Kristensen et al. 1985). Irrigation of burrows for respiration causes an increase in the uptake of glycine by the bacteria living in the burrows (Jorgensen et al. 1980). Ventilation

of the burrow creates a halo of oxidized sediment along the length of the burrow. It is not surprising that small zoobenthos aggregate in the oxidized regions outside of sandworm burrows; nematode and gnathostomid abundances were increased by 94% and 200% respectively, in the proximity of oxygen burrows (Reise 1981).

ENVIRONMENTAL REQUIREMENTS

Substratum

Nereis virens has been reported from a range of sediment types, varying from sandy muds to fine sands (Pettibone 1963; Bass and Brafield 1972; Snow and Marsden 1974; Reise 1981). Middier sediments seem to be preferred. Highest densities, up to 700/m², are found in the lower portions of the intertidal zone (Bass and Brafield 1972; Rasmussen 1973; Snow and Marsden 1974). The migration of nonreproductive adults in the water column in the winter (Dean 1978) may be a mechanism to allow sandworms to find more suitable benthic habitats.

Salinity

Nereis virens is euryhaline (Sayles 1935; Jørgensen and Dales 1957; Richards 1969; Wålmsby 1970; Appy et al. 1980), tolerating salinities as low as 0.5 ppt (Larsen and Doggett 1978). Nereis virens is intermediate in its ability to tolerate low and high salinity stress relative to three congeneric species: N. diversicolor, N. succinea, and N. pelagica (Theede et al. 1973). Reduced salinities cause an increase in ammonia excretion (Haberfield 1977) and tachycardia (deFur and Mangum 1979).

Dissolved Oxygen

Nereis virens has blood containing a hemoglobin used for oxygen transport rather than storage (Economides and

Wells 1975). Decreased oxygen tension results in increased ventilatory pumping of the burrow to increase oxygen transport to nonvascularized tissues (Lindroth 1938; deFur and Mangum 1979). Hymn (1932) noted that oxygen intake is independent of surrounding tension within moderate ranges of tension. The ventilation amplitude increases with increasing temperature (Kristensen 1981, 1983a, b, c).

When sandworms are exposed at low tide and oxygen tensions decline, an anaerobic pathway is utilized (Scott 1976; Scott et al. 1976). The worms produce large amounts of d-lactate and later pay an oxygen debt. Under long periods of anaerobiosis, sandworms switch to glycogen degradation which results in the production of succinate and volatile fatty acids (Schottler 1979).

Temperature

Kristensen (1983b) states that optimal temperatures are between 11 °C and 20 °C, although sandworms can tolerate temperatures as high as 37.5 °C in the laboratory. Richards (1969) claimed that sandworms are highly tolerant of changes in temperature.

Adaptability to Laboratory Conditions

Nereis virens is a potentially valuable research organism because it can be maintained in healthy culture in the laboratory (Goerke 1979, 1984b; Kristensen 1983c). Its adaptability to the laboratory led to its use in some of the first studies on conditioned response and habituation in invertebrates (Copeland 1930, 1934; Clark 1960; Evans 1963a, b, 1966). A word of caution is in order for any who use sandworms as bioassay organisms: sandworms maintained in seawater without sediment, where the worms cannot form burrows, may show abnormal metabolism (Pamatnat 1982).

Toxicology

Sandworms have been the focus of many studies on the bioavailability of heavy metals and organic pollutants. A significant fraction (30%-40%) of the total body burden of zinc is always found in the jaws (Bryan and Gibbs 1979, 1980), so concentrations of zinc in sandworms do not closely follow environmental concentrations, and sandworms are poor indicators of zinc contamination. The jaws contribute less than 1% of the total body burden of silver, cadmium, copper, iron, and lead. Cadmium uptake increases with increasing concentration in the environment; uptake, primarily from interstitial water, is greater in small worms (Ray et al. 1980). Rice and Chien (1977) suggested that there may be a cadmium detoxification mechanism in the coelomic fluid; body concentrations may be 1,000 times the seawater concentration. Biochemical stress indices have been determined for sublethal cadmium dosages (Carr and Neff 1982). Ray et al. (1981) indicated that the body burden of copper and zinc did not vary between clean and contaminated environments but significantly greater body burdens of lead and cadmium were found in worms from contaminated sites. Pereira and Kanungo (1981) demonstrated significant effects of

silver on respiration and osmotic balance.

Among organic contaminants, Eisler et al. (1972) determined that nitroacetic acid (NTA) at a concentration of 5,500 mg/l resulted in 50% mortality of sandworms. Sandworms are intermediate in tolerance to NTA compared to many other marine species (Eisler et al. 1972). Sandworms have been shown to accumulate and metabolize PCB's, with small worms accumulating 10.8 times the environmental concentration of 0.04-0.58 ppm and adults 3.8 times (Ernst et al. 1977; Goerke and Ernst 1977; Goerke 1979; McLeese et al. 1981). Excretion of PCB's can be described by an exponential function which varies with temperature; the maximum rate of elimination occurs at 12 °C (Goerke 1984c). Biochemical stress indices have been measured in response to pentachlorophenol (Carr and Neff 1981) and to refined oil products (Carr and Neff 1984). McElroy (1985) showed that a polycyclic aromatic hydrocarbon (PAH) was metabolized by Nereis virens. Sandworms accumulate and metabolize the insecticide Lindane, reaching equilibrium in 10-14 days (Goerke and Ernst 1980). Sandworms are much more tolerant of organochlorine pesticides than the shrimp Crangon septemspinosus (McLeese et al. 1982; Haya et al. 1984).

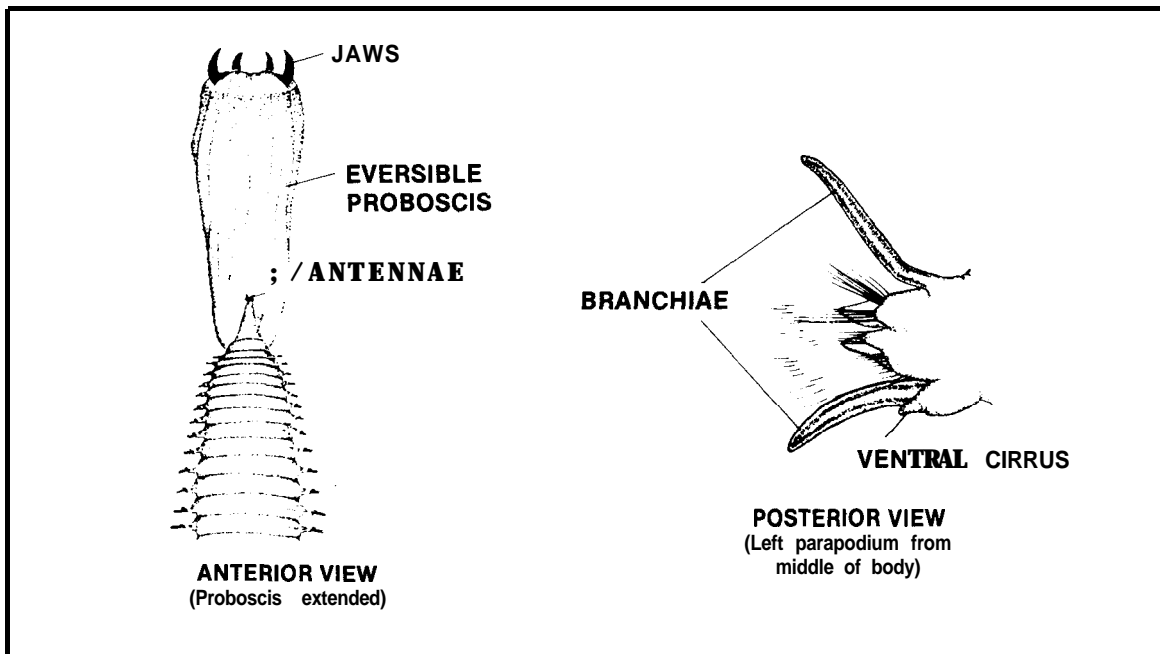


Figure 3. Bloodworm (Glycera dibranchiata).

BLOODWORM

NOMENCLATURE/TAXONOMY/RANGE

Scientific name.....Glycera dibranchiata Ehlers, 1868 (Figure 3)
 Preferred common name.....Bloodworm
 Other common names.....Beakworm
 beak-thrower
 Phylum.....Annelida
 Class.....Polychaeta
 Order.....Phyllodoidea
 Family.....Glyceridae

Geographic range: Found from low water out to about 400 m along the Atlantic coast from the Gulf of St. Lawrence to Florida. Also recorded in the Gulf of Mexico, and in the eastern Pacific from central California to Mazatlan, Mexico. Figure 4 gives the distribution of this species in the North Atlantic region.

MORPHOLOGY/IDENTIFICATION AIDS

Description

Body elongate, robust, having up to 300 segments. Largest individuals exceed 370 mm in length and 11 mm in width. Prostonium (head) conical, with 14-15 annulations and two distal pairs of antennae (Figure 3). Indistinct eyes on the basal annulation of the head, or eyes absent. Eversible proboscis with four dark, curved, hollow terminal jawpieces. Proboscis covered with small, conical proboscidean organs. Parapodia with dorsal and ventral lobes (biramous), bearing short dorsal cirri and more elongate ventral cirri. Paired, nonretractile gills or branchiae beginning on segments 15-20 and continuing to near

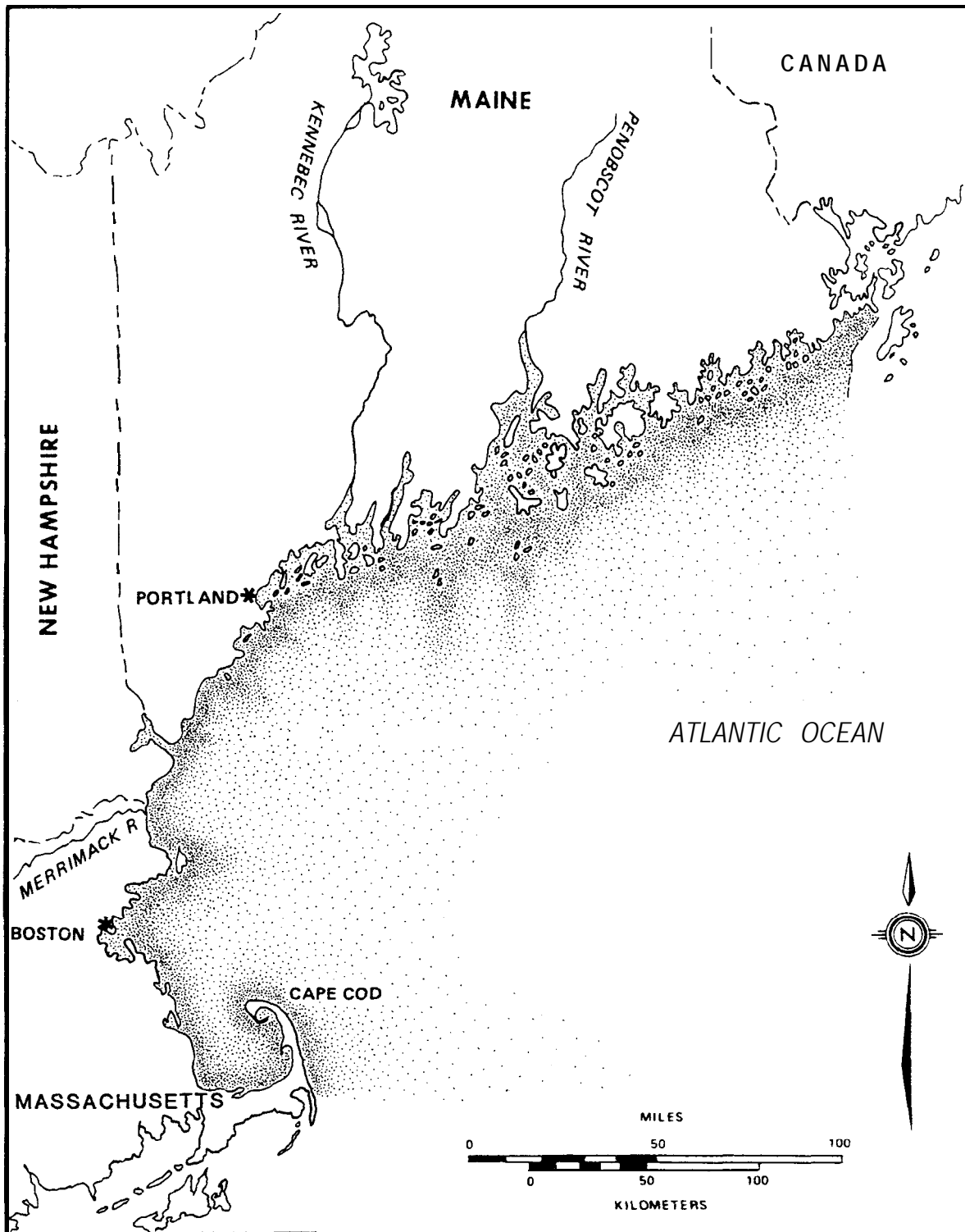


Figure 4. Distribution of bloodworm in the North Atlantic region. Heavier stippling indicates regions of higher abundance.

the posterior of the body; gills elongate or inflated, exceeding the length of the parapodia (Figure 3). Dorsal lobe of parapodia (notopodia) with simple, elongated, finely serrated setae. Ventral lobe (neuropodia) with simple and jointed elongated, finely serrated setae.

Identification Aids

The animals are bright pink. The species is characterized by the pair of enlarged gills above and below each of the middle parapodia. Glycera dibranchiata can be distinguished from the similar G. americana in that the latter has retractile, bush-like gills above the parapodia.

Taxonomic References

Refer to Ehlers 1868; Verrill 1881; Webster and Benedict 1884; Arwidsson 1898; Hartman 1940; Pettibone 1963.

REASON FOR INCLUSION IN SERIES

Baitworms (bloodworms and sandworms) are an important fishery in the Northeastern United States and Nova Scotia (MacPhail 1954; Klawe and Dickie 1957; Dow and Creaser 1970; Schroeder 1978). Baitworms form the fourth largest fishery in Maine, trailing only lobsters, clams, and total finfish. In the past 30 years, professional bait-diggers have removed nearly one billion bloodworms (Dow 1978). Over 90% of the bloodworms in the United States come from Maine with the remainder from Nova Scotia (7%) and Massachusetts (2%). Recent evidence, based on sampling of the worm sizes of commercial landings, indicates that 2-year old worms, rather than the larger 5-year old worms, are presently being harvested, suggesting that the populations are being overharvested (Dow 1978; but see Schroeder [1978] for an alternative interpretation of the data). Overharvesting of mudflats in two Maine counties has

eliminated bloodworms (Anonymous 1979). Genetic evidence also indicates that some populations are being overharvested (Vatias and Bristow 1985). Dow (1978) believes the only long-term solution to maintaining sufficient standing stock to support present intensities of harvesting is to culture worms under controlled environmental conditions. Creaser et al. (1983) presented models for the determination of Maximum Sustainable Yield and Optimal Sustainable Yield. The imposition of size-limits has been suggested (Saft 1978). Confounding attempts at managing stocks is an inverse correlation between bloodworm production and mean annual temperature; this relationship may explain some of the temporal variance in bloodworm densities (Dow 1978).

LIFE HISTORY

Gametogenesis

Separate sexes are found in bloodworms. Gametogenesis occurs in the undivided body cavity (coelom) and requires about 1 year (Simpson 1962a, b). Oocytes are released into the coelom when they are about 21 μm in diameter. Mature oocytes are 151-160 μm in diameter.

Spawning

Populations in Maine and southwestern Nova Scotia reproduce from mid-May until early June (Klawe and Dickie 1957; Creaser 1973). Populations from Maryland reproduce in the fall and possibly in late spring (Simpson 1962b). Shortly before reproduction, bloodworms undergo radical morphological changes. Their alimentary tract and musculature atrophy. Their parapodia and setae elongate. These sexual forms (epitokes) swarm in shallow water over a period of 1 to 3 days at high tide in the afternoon (Simpson 1962a, 1973). Males emit sperm while swimming. Females rupture, releasing up to 10 million

eggs per individual (Creaser 1973). Both males and females die after spawning.

Larval Development

The early development of Glycera dibranchiata apparently occurs on the sediment surface (Simpson 1962b). Development proceeds to swimming stages in 14-20 h after fertilization, giving rise to unspecialized, planktotrophic larvae (Simpson 1962a). The larvae are not found in plankton tows, suggesting that their planktonic life is short or that they are demersal (living just above the bottom).

Population Structure

Klawe and Dickie (1957) and Creaser (1973) found that Glycera dibranchiata has a maximum life span of 5 years. The most rapid growth occurs during the second and third years. Most bloodworms reproduce and die at 3 years of age although some postpone reproduction until the fourth or fifth year.

ECOLOGICAL ROLE

Feeding

There has been much debate about whether bloodworms are deposit-feeders or predators. Sanders et al. (1962) suggested that Glycera dibranchiata is a deposit-feeder, based on gut contents. Frankenberg and Smith (1967) and Adams and Angelovic (1970) demonstrated significant utilization of dead organic matter by bloodworms in the laboratory. Such findings are puzzling in light of the formidable feeding apparatus of G. dibranchiata. These worms possess an eversible proboscis which contains four terminal jaws (Wells 1937). The jaws are strengthened, particularly distally, by accumulation of copper; 13% of the distal tip is composed of copper (Gibbs and Bryan 1980). Each jaw is

coursed by a canal with numerous pores to the exterior through which a secretion from associated glands can flow (Michel 1966; Wölff 1976, 1977). The secretion is a neurotoxin, especially effective on crustaceans (Michel and Keil 1975). It is therefore not surprising that bloodworms have been found to feed on amphipods (Dubois-Laviolette 1985) and polychaetes (Ambrose 1984a, b).

A congeneric species, G. alba, has been shown to maintain a permanent gallery of burrows (Ockelmann and Vahl 1970). Prey are detected by mechanoreception and ambushed at the sediment surface. Glycera dibranchiata occupies burrows (Klawe and Dickie 1957), but their exact configuration has not been observed. Anecdotal evidence for G. dibranchiata as an ambush predator derives from the foraging behavior of Black-bellied Plovers (Pluvialis squatarola), specialized predators on G. dibranchiata (Dubois-Laviolette 1985). To bring bloodworms near the sediment surface, these plovers engage in foot-trembling behavior, setting up vibrations at the sediment surface. Bloodworms apparently mistake these vibrations for the vibrations of a potential prey item. Stolte (1932) described the complex innervation of the mechanoreceptive sense organs of bloodworms. Bloodworms refused to eat dead prey in the laboratory, indicating the importance of mechanoreception in prey location (Klawe and Dickie 1957; Fauchald and Jumars 1979).

Several features make it likely that Glycera dibranchiata is primarily a predator: the proboscis armed with neurotoxin-injecting jaws, mechanoreceptive abilities, lack of a complete gut (Ockelmann and Vahl 1970), and the presence of proteolytic enzymes in the gut (Vahl 1976). Evidence does exist indicating that bloodworms can successfully utilize detritus (Frankenberg and Smith 1967; Adams and Angelovic 1970). It seems

likely that detritivory is manifested only in the absence of suitable animal prey.

Bloodworms are capable of utilizing dissolved organic matter. Stephens et al. (1965) showed that bloodworms take up creatine opportunistically. Stevens and Preston (1981a, b, c) showed that alanine can be concentrated against a concentration gradient. Preston and Stephens (1969), Preston (1970) and Chien et al. (1972) indicate that a number of other amino acids can be concentrated.

Predator-Prey Relations

Bloodworms can significantly affect populations of other infaunal organisms. Wilson (1979) showed a correlation between bloodworm abundance and the number of maldanid polychaetes regenerating their anterior ends and argued that bloodworms were browsing on the maldanids. Ambrose (1984a, b) showed that bloodworms consume significant numbers of the sandworm Nereis virens. Dubois-Laviolette (1985) reported that bloodworm guts contained the amphipod Corophium volutator.

Predators on G. dibranchiata seem to be few. They were rarely found in fish guts (Klawe and Dickie 1957). Dubois-Laviolette (1985) reported that bloodworms are the major prey of Black-bellied Plovers (Pluvialis squatarola) in the upper Bay of Fundy. The striped bass, Morone saxatilis, and the sand shrimp, Crangon septemspinosa, consume large numbers of spent, dead bloodworms.

ENVIRONMENTAL REQUIREMENTS

Substratum

Bloodworms live in a range of substratum types, but seem to be most abundant in very fine muds with high organic content (Klawe and Dickie 1957; Creaser 1973; Dubois-Laviolette

1985). Bloodworms are conspicuous in the water column during the fall and winter (Dean 1978b; Graham and Creaser 1979). Such swimming worms are not reproductive; they may be searching for more suitable benthic habitat.

Salinity

There are no published data on tolerance limits of bloodworms to salinity stress. Costa et al. (1980) demonstrated that bloodworms are osmoconformers. Bloodworms use free amino acids to decrease intracellular solute concentrations during hypo-osmotic stress. Machin (1975) found that these animals equilibrated to 50% and 150% seawater after 10-25 h, producing a urine that is iso-osmotic to the coelomic fluid. The volume of coelomocytes changes rapidly in response to different osmotic pressures (Machin and O'Donnell 1977).

Dissolved Oxygen

Glycera dibranchiata is called a bloodworm because its hemoglobin imparts a reddish color to the body. The hemoglobin is found in cells in the body cavity (coelom); a circulatory system is lacking. No data exist on the minimum dissolved oxygen concentration needed for survival. The hemoglobin of bloodworms consists of two different molecules, differing greatly in molecular weight and oxygen affinity (e.g., Weber et al. 1977; Harrington et al. 1978; Parkhurst et al. 1981). The two hemoglobin types allow for the storage of oxygen under conditions of low oxygen tension and for the transport of oxygen under conditions of high oxygen tension. Mangum (1970) and Hoffman and Mangum (1970) showed that much of the oxygen transport in bloodworms continues after experimentally blocking the hemoglobin, implying that the storage capability of hemoglobin is the more important use. In addition to hemoglobin, the muscles of the proboscis contain a myoglobin which facilitates

transfer of oxygen (Terwilliger and Terwilliger 1981).

Toxicology

Limited information is available on the effect of heavy metals and organic pollutants on bloodworms. In contaminated sites, copper may increase in the body but not in the jaws; 67% of the body burden of copper is in the jaws (Gibbs and Bryan 1980). Zinc concentrations remain reasonably constant in both the jaws and body for worms exposed to different levels of

environmental zinc. Rice and Chien (1979) showed that cadmium accumulates through both the body surface and the intestine. They argued that the coelomic fluid may act like mammalian metallothioneins to bind the metal ions. Medeiros et al. (1981) showed that mercury uptake is very rapid, with 75% of the equilibrium value being attained after only 2 h of exposure. PCB's do not produce increased mortality in bloodworms but may affect the ability of coelomocytes to phagocytize pathogens (Anderson et al. 1984).



LITERATURE CITED

- Adams, S.A., and J.W. Angelovic. 1970. Assimilation of detritus and its associated bacteria by three species of estuarine animals. Chesapeake Sci. 11:249-254.
- Anbrose, W.G., Jr. 1984a. Influences of predatory polychaetes and epibenthic predators on the structure of a soft-bottom community in a Maine estuary. J. Exp. Mar. Biol. Ecol. 81:115-145.
- Anbrose, W.G., Jr. 1984b. Influence of residents on the development of a marine soft-bottom community. J. Mar. Res. 42:633-654.
- Anbrose, W.G., Jr. 1986. Estimate of removal rate of *Nereis virens* (Polychaeta: Nereidae) from an intertidal mudflat by gulls (*Larus* spp.). Mar. Biol. (Berl.) 90:243-247.
- Anderson, R.S., C.S. Giam and L.E. Ray. 1984. Effects of hexachlorobenzene and pentachlorophenol on cellular and humoral immune parameters in *Alydina nchiata*. Mar. Environ. Res. 14:317-326.
- Anonymous. 1979. Short-sighted Maine worm industry jeopardizing its future. Natl. Fisherman 59(9):77.
- Apy, T.D., L.E. Linkletter, and M.J. Dadswell. 1980. A guide to the marine flora and fauna of the Bay of Fundy: Annelida: Polychaeta. Can. Fish. Mar. Serv. Tech. Rep. 920:1-124.
- Arwidsson I. 1898. Studien uber die Familien Glyceridae und Goniadidae. Bergens Mus. Aarborg 11:1-70.
- Bass, N.R., and A.E. Brafield. 1972. The life cycle of the polychaete *Nereis virens*. J. Mar. Biol. Assoc. U.K. 52: 701-726.
- Bass, N.R., G. Chapman, and J.M. Chapman. 1969. Uptake of leucine by larvae and adults of *Nereis*. Nature (Lond.) 221:467-477.
- Bell, K., and J.R. Marsden. 1980. Age-related histological changes in neurosecretory cells in the brain of *Nereis virens* (Annelida, Polychaeta). Can. J. Zool. 58:1735-1740.
- Blake, R.W. 1979. On the exploitation of a natural population of *Nereis virens* from the northeast coast of England. Estuarine Coastal Mar. Sci. 8:141-148.
- Brafield, A.E., and G. Chapman. 1967. Gametogenesis and breeding in a natural population of *Nereis virens*. J. Mar. Biol. Assoc. U.K. 47:619-627.
- Bryan, G.W., and P.E. Gibbs. 1979. Zinc--a major inorganic component of nereid polychaete jaws. J. Mar. Biol. Assoc. U.K. 59:969-973.
- Bryan, G.W., and P.E. Gibbs. 1980. Metals in nereid polychaetes: the contribution of metals in the jaw to the total body burden. J. Mar. Biol. Assoc. U.K. 60:641-654.

- Bumpus, H.C. 1898. The breeding of animals at Woods Hole during the month of March, 1898. *Science* 7:485-487.
- Cantin, M., J. Bedard, and H. Milne. 1974. The food and feeding of common eiders in the St. Lawrence Estuary in summer. *Can. J. Zool.* 52:319-324.
- Carr, R.S., and J.M. Neff. 1981. Biochemical indices of stress in the sandworm Neanthes virens (Sars). I. Responses to pentachlorophenol. *Aquat. Toxicol.* 1:313-327.
- Carr, R.S., and J.M. Neff. 1982. Biochemical indices of stress in the sandworm Neanthes virens (Sars). II. Sublethal responses to cadmium. *Aquat. Toxicol.* 2:319-333.
- Carr, R.S., and J.M. Neff. 1984. Field assessment of biochemical stress for the sandworm Neanthes virens (Sars). *Mar. Environ. Res.* 14:267-279.
- Case, J. 1962. Responses of Nereis virens to alcohols. *Comp. Biochem. Physiol.* 6:47-56.
- Chapman, G., and A.G. Taylor. 1968. Uptake of organic solutes by Nereis virens. *Nature* 217:763-764.
- Chien, P.K., G.C. Stephens, and P.L. Healy. The role of ultrastructure and physiological differentiation of epithelia in amino acid uptake by the bloodworm Glycera. *Biol. Bull. (Woods Hole)* 142:219-234.
- Clark, R.B. 1960. Habituation of the polychaete Nereis to sudden stimuli. I. General properties of the habituation process. *Anim Behav.* 8:82-91.
- Comito, J.A. 1982. Importance of predation by infaunal polychaetes in controlling the structure of a soft-bottom community in Maine, USA. *Mar. Biol. (Berl.)* 68:77-81.
- Comito, J.A., and P.B. Schrader. 1985. Benthic community response to experimental additions of the polychaete Nereis virens. *Mar. Biol. (Berl.)* 86:101-107.
- Copeland, M. 1930. An apparent conditioned response in Nereis virens. *J. Comp. Psychol.* 10:339-354.
- Copeland, M. 1934. Modification of behavior in Nereis virens. *Biol. Bull. (Woods Hole)* 67:356-364.
- Copeland, M., and H.L. Wieman. 1924. The chemical sense and feeding behavior of Nereis virens Sars. *Biol. Bull. (Woods Hole)* 47:231-238.
- Costa, C.J., S.K. Pierce, and M.K. Warren. 1980. The intracellular mechanism of salinity tolerance in polychaetes: volume regulation by isolated Glycera dibranchiata red coelomocytes. *Biol. Bull. (Woods Hole)* 159:626-638.
- Creaser, E.P., Jr. 1973. Reproduction of the bloodworm (Glycera dibranchiata) in the Sheepscot Estuary, Maine. *J. Fish. Res. Board Can.* 30:161-166.
- Creaser, E. P., Jr., and D.A. Clifford. 1982. Life history studies of the sandworm Nereis virens Sars, in the Sheepscot Estuary, Maine. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 80:735-743.
- Creaser, E.P., Jr., D.A. Clifford, M.J. Hogan, and D.B. Sampson. 1983. A commercial sampling program for sandworms Nereis virens Sars, and bloodworms, Glycera dibranchiata Ehlers, harvested along the Maine coast. NOAA Tech. Rep. NMFS SSRF-767:1-56.
- Dean, D. 1978a. Migration of the sandworm Nereis virens during winter nights. *Mar. Biol. (Berl.)* 45:165-173.

- Dean, D. 1978b. The swimming of bloodworms (*Glycera* spp.) at night, with comments on other species. *Mar. Biol.* (Berl.) 48:99-104.
- deFur, P.C., and C.P. Mangum. 1979. The effects of environmental variables on the heart rates of invertebrates. *Comp. Biochem Physiol.* (A) 62:283-294.
- Dow, R.L. 1978. Few ways are open for increasing wild stocks of Maine's bloodworms. *Natl. Fisherman* 58 (10):33.
- Dow, R.L., and E.P. Creaser, Jr. 1970. Marine bait worms, a valuable inshore resource. *Atl. States Mar. Fish. Comm. Leaflet* 12:1-4.
- Dubois-Lavolette, A. G. T. M. 1985. Foraging and energetics of the Black-bellied Plover *Pluvialis squatarola* (Linnaeus) and related aspects of its prey *Glycera dibranchiata* Ehlers on the Starrs Point mudflat, Minas Basin, N.S. M.S. Thesis, Acadia University, Wolfville, Nova Scotia. 150 pp.
- Economides, A.P.M. and R.M.G. Wells. 1975. The respiratory function of the blood of *Neanthes* (=Nereis) *virens* (Sars) (Polychaeta: Nereididae). *Comp. Biochem Physiol.* (A) 51:219-223.
- Ehlers, E. 1868. Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt. Volume 2. pp. 269-748.
- Eisler, R., G. R. Gardner, R. J. Hennekey, G. LaRoche, D.F. Walsh, and P.P. Yevich. 1972. Acute toxicology of sodium nitriloacetic acid (NTA) and NTA-containing detergents to marine organisms. *Water Res.* 6:1009-1027.
- Ernst, W, H. Goerke, and K. Weber. 1977. Fate of ¹⁴C-labelled di-, tri- and pentachlorobiphenyl in the marine annelid *Nereis virens*. 2. Degradation and faecal elimination. *Chemosphere* 6:559-568.
- Evans, S. 1963a. The effect of brain extirpation on learning and retention in nereid responses. *Anim. Behav.* 11:172-178.
- Evans, S. 1963b. The behaviour of the polychaete *Nereis* in T mazes. *Anim. Behav.* 11:379-392.
- Evans, S. 1966. Non-associative avoidance learning in the nereid polychaetes. *Anim. Behav.* 14:102-106.
- Fauchald, K., and P.A. Jumars. 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol. Annu. Rev.* 17:193-284.
- Fauvel, P. 1923. Polychetes errantes. *Faune Fr.* 5:1-488.
- Fischer, A., and K. Schmitz. 1981. Preparation, properties and composition of *Nereis vitellin*, the yolk protein of the annelid, *Nereis virens*. *Differentiation* 19:103-108.
- Frankenberg, D., and K.L. Smith, Jr. 1967. Coprophagy in marine animals. *Limnol. Oceanogr.* 12:443-450.
- Gibbs, P.E., and G.W. Bryan. 1980. Copper--the major metal component of glycerid polychaete jaws. *J. Mar. Biol. Assoc. U.K.* 60:205-219.
- Goerke, H. 1971a. Die Ernährungsweise der *Nereis*-Arten (Polychaeta, Nereidae) der deutschen Küsten. *Veroeff. Inst. Meeresforsch. Bremerhaven* 13:1-50.
- Goerke, H. 1971b. Nahrungsaufnahme, Nahrungsausnutzung und Wachstum von *Nereis virens* (Polychaeta, Nereidae). *Veroeff. Inst. Meeresforsch. Bremerhaven* 13:51-78.

- Goerke, H. 1979. Nereis virens (Polychaeta) in marine pollution search: culture methods and oral administration of a polychlorinated biphenyl. Veroeff. Inst. Meeresforsch. Bremerhaven 17:151-161.
- Goerke, H. 1984a. Temperature-dependence of swarming in North Sea Nereidae. Fortschr. Zool. 29:39-43.
- Goerke, H. 1984b. Testing the fate of xenobiotics in Nereis diversicolor and Nereis virens (Polychaeta). Pages 53-66 in G. Persoone, E. Jaspers, and C. Claus, eds. Ecotoxicological testing for the marine environment, Vol. 2. Ghent, Belgium
- Goerke, H. 1984c. Temperature-dependent elimination of 2, 4, 6, 2', 4' - pentachloro[U-14]biphenyl in Nereis virens (Polychaeta). Arch. Environ. Contam. Toxicol. 13:347-355.
- Goerke, H., and W Ernst. 1977. Fate of ¹⁴C-labelled di-, tri- and pentachlorobiphenyl in the marine annelid Nereis virens. 1. Accumulation and elimination after oral administration. Chemosphere 6:551-558.
- Goerke, H., and W Ernst. 1980. Accumulation and elimination of ¹⁴C-8 HCH (lindane) in Nereis virens (Polychaeta) with considerations metabolites. Helgol. Meeresunters. 33:313-326.
- Graham, J.J., and E.P. Creaser, Jr. 1979. Tycho planktonic bloodworms, Glycera dibranchiata, in Sullivan Harbor, Maine. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 76:480-483.
- Gross, A.O. 1921. The feeding habits and chemical sense of Nereis virens Sars. J. Exp. Zool. 32:427-442.
- Haberfield, E.C. 1977. Early ammonia release by a polychaete Nereis virens and a crab Carcinus maenas in diluted sea water. Comp. Biochem Physiol. (A) 52:501-503.
- Hamaker, J.I. 1898. The nervous system of Nereis virens Sars. Bull. Mus. Comp. Zool. 32:89-124.
- Harrington, J.P., G. Suarez, T.A. Borgese, and R.L. Nage. 1978. Subunit interactions of Glycera dibranchiata hemoglobin. J. Biol. Chem 253:6820-6825.
- Hartman, O. 1940. Chrysopetalidae to Gonaididae. Allan Hancock Found. Pacif. Exped. 7:173-287.
- Haya, K., O.W. McLeese, B.A. Whiwood, and L.E. Burridge. 1984. Organochlorine pesticides and the metabolic energy state of Nereis virens. Mar. Environ. Res. 14:482.
- Henriksen, K., J.I. Hansen, and T.H. Blackburn. 1980. The influence of benthic infauna on exchange rates of inorganic nitrogen between sediment and water. Ophelia (Suppl.) 1:249-256.
- Hoffman, R.J., and C.P. Mangum. 1970. The function of coelomic cell hemoglobin in the polychaete Glycera dibranchiata. Comp. Biochem Physiol. 36:211-228.
- Hyman, L.H. 1932. Relation of oxygen tension to oxygen consumption in Nereis virens. J. Exp. Zool. 61:209-221.
- Imajima, M. 1972. Review of the annelid worms of the family Nereidae of Japan with descriptions of five new species or subspecies. Bull. Natl. Sci. Mus. Tokyo 15:37-153.
- Jorgensen, N.O.G. 1979. Uptake of L-valine and other amino acids by the polychaete Nereis virens. Mar. Biol. (Berl.) 52:45-52.
- Jorgensen, N.O.G. 1980. Uptake of glycine and release of primary amines by the polychaete Nereis

- virens (Sars) and the mud snail Hydrobia neglecta Muus. *J. Exp. Mar. Biol. Ecol.* 47:281-297.
- Jorgensen, N. O. G., and R. P. Dales. 1957. The regulation of volume and osmotic regulation in some nereid polychaetes. *Physiol. Comp. Oecol.* 4:357-374.
- Jorgensen, N. O. G., and E. Kristensen. 1980a. Uptake of amino acids by three species of Nereis (Annelida: Polychaeta). I. Transport kinetics and net uptake from natural concentrations. *Mar. Ecol. Prog. Ser.* 3:329-340.
- Jorgensen, N. O. G., and E. Kristensen. 1980b. Uptake of amino acids by three species of Nereis (Annelida: Polychaeta). II. Effects of anaerobiosis. *Mar. Ecol. Prog. Ser.* 3:341-346.
- Jorgensen, N. O. G., K. Mopper, and P. Lindroth. 1980. Occurrence, origin, and assimilation of free amino acids in an estuarine environment. *Ophelia* (Suppl.) 1:179-192.
- Kay, D. G. 1974. The distribution of the digestive enzymes in the gut of the polychaete Neanthes virens (Sars). *Comp. Biochem Physiol. (A)* 47:17-22.
- Kay, D. G., and A. E. Brafield. 1973. The energy relations of the polychaete Neanthes (=Nereis) virens (Sars). *J. Anim. Ecol.* 42:673-692.
- Klawa, W. L., and L. M. Dickie. 1957. Biology of the bloodworm Glycera dibranchiata Ehlers, and its relation to the bloodworm fishery of the Maritime Provinces. *Bull. Fish. Res. Board Can.* 115:1-37.
- Kristensen, E. 1981. Direct measurement of ventilation and oxygen uptake in three species of tubicolous polychaetes (Nereis spp.). *J. Comp. Physiol.* 145:45-50.
- Kristensen, E. 1983a. Ventilation and oxygen uptake by three species of Nereis (Annelida: Polychaeta). I. Effects of hypoxia. *Mar. Ecol. Prog. Ser.* 12:289-297.
- Kristensen, E. 1983b. Ventilation and oxygen uptake by three species of Nereis (Annelida: Polychaeta). II. Effects of temperature and salinity changes. *Mar. Ecol. Prog. Ser.* 12:299-306.
- Kristensen, E. 1983c. Comparison of polychaete (Nereis spp.) ventilation in plastic tubes and natural sediment. *Mar. Ecol. Prog. Ser.* 12:307-309.
- Kristensen, E. 1984a. Life cycle, growth and production in estuarine populations of the polychaetes Nereis virens and N. diversicolor. *Holarctic Ecol.* 7:249-256.
- Kristensen, E. 1984b. Effect of natural concentrations on nutrient exchanges between a polychaete burrow in estuarine sediment and the overlying water. *J. Exp. Mar. Biol. Ecol.* 75:171-190.
- Kristensen, E. 1985. Exchange of oxygen and inorganic nitrogen in a bioturbated estuarine sediment-water system. *J. Coastal Res.* 2:14-23.
- Kristensen, E., M. H. Jensen, and T. K. Andersen. 1985. The impact of polychaete (Nereis virens Sars) burrows on nitrification and nitrate reduction in estuarine sediments. *J. Exp. Mar. Biol. Ecol.* 85:75-91.
- Larsen, P. F., and L. F. Doggett. 1978. Benthos study of the Sheepscot River Estuary. Tech. Rep. 10-78, Bigelow Laboratories, West Boothbay Harbor, Maine.
- Lewis, D. B., and P. J. Whitney. 1968. Cellulase in Nereis virens. *Nature (Lond.)* 220:603-604.

- Lindroth, A. 1938. Studien uber die respiratorischen Mechanismen von Nereis virens Sars. Zool. Bidr. Uppsala 17:367-497.
- Machin, J. 1975. Osmotic responses of the bloodworm Glycera dibranchiata Ehlers: a graphical approach to the analysis of weight regulation. Comp. Biochem Physiol. (A) 52:49-54.
- Machin, J., and M.J. O'Donnell. 1977. Volume regulation in the coelomocytes of the blood worm Glycera dibranchiata. J. Comp. Physiol. 117:303-311.
- MacPhail, J.S. 1954. Marine bait worms--a new maritime industry. Prog. Rep. Atl. Coast. Stn., Fish. Res. Board Can. 58:11-17.
- Mangum, C.P. 1970. Respiratory physiology in annelids. Am Sci. 58:641-647.
- Marsden, J.R. 1971. Phospholipid activity in the supra-esophageal ganglion of the polychaetous annelid, Nereis virens. Comp. Biochem Physiol. (B) 40:871-874.
- Marsden, J.R. 1978. A ¹⁴C myoinositol radioautographic and morphologic study of the posterior brain of Nereis virens (Sars) (Polychaeta: Annelida). Comp. Biochem Physiol. 60:353-363.
- Marsden, J.R., and J. Jost. 1975. The radiotracer labelling of the phospholipids of the brain of Nereis virens (Polychaeta) in very young and older animals. Can. J. Zool. 53:278-284.
- Maxwell, S.S. 1897. Beitrage zur Gehirnphysiologie der Anneliden. Arch. gesante Physiol. 67:263-297.
- McElroy, A.E. 1985. In vivo metabolism of benz[a]anthracene by the polychaete Nereis virens. Bull. Environ. Res. 17:133-136.
- McLeese, D.W., C.D. Metcalfe, and D.S. Pezzack. 1981. Uptake of PCBs from sediment by Nereis virens and Cragon septemspinosa. Arch. Environ. Contam. Toxicol. 9:507-518.
- McLeese, D.W., L.E. Burrige, and J. Van Dinter. 1982. Toxicities of five organochlorine compounds in water and sediment to Nereis virens. Bull. Environ. Contam. Toxicol. 28:216-220.
- Medeiros, D.M., L.L. Caldwell, and R.L. Preston. 1981. A possible physiological uptake mechanism of methylmercury by the marine bloodworm (Glycera dibranchiata). Bull. Environ. Contam. Toxicol. 24:97-101.
- Michel, C. 1966. Mchoires et glandes annexes de Glycera convoluta (Keferstein), Annelide, Polychete, Glyceridae. Cah. Biol. Mar. 7:367-373.
- Michel, C., and E.J. DeVillez. 1979. Secretion of trypsin in the esophagus of Nereis virens Sars (Polychaeta, Errantia). A biochemical and histological study. Biol. Bull. (Woods Hole) 156:224-233.
- Michel, C., and E.J. DeVillez. 1980. Cuticles and mucous glands in the oesophagus of an annelid (Nereis virens). Tissue Cell 12:673-683.
- Michel, C., and B. Keil. 1975. Biologically active proteins in the venomous glands of the polychaetous annelid, Glycera convoluta Keferstein. Comp. Biochem Physiol. (B) 50:29-33.
- Neuhoff, H.G. 1979. Influence of temperature and salinity on food conversion and growth of different Nereis species (Polychaeta: Annelida). Mar. Ecol. Prog. Ser. 1:255-262.
- Ockelmann, K.W., and O. Vahl. 1970. On the biology of the polychaete

- Glycera especially its burrowing and feeding. *Ophelia* 8:275-294.
- Pamatmat, M.M. 1982. Metabolism of a burrowing polychaete: precaution needed when measuring toxic effects. *Mar. Pollut. Bull.* 13:364-367.
- Parkhurst, L.J., P. Sima, and D.J. Gross. 1981. Kinetics of oxygen and carbon monoxide binding to the hemoglobin of Glycera dibranchiata. *Biochem* 19:2688-2692.
- Pereira, J.J., and K. Kanungo. 1981. Effects of silver on respiration and on ion and water balance in Neanthes virens. Pages 107-125 in F.J. Vernberg, A. Calabrese, F.P. Thurberg and W.B. Vernberg, eds. *Biological monitoring of marine pollutants*. Academic Press, New York.
- Pettibone, M.H. 1963. Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. *Bull. U.S. Natl. Mus.* 227:1-356.
- Preston, R.L. 1970. The accumulation of amino acids by the coelomocytes of the bloodworm, Glycera dibranchiata. Ph.D. Dissertation. University of California-Irvine, 101 pp.
- Preston, R.L., and G.C. Stephens. 1969. The accumulation of amino acids by coelomocytes of Glycera dibranchiata. *Am Zool.* 9:1116.
- Rasmussen, E. 1973. Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* 11:1-507.
- Ray, S., D. W. McLeese, and M. R. Peterson. 1981. Accumulation of copper, zinc, cadmium and lead from two contaminated sediments by three marine invertebrates--a laboratory study. *Bull. Environ. Contam. Toxicol.* 26:315-322.
- Ray, S., D. McLeese, and D. Pezzack. 1980. Accumulation of cadmium by Nereis virens. *Arch. Environ. Contam. Toxicol.* 9:1-8.
- Reise, K. 1981. High abundance of small zoobenthos around biogenic structures in tidal sediment of the Wadden Sea. *Helgol. Meeresunters.* 34:413-425.
- Retzius, G. 1895. Zur Kenntnis der Gehirnganglions und des sensiblen Nervensystems der Polychaeten. *Biol. Unters.* 7:6-11.
- Rice, M.A., and P.K. Chien. 1977. The effects of divalent cadmium on the uptake kinetics of glycine by the polychaete, Neanthes virens. *Wasmann J. Biol.* 35:137-143.
- Rice, M.A., and P.K. Chien. 1979. Uptake, binding and clearance of divalent cadmium in Glycera dibranchiata (Annelida: Polychaeta). *Mar. Biol. (Berl.)* 53:33-39.
- Richards, T.L. 1969. Physiological ecology of selected polychaetous annelids exposed to different temperature, salinity and dissolved oxygen combinations. Ph.D. Dissertation. University of Maine, Orono. 171 pp.
- Saft, S. 1978. Maine worm industry moves to abolish conservation committee. *National Fisherman* 59 (7):53.
- Sanders, H.L., E.M. Goudsmit, E.L. Mills, and G.E. Hampson. 1962. A study of the intertidal fauna of Barnstable Harbor, Massachusetts. *Limnol. Oceanogr.* 7:63-79.
- Sars, M. 1835. Beskrivelser og lagtagelser over nogle mækkelige eller nye i Havet bed den Bergenske Kyst levende Dyr af Polypernes, Acalepernes, Radiaternes, Annelidernes og Molluskernes classer, med en kort Oversigt over de hidtil af Forfatteren samstedes fundne Arter og deres Forekommen. Bergen. 81 pp.

- Sayles, L.P. 1935. The effect of salinity changes on body weight and survival of Nereis virens. Biol. Bull. (Woods Hole) 69:233-244.
- Schottler, U. 1979. On the anaerobic metabolism of three species of Nereis (Annelida). Mar. Ecol. Prog. Ser. 1:249-254.
- Schroeder, P. 1978. Marine worm industry unhappy with research program Natl. Fisherman 59:28-29, 32.
- Scott, D.M. 1976. Circadian rhythm of anaerobiosis in a polychaete annelid. Nature (Lond.) 262:811-813.
- Scott, D.M., M. Mazurkiewicz, and P. Leeman. 1976. The long term monitoring of the ventilation rhythms of the polychaetous annelid Nereis virens Sars. Comp. Biochem Physiol. (A) 53:65-68.
- Shklyarevich, G.A. 1979. Role of Nereis virens Sars in the feeding of marine birds of Kankalaksha Bay of the White Sea. Sov. J. Ecol. 10:158-160.
- Simpson, M. 1962a. Reproduction of the polychaete Glycera dibranchiata at Solomons, Maryland. Biol. Bull. (Woods Hole) 123:396-411.
- Simpson, M. 1962b. Gametogenesis and early development of the polychaete Glycera nchiata. Biol. Bull. (Woods Hole) 123:412-423.
- Snow, D.R., and J.R. Marsden. 1974. Life cycle, weight and possible age distribution in a population of Nereis virens (Sars) from New Brunswick. J. Nat. Hist. 8:513-527.
- Spaans, A.L. 1971. On the feeding ecology of the Herring Gull Larus argentatus Pont. in the northern part of the Netherlands. Ardea 59:73-188.
- Stephens, G.C., J.F. Von Pilsum and D. Taylor. 1965. Phylogeny and the distribution of creatine in invertebrates. Biol. Bull. (Woods Hole) 129:573-581.
- Stevens, B.R., and R.L. Preston. 1981a. The transport of L-alanine by the integument of the marine polychaete, Glycera dibranchiata. J. Exp. Zool. 212:119-127.
- Stevens, B.R., and R.L. Preston. 1981b. The effect of sodium on the kinetics of L-alanine flux by the integument of the marine polychaete, Glycera dibranchiata. J. Exp. Zool. 212:129-138.
- Stevens, B.R., and R.L. Preston. 1981c. Sodium dependent steady state L-alanine accumulation in the body wall of Glycera dibranchiata. J. Exp. Zool. 212:139-146.
- Stolte, H.A. 1932. Untersuchungen über Bau und Funktion der Sinnesorgane der Polychatengattung Glycera. Sav. Z. Wss. Zool. 140:421-538.
- Sveshnikov, V.A. 1960. Pelagic larvae of some Polychaeta in the White Sea. Zool. Zh. 39:343-355.
- Taylor, A.G. 1969. The direct uptake of amino acids and other small molecules from sea water by Nereis virens Sars. Comp. Biochem Physiol. 29:243-250.
- Tenore, K.R., M.G. Brown, and E.J. Chesney, Jr. 1978. Polyspecies aquaculture systems: the detrital trophic level. J. Mar. Res. 32:425-432.
- Tenore, K.R., and U.K. Gopalan. 1974. Feeding efficiencies of the polychaete Nereis virens cultured on hard-clam tissue and oyster detritus. J. Fish. Res. Board Can. 31:1675-1678.

- Terwilliger, R.C., and N.B. Terwilliger. 1981. Proboscis myoglobin of Glycera dibranchiata. *Comp. Biochem Physiol.* (B) 70:169-171.
- Theede, H., J. Schaudinn, and F. Saffe. 1973. Ecophysiological studies of four Nereis species of the Kiel Bay. *Oikos* (Suppl.) 15:246-252.
- Treadwell, A.L. 1939. New polychaetous annelids from New England, Texas and Puerto Rico. *Am Mus. Novit.* 1023:1-7.
- Treadwell, A.L. 1941. Polychaetous annelids from the New England region, Puerto Rico and Brazil. *Am Mus. Novit.* 1089:1-4.
- Turnbull, F. 1876. On the anatomy and habits of Nereis virens. *Trans. Conn. Acad. Arts Sci.* 3:265-281.
- Vadas, R.L., and G. Bristow. 1985. Genetic changes associated with a bottleneck in an overharvested population of Glycera dibranchiata (Polychaeta). Pages 617-629 in J.S. Gray and M.E. Christiansen, eds. *Marine biology of polar regions and Effects of stress on marine organisms*. John Wiley and Sons, New York.
- Vahl, O. 1976. On the digestion of Glycera alba (Polychaeta). *Ophelia* 15:49-56.
- Verrill, A.E. 1873. Report upon the invertebrate animals of Vineyard Sound and adjacent waters, with an account of the physical features of the region. *Rep. U.S. Fish. Comm* 1871-1872:295-852.
- Verrill, A.E. 1881. New England Annelida. Part 1. Historical sketch, with annotated lists of the species hitherto recorded. *Trans. Conn. Acad. Arts Sci.* 4:285-324.
- Walmsby, J.R. 1970. The effects of osmotic stress and other factors on the respiration of the polychaete Nereis virens. Ph.D. Dissertation. University of London.
- Weber, R.E., B. Sullivan, J. Bonaventura, and C. Bonaventura. 1977. The haemolobin systems of the bloodworms Glycera dibranchiata and G. americana. Oxygen binding properties of haemolysates and component haemoglobins. *Comp. Biochem Physiol.* (B) 58:183-187.
- Webster, H.E., and J.E. Benedict. 1884. The Annelida Chaetopoda from Provincetown and Wellfleet, Massachusetts. *Rep. U.S. Fish. Comm* 1881:699-747.
- Webster, H.E., and J.E. Benedict. 1887. The Annelida Chaetopoda of Eastport, Maine. *Rep. U.S. Fish. Comm* 1885:707-755.
- Wells, G.P. 1937. The movements of the proboscis in Glycera dibranchiata Ehlers. *J. Exp. Biol.* 14:290-301.
- Wilson, W.H., Jr. 1979. Community structure and species diversity of the sedimentary reefs constructed by the Petaloproctus socialis (Polychaeta: Maldanidae). *J. Mar. Res.* 37:623-641.
- Wolff, G. 1976. Bau und Funktion der Kieferorgane von Polychaeten. *Eigen-druck* 1:1-70.
- Wolff, G. 1977. Kieferorgane von Glyceriden (Polychaeta)--ihre Funktion und ihr taxonomischer Wert. *Senckenb. Marit.* 9:261-283.
- Yokouchi, K. 1985. Reproduction and larval ecology of the sandworm Neanthes virens (Sars) from the southern Hokkaido. *Bull. Plankt. Soc. Japan* 32:1-13.

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