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Ecology and biology of marine oligochaeta – an inventory rather than another review

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Abstract

Instead of updating the1982-review by Giere & Pfannkuche, it was deemed more useful to highlight some recent and relevant studies given the limited number of new and pertinent publications. In addition, new data on population ecology, some recent results on symbiotic associations and descriptions of adaptations to oxygen deficiency and hydrogen sulfide will be commented on. The scarcity of new ecological and biological studies on marine Oligochaeta, an animal group that often attains key positions in important shore areas, is alarming. Future research efforts on this ecologically relevant annelid group are seriously needed.

Introduction

In an earlier review (Giere & Pfannkuche, 1982), we described the pertinent literature up to 1980. The original aim of this contribution was to provide an update with more recent important data. However, a literature research showed only some sixty references directed specifically at oligochaetes over the past 20 years. Some of these publications were of more general interest and/or point to directions of future relevance. Those will be briefly mentioned. Therefore, this compilation represents more an inventory rather than another review. If relevant, selected studies of brackish water and freshwater oligochaetes have also been included. For comparison, the topics in this update are the same as those in our previous review.

Topics considered

Methods

In field, culture and experimental techniques, studies on marine oligochaetes do not need novel or specific approaches other than those established methods for the general benthos or previously described. The main changes have been in the development of mathematical and statistical evaluation methods. These have been summarized by Burd et al. (1990) and they describe examples explicitly referring to oligochaetes. Burd et al. (1990) first evaluate sampling patterns and efforts to analyze data matrices. Classical univariate descriptors such as various diversity indices and their application are covered. The use of biomass/size spectra is also discussed as well as the value of multivariate statistics such as Multidimensional Scaling and other ordination techniques.

Faunistics, distribution, zoogeography

There are numerous papers in this field that are of local faunistic relevance only. Focus is given here only to those with wider than regional aspects or with generalizable conclusions. Erséus (2002) summarized the knowledge on oligochaetes from mangrove habitats. This ecotone harbors more than 50 species. The majority (38 spp), aquatic tubificids, occur in more marine habitats, while the more terrestrial enchytraeids (16 spp.) dominated in the upper reaches of the mangrove belt. This pattern conforms to the distribution ascribed to meiobenthic oligochaetes (Fig. 1) on marine shores in general (Giere, 1993).

Brackish-water tolerance appears to be a prerequisite for colonizing mangrove biotopes where typical taxa like *Paranais*, *Ainudrilus*, *Rhizodrilus*, *Monopylephorus* occur. The second dominant factor for mangrove benthos is the absence of an interstitial system. This is the reason for the absence of the mostly interstitial phallodriline Tubificidae, a group that is species-rich in sandy habitats in warm water regions (e.g., Erséus, 2003). The absence of oxygen in the sediment is not mentioned as an important factor in worm distribution by Erséus (2002).

Mangroves are ecologically important but rather exotic habitats. The same can be said for *Spartina* salt marshes along the North American Atlantic coast, a rapidly disappearing habitat. Here, biological diversity and productivity is of prime importance and seems well assessed. Examination of the air passages in *Spartina* stems has revealed this to be a preferred habitat for enchytraeid species (Healy & Walters, 1994), which has generally been disregarded. At the present time the trophic basis of these rich oligochaete populations (*Marionina* spp, *Monopylephorus parvus*) is unclear. However, this one habitat alone can increase estimates of oligochaete abundance by an order of magnitude from 1150 to 10,250 ind. m^{-2}.

High ecological relevance is also attributed to another unusual habitat, the drift zone of beaches, where debris from plants and animals tends to accumulate and decomposing organisms prevail. Here, Koop & Griffiths (1982) studying the meiofauna of South African beaches, found accumulations of meiobenthic oligochaetes (taxa unidentified). They suggest that this wrack zone is a center of oligochaete distribution. As assumed in earlier studies from boreal shores (Giere, 1970), these detritivorous oligochaetes play an important role in the breakdown of larger organic particles thus facilitating bacterial decomposition. The exceptional role of this zone is emphasized by the fact that other beach habitats also contain considerable amounts of organic matter, yet are less attractive to the meiofauna (Giere, 1993).

Life history

This general heading includes studies on development, reproductive biology, life cycles with the

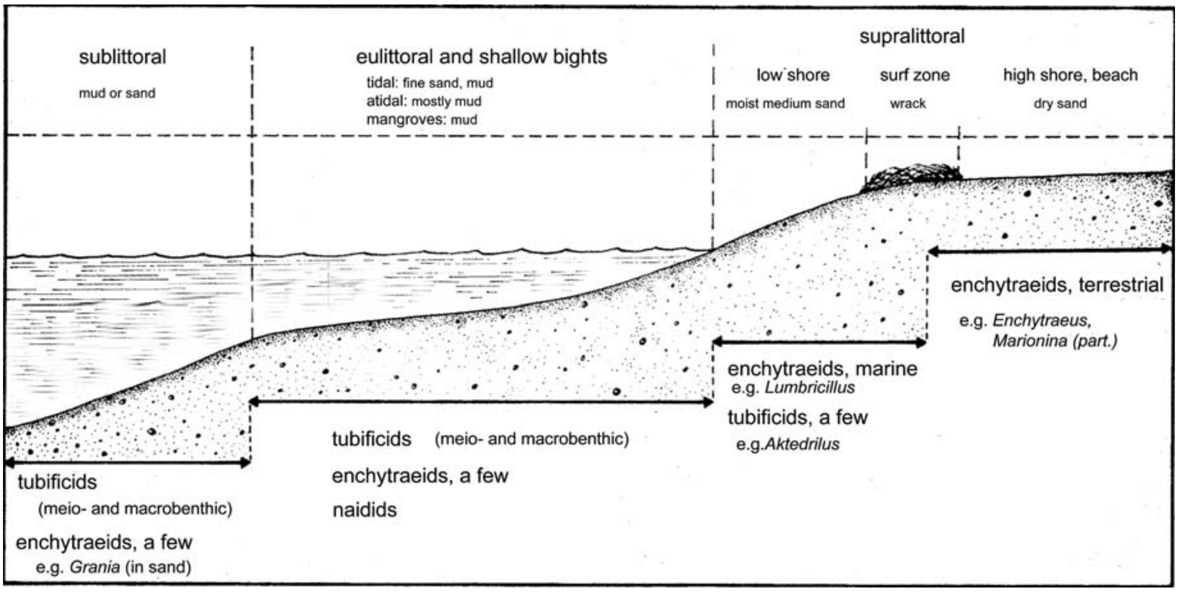

Figure 1. Generalized distribution pattern of marine oligochaetes (from Giere, 1993, modified).

annual fluctuations as well as patterns of symbiotic coexistence.

General aspects

Working on general developmental and genetic problems, Levinton's group chose the asexually reproducing *Paranais litoralis* (Naididae) as their animal model. Investigating the senescence of animals without a specific germ line, Martinez & Levinton (1992) found that asexually reproducing animals are also subject to aging and they reason that senescence is linked to somatic differentiation rather than germ line sequestration.

Nilsson et al. (1997) revealed that several clones belonging to subpopulations of *P. litoralis* from different environments showed marked differences in life span, production of offspring, growth etc. DNA-analysis revealed not only a genetic interclonal difference, but that the sequences were unstable and seemed to interact with the environment. The authors interpret this flexibility as adaptive, creating a mosaic of local reactions to a shifting environment. In a later study (Nilsson et al., 2000), observations from the field and from cultures showed that in times of resource depletion, the clones grew longer and thinner and become migratory, swimming up in the water column. Thus, areas of food scarcity may be avoided and migration helps the populations not only to persist but also to maintain a genetic flux and variability between metapopulations.

Reproductive biology

Oligochaeta, especially many Tubificidae, are characterized by their complex and elaborate reproductive organs which have become the basis for identification. Yet, we are far from understanding the reproductive biology of these animals and cannot even guess at the interrelations between the form and function of external genital structures in these hermaphroditic organisms. The paper by Cuadrado & Martinez-Ansemil (2001), although dealing with limnetic tubificid species, gives an example about differentiation of structures required for copulation and sperm exchange. Our lack of knowledge in this field is apparent in those species where number and position of genital organs and openings deviates from normal (e.g., mid-dorsal opening of spermathecae).

Takashima & Mawatari (1998) concluded that the function of the genital structures and, thus, the mode of sperm transfer remains mostly enigmatic. Accordingly, the autapomorphic character of many genital structures cannot be relied on from extrapolation of old observations on earthworms and we cannot consider the megadriles to be representative for all the oligochaeta. What is required in this somewhat mundane, but much needed, research field is patience, appropriate culture techniques and modern documentation methods, best characterized by the film of Westheide & Müller (1995) on the reproductive behavior of terrestrial enchytraeids.

Symbioses

A remarkable biological and ecological feature of some marine oligochaetes is the existence of complex and obligatory symbioses with bacteria. Occurring in two phallolodriline genera (Tubificidae). These associations parallel the symbiotic trends in deep-sea hydrothermal vents, but differ in the diversity of symbionts participating in the relationships (Giere & Langheld, 1987; Giere & Krieger, 2001). Since the discovery of two gutless species in coralline sands of Bermuda (Giere, 1979) some 100 species of the monophyletic genera *Olavius* und *Inanidrilus* completely lacking digestive and excretory organs have been described (Erséus, 2003) (Fig. 2).

The bacteria–symbiotic worms occur in shallow sulfidic sediments of warm water areas from all major seas. At present approximately 30 spp. have been studied in detail. They all have incorporated a fairly thick layer of extracellular bacteria beneath the cuticle while the wide body cavity is devoid of an intestine (Giere et al., 1995). Only in two species from the Mediterranean island of Elba, are the bacteria mostly found enclosed by the epidermal cells, thus often attaining an intracellular position (Giere & Erséus, 2002). The symbiotic bacteria in the gutless worms belong to different morphotypes. Large, oval ones are frequently combined in dual symbiosis with smaller, rod-shaped ones (Fig. 3). However, in some cases the picture becomes complicated by additional morphologically divergent types of different

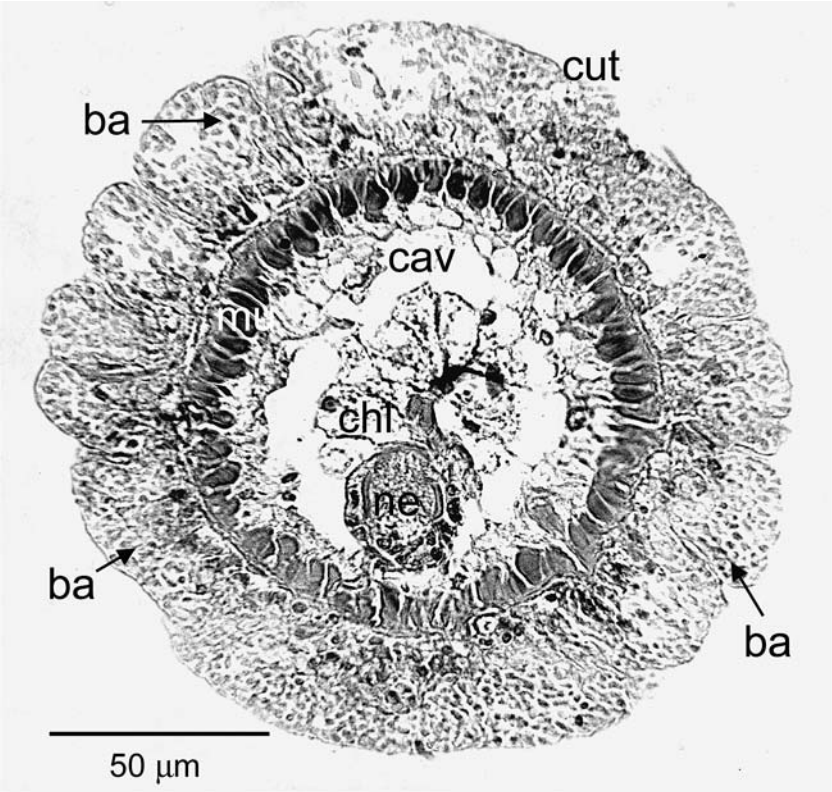

Figure 2. Cross-section through *Inanidrilus leukodermatus* (Tubificidae, Oligochaeta) from Bermuda. Light micrograph. Abbreviations: ba = symbiotic bacteria, cav = body cavity, chl = chloragogue cells, cut = cuticle, mu = dermal musculature, ne = ventral nerve cord.

shapes and sizes, including long, twisted filiforms (Giere & Krieger, 2001; Fig. 4).

It was not till molecular methods were developed that the function of some of the various symbionts could be revealed. The large oval symbionts belonging to the gamma-Proteobacteria have been shown to be sulfide oxidizers (Dubilier et al., 1995), while the function of the smaller ones, often alpha-Proteobacteria, still remains unclear. In *Olavius algarvensis*, from Elba, close functional cooperation between the two bacterial types has been documented (Dubilier et al., 2001). Here sulfide, oxidized by the larger gamma-Proteobacteria into sulfate, was then reduced again into sulfide by the small rod-shaped alpha-Proteobacteria (Fig. 5).

This unique bacterial 'cyclotrophism' of directly adjoining symbionts enables the gamma-Proteobacteria to obtain sulfide (as electron donor) even in sand poor in, or temporally devoid, of free sulfide. In this case, the gutless hosts, obligately dependent on their bacteria, are not any longer strictly bound to sulfidic/oxic interfaces (Giere et al., 1991) but can remain in the oxic layer. Further molecular studies have recently revealed that the two tubificid species found in Elba harbor even a set of up to five bacterial phylotypes (Dubilier et al., in press). Other bacterial phylotypes, including Spirochaeta, have been identified by molecular methods as symbionts in various gutless species from Australian, Caribbean and Peruvian regions.

Obligate reliance of the hosts on their bacterial partners, the internal position of the bacteria, and the complicated mode of reproduction in oligochaetes (see above) suggest vertical pathways of bacterial transmittance, i.e. from the parental generation directly to their offspring. On the other hand, the divergence of bacterial associations in closely related worm species rather speaks for a horizontal uptake, i.e. uptake from the environment. Sometimes (e.g. in *O. algarvensis*), the symbionts differ even in separate populations of

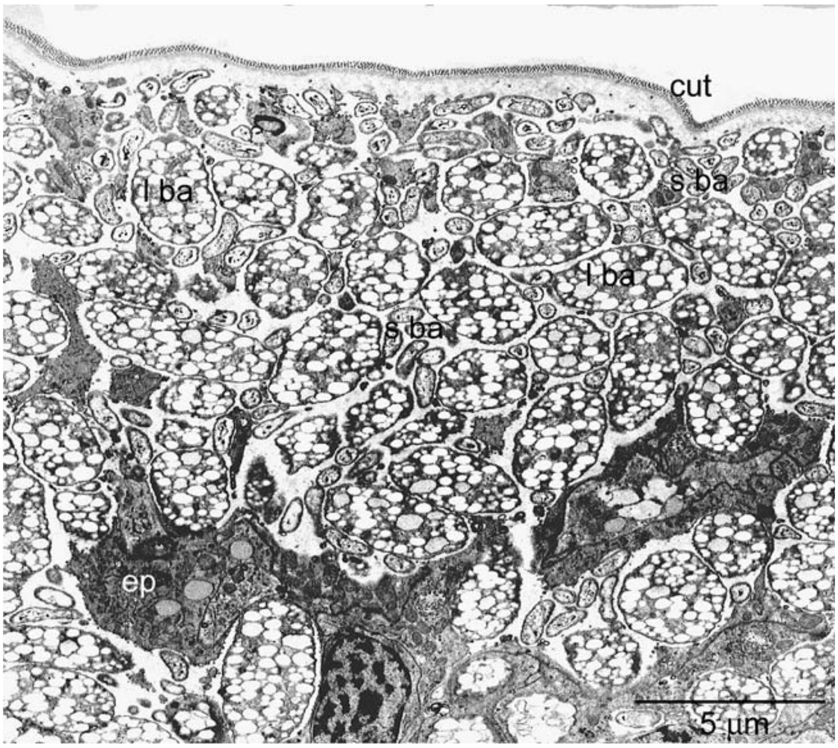

Figure 3. Cross-section through *Inanidrilus leukodermatus* (Tubificidae, Oligochaeta) from Bermuda showing subcuticular symbiotic bacteria of two different morphotypes. Transmission electron micrograph. Abbreviations: cut = cuticle, ep = epidermal cell, l ba = large γ-Proteobacteria, s ba = small α-Proteobacteria.

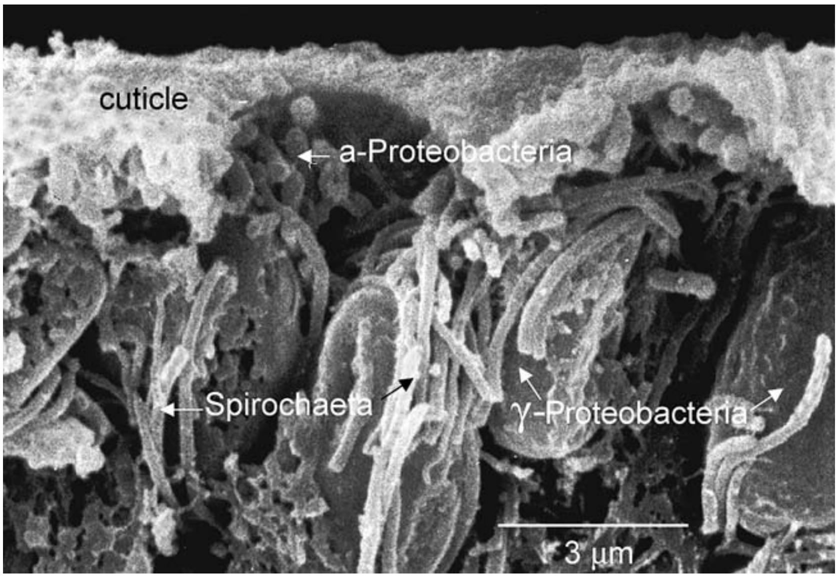

Figure 4. Longitudinal micropreparation of *Olavius crassitunicatus* (Tubificidae, Oligochaeta) from the shelf off Peru showing spirochete symbionts together with oval γ-Proteobacteria and small α-Proteobacteria. Scanning electron micrograph.

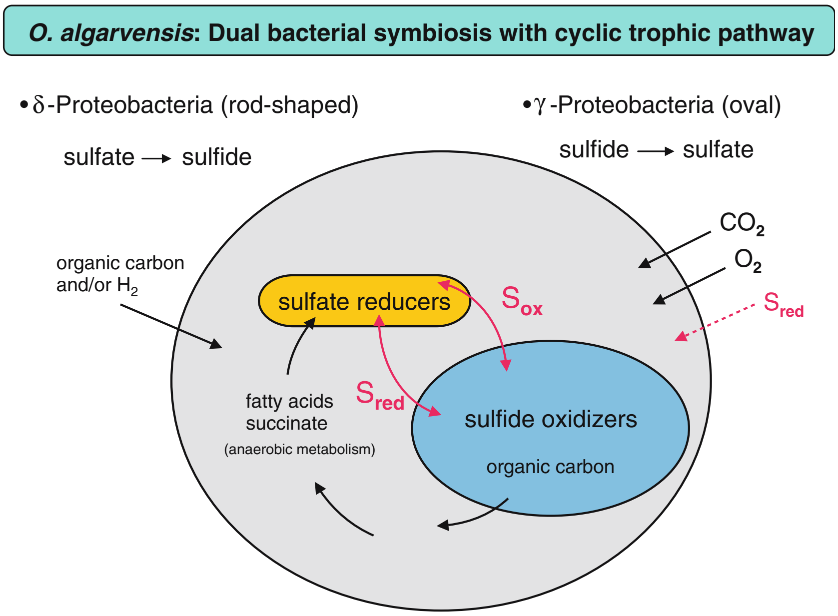

Figure 5. Functional diagram of symbiotic bacteria and their metabolic pathways in *Olavius algarvensis* from Elba (from Dubilier et al., 2001, modified).

the same host species. This also supports the view of environmental transmission of the bacteria. Our studies on *I. leukodermatus* from Bermuda have revealed that only the oval sulfide oxidizing gamma-Proteobacteria are vertically transmitted (Krieger, 2001), ‘infecting’ the egg at the moment of deposition (the sticky eggs in these gutless oligochaetes are layed singly onto the sediment grains and not deposited in cocoons as usual in oligochaetes). Hence, we have to assume that there is a combination of vertical and environmental transmission, at least in the species studied (Fig. 6).

Though there are many parallels that can be drawn between the bacteria–symbiotic associations in these gutless Oligochaeta and the deep-sea gutless tube worms and molluscs in sulfide-emanating hydrothermal vents, the complexity, variability, and diversity of the symbiotic pattern in the gutless tubificids seem unique. Their various bacterial associations, each perhaps with specific metabolic requirements, might be a clue to the syntopic occurrence of various gutless species (see below).

Life cycle studies

The assessment of life cycles has been a neglected, but is an ecologically important field of oligochaete research. This type of study requires patient long-term data collection with numerous sampling campaigns and/or tedious culturing to separate the ‘noise’ from the trend, so as to reveal the role of environmental factors (temperature, salinity) and demonstrate true life cycle attributes. This long-term approach was adopted in the comprehensive study by Erséus & Diaz (1989) on *Tubificoides amplivasatus* (Tubificidae) from the Kattegat. The subtidal species reproduces year round without clear cohort formation. It has a very patchy distribution with irregular peaks of abundance, which can be related to the warmer temperatures in late summer and autumn. The long time to maturity (200 days) infers a life span of several years. Recruitment in the warmer season and for prolonged periods is also reported for the congener *T.* cf. *brownae* in North American brackish water (Diaz, 1984).

A relationship with temperature was not found in *Tubificoides benedii* from the shallow Forth estuary (Bagheri & McLusky, 1982). Here, the erratic annual population curves with peaks also in the winter did not show any clear seasonality and no marked period of recruitment. This was in contrast to the other dominant oligochaetes in this brackish water habitat, the naidid species *Amphichaeta sannio* and *P. litoralis*. Their population

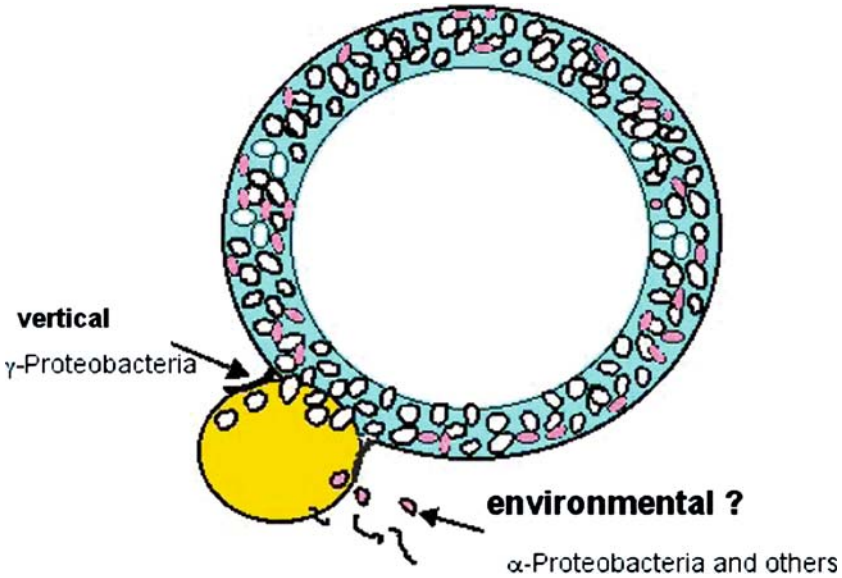

Figure 6. Schematic pathways of bacterial transmission in symbiotic oligochaetes.

peaks could be correlated to periods of algal blooms. The prevailing asexual reproduction by fission supports erratic population fluctuations as soon as algal blooms arise.

Quantitative population data, production

"Few estimates of production in aquatic oligochaetes have been made. Those, that have vary considerably in methodology, the units employed, the values obtained, and sometimes in the concept of production used." (R.O. Brinkhurst, 1st. Olig. Symposium, Sidney, Can., 1979)

By and large, this statement (Brinkhurst, 1980) is still valid, with the result that in the field of marine oligochaeta, we have to rely on a few isolated publications.

Using respiration values combined with biomass data, Bagheri & McLusky (1984) calculated production of *T. benedii* and the naidid species *A. sannio* and *P. litoralis* together with that of the small polychaete *Manayunkia aestuarina*. These species are dominant in the Forth estuary, Scotland, contributing about half and sometimes up to >90% of the total invertebrate production of this brackish water area.

Tubificoides benedii is a species which contradicts general ecological classification: This common oligochaete is dominant in coastal areas that are highly enriched in organic matter, and is often typified as 'opportunist' that is adapted to the rapid environmental fluctuations and harsh conditions in estuaries (see Bagheri & McLusky, 1982). The behavior of this oligochaete species does not conveniently fit into the concepts of, 'r' and 'K' strategies described in the ecological literature. Despite its huge population density (1×10^6 m^{-2}) and production (14–27 g wet wt. m^{-2} a^{-1}). *T. benedii* is not a typical r-strategist. Its long life span (a few years, see also *T. amplivasatus*, above), discontinuous breeding, internal fertilization with brooding and low P/B-ratio (0.85:1) contradict the classical 'r'-strategy. Among the aquatic groups, this contradiction refers mainly to the long-lived tubificids and to many larger terrestrial oligochaetes as well, so that oligochaetes do not fit the simplified pattern of r- and K-strategists.

The low P/B-ratio of *T. benedii* is in contrast to that of some enchytraeids, e.g., the small enchytraeid *M. southerni* (oligohaline to limnic species, P/B ratio of 2.5) which only has a 1-year life cycle (Lindegaard et al., 1994). Reliable calculations of annual P/B ratios in naidids are impaired by their excessive multiplication through asexual fission in periods of algal blooms.

Obtaining more reliable life history data for marine oligochaeta for calculating production will require both field sampling and laboratory cultures. The work of Bouguenec & Giani (1989) on *Enchytraeus variatus*, a terrestrial species with both sexual and asexual reproduction is an excellent example of the type of study required. Using cultures the relevant life history data for the complete calculation of growth and production were acquired including: embryonic development, post-embryonic, maturity period, laying period, individual life time, production, biomass, and growth curves of populations.

Abiotic habitat factors

The impact of habitat on distribution and life history is one of the basic ecological questions. Nevertheless, multifactorial interactions render its assessment difficult. For oligochaetes, this complexity is summarized by Diaz (1984) "... The complexity of species interactions... combined with climatic, or salinity, or substrate changes may overshadow any progressive tendencies in the benthos."

Sediment

One of the most puzzling features of marine oligochaete communities is the diversity of closely related species in seemingly uniform sediments and syntopic occurrence. An analysis of the speciose tubificid fauna in shallow water sediments of the Caribbean (Diaz & Erséus, 1994) explained the co-occurrence of species by strong niche partitioning and by differences in organic contents of the sediment. Using cluster analysis these authors classified species associations and related them to sediment granulometry and water depth.

Oxygen/hydrogen sulfide

Sediment structure and organic content are likely the main factors affecting community structure, especially in marine habitats: The supply of oxygen and exposure to hydrogen sulfide have often been found to be key factors in the distribution of marine oligochaetes (Giere & Pfannkuche, 1982). "To fully understand the distribution and ecology of aquatic plants and animals, sulfide must be taken into account along with temperature, salinity, oxygen, and other environmental factors" (Bagarinao, 1992). In the preferred coastal habitat of many marine oligochaetes, periods of oxygen deficiency and strong sulfide formation are frequently observed as a result of high enrichment with organic matter. The general importance of oxygen/free sulfide in affecting the distribution of marine oligochaetes is reflected in four pertinent reviews published in the 90s: although not restricted to oligochaetes, the conclusions of these reviews can be generalized and are of broad importance. Giere (1992) considered the tolerance of many specialized marine animals to hypoxia and sulfide from an ecological point of view, while Grieshaber et al. (1992), in a parallel paper, considered the physiological mechanisms involved in survival under sulfidic conditions. Grieshaber et al. (1994) supplemented this paper with a compilation of physiological and metabolic responses to hypoxia. A more ecophysiological view was taken in the paper by Bagarinao (1992) who also covered some of the symbioses developed in sulfide-rich environments. In the context of this paper, these review papers can be summarized:

1. Hypoxia and sulfide closely interact physiologically, the presence of hydrogen sulfide exacerbates the effects of hypoxia ("sulfide dependent anaerobiosis").
2. Different taxa use different mechanisms of detoxification and adaptation.
3. The main defense against hydrogen sulfide is the capacity for intermittent anaerobiosis and/or oxidation by the mitochondria. During anaerobiosis, succinate is accumulated, possibly in all aquatic oligochaetes, and can be used as an indicator of an anaerobic metabolism.
4. The frequently observed precipitation of metal-sulfides in various tissues of the body often interpreted as a mechanism for detoxification needs scrutiny, since it will not cope with the rapid sulfide influx and export pathways have never been reported (see also Dubilier et al., 1995).
5. Most enchytraeids and naidids are sensitive to hydrogen sulfide and hypoxia, while tubificids often are more resistant, some of them having special physiological adaptations (see below).
6. The ecological advantage of living in hypoxic, temporarily sulfidic sediments is the ample supply of organic matter and the reduced interspecific competition.

Lindegaard et al. (1994) in their study on *Marionina southerni* from Danish brackish waters, confirmed the limited capacity of many enchytraeids to regulate in low oxygen conditions. This species was a relatively good regulator but only at low temperatures. Between 10 and 20 °C, it reached its critical oxygen partial pressure ($P_{\text{crit.}}$) at 60% saturation (=12.6 kPa). This corresponds to the average field occurrence of marine enchytraeids, which are never encountered in severely hypoxic sediments (Giere, 1973).

In contrast, our own studies on *T. benedii* (Tubificidae), often a 'pioneer' in hypoxic and sulfidic environments (Giere et al., 1999), resulted in a $P_{\text{crit.}}$ of only 10% (=2.1 kPa) at 15 °C. This value is extremely low compared to other aquatic oligochaetes and polychaetes (Table 1) documenting that *T. benedii* is one of the best annelid oxyregulators, even under sulfidic conditions. Its extreme oxygen tolerance corresponds with its unusually low respiration rate, compared to limnetic oligochaetes and polychaetes of comparable size (Table 1).

Salinity

In coastal marine areas, especially in tidal flats and estuaries, salinity fluctuations also play an important role in the distribution of oligochaetes. This is especially evident from studies in long tidal estuaries such as the Rhine delta where Verdonschot (1981) and Verdonschot et al. (1982) could relate salinity to field distribution. It was shown that *Heterochaeta costata* (=*Tubifex costatus*) preferred shallow-water brackish stations avoiding areas of usually euhaline salinity, while *T. benedii* covered a range from meso- to euhaline stations.

To examine the salinity-dependent osmoregulatory potential of aquatic oligochaetes, comparative tolerance experiments have been conducted (Generlich & Giere, 1996). Using terrestrial and coastal marine populations of *Enchytraeus albidus* (Enchytraeidae) the osmolality of the coelomic fluid was measured after varying acclimation times in a range of salinities. The enormous regulatory potential of *E. albidus* was underlined not only by the survival of test animals in concentrations from freshwater to fully marine conditions (after long-term acclimation), but particularly by the continuous maintenance of a hyperosmotic coelomic fluid. The main difference in populations of *E. albidus* from the seashore and garden soil was the higher stability of the osmotic barrier inside/outside in the shore populations.

Rapid salinity change (hyperosmotic shock) can result in a similarly rapid adjustment of the internal fluid concentration to the changed external conditions. However, it took longer for the animals to regulate their body volume by adjustment of the water content. Molecular studies are required to show to what extent ecophysiological differences in terrestrial and marine populations of *E. albidus* relate to differences in their genetic background. Comparison with other annelids suggests that different regulatory pathways exist in the various test animals. In the tubificid

Table 1. Inter-annelid comparison of critical oxygen concentrations ($P_{\text{crit.}}$) and respiration at about 15 °C

Species	Critical PO_2 (kPa)	Respiration rate, 15 °C (nmol O_2 g^{-1} fwt min^{-1})	Reference
Tubificoides benedii	–	37	Bagheri & McLusky (1984)
T. benedii	1		Dubilier et al. (1994)
	2	63	Giere et al. (1999)
Limnodrilus hoffmeisteri	4	357	Schneider (1994)
Tubifex tubifex	4	218	Schneider (1994)
Marionina achaeta	3.2	570	Lasserre (1976)
M. southerni	12.6	169	Lindegaard et al. (1994)
Scoloplos armiger	2.1	–	Schöttler & Grieshaber (1988)
Capitella capitata (large form)	17		Gamenick (1997)
		125	Gamenick et al. (1998)
Arenicola marina	16	–	Hauschild & Grieshaber (1997)

Heterochaeta costata, regulation of water loss in a hyperosmotic medium was more limited.

Biotic habitat factors

Bioturbation

For endobenthos bioturbative reworking of the sediment is one of the most effective environmental factors. In the marine realm most work in this field has been done with polychaetes, but the paper by Reible et al. (1996), although dealing with the limnetic tubificid *Limnodrilus hoffmeisteri*, may also parallel conditions in marine sediments. From experimental sediment arrays contaminated with pyrene it was concluded that the intense bioturbative activity of these tube-building worms would lead to an enhanced long-term diffusion of pore water into the overlying water column (about 370 times greater than in non-bioturbated sediment).

Given the frequent high abundance of common littoral oligochaetes (e.g., 10^5–10^6 ind. m^{-2}, Giere & Pfannkuche, 1982), the burrows of these non-tube builders would likely cause a considerable 'secondary porosity' in muddy sediments which adds to that created by other marine burrowers (mainly polychaetes and bivalves). The exchange of solutes and pollutants at the water/sediment interface is further increased by the continuous reworking of sediment through the digging and feeding activity of most endobenthic fauna. Kaster et al. (1984) calculated for *Limnodrilus* that sediment up to several times its own body weight is brought to the surface every day *via* defecation. Grossly enhanced diffusion and reworking of sediment by the various littoral oligochaete species will substantially contribute to the overall exchange of solutes, an important factor in sediment biogeochemistry.

Disturbance

Another important effect of bioturbation is disturbance, particularly between similar functional groups, e.g., deposit feeders (Rhoads & Young, 1970) or between benthic adults and settling larvae (adult – larvae interaction, Woodin, 1976). McCann & Levin (1989) examined the disturbance associated with dense populations of a marine tubificid (*Monopylephorus evertus*). Surprisingly, the experiments showed that there was no measurable negative impact between the large populations of the oligochaete and the adults of another common surface deposit feeder, the polychaete *Streblospio benedicti*. Even negative 'adult-larval interaction' between the mobile burrower (*Monopylephorus*) and the settling planktonic larvae of the polychaete were not observed. But this absence of effect seemed stage-specific: *M. evertus* did inhibit the development and survival of newly settled juveniles of *S. benedicti*.

In another study, Commito (1987) used the marine tubificid *T. benedii* to test the general applicability of the 'trophic group amensalism' hypothesis (Woodin, 1976). Do dense populations of filter feeders (mussels) prevent colonization of *all* deposit feeding benthos, regardless of developing a planktonic or benthic larval/juvenile phase? He showed that population density of *T. benedii* was the same or even higher in mussel beds than in open mud areas. Absence of an inhibitory effect was also found by Bagheri & McLusky (1982) studying the interaction between the filter feeding polychaete *M. aestuarina* and the grazer/deposit feeder *P. litoralis*. Thus, amensalism between filter feeders and deposit feeders is not evident for holobenthic deposit feeding species, based on these data (and in fact amelioration may be true). The only demonstrated interactions are inhibitory effects by the filtering activity reducing the planktonic larvae of deposit feeders that settle onto the bottom.

The results of Bagheri & McLusky (1982) provide some explanation of disturbance effects. The naidid *P. litoralis* differs from *T. benedii* in its biology: It often occurs in the suprabenthic water layer actively swimming above the sediment/water interface and potentially interferes with the filtering structures of *Manayunkia*. In the absence of negative interaction by disturbance, explanations for the general ecological interactions are ascribed to predator/prey relationships. And these relationships are highly dependent on size classes and life history characteristics.

An example of the effect of size class on competition for food, between oligochaetes and polychaetes was given in experiments, which artificially inhibited the viability of diatoms (Hentschel & Jumars, 1994). The breakdown of diatom populations reduced the stocks of the brackish water naidid *Amphichaeta leydigi* and the polychaete *Hobsonia florida* only in the larger life stages. The smaller juveniles showed no reduction in abundance, indicating a different feeding strategy.

The lack of disturbance interactions, the extreme adaptation to hypoxic and sulfidic sediments, described above, and the predilection for centers of biodeposits would explain the particularly rich populations of *T. benedii* in the bottom sediment of mussel beds with their masses of feces and pseudofeces. Despite the intense predation by *Nereis diversicolor* on *T. benedii* in mussel beds, recruitment of this opportunistic oligochaete seems to compensate for its losses, while predatory pressure on another oligochaete of a similar ecological character, *Tubifex pseudogaster*, was much less (Dittmann, 1990).

Oligochaetes as food

The different fate of the two eulittoral tubificid species in mussel beds leads to consideration of the fate of the rich oligochaete production as a prey for higher trophic levels. Eulittoral tidal flats are known as nursery and over-wintering grounds for many marine fauna. Here, the rich biomass of marine oligochaeta results in them playing an important role in the coastal food web (Giere & Pfannkuche, 1982). This was confirmed in the experiments of Dittmann (1990) with the polychaete *N. diversicolor*. In our own studies (unpubl.) juvenile *Crangon crangon* and gobiid fish consume *T. benedii* in large amounts preferring it to polychaetes of similar size. For some migratory birds *T. benedii* is a 'significant part of the diet' (Bagheri & McLusky, 1984). Finally, the meiofauna also utilize marine oligochaetes. Watzin (1986) found severe depletion of oligochaetes (unidentified) in experimental boxes after the addition of two turbellarian species as predators. Virnstein (1977), however, showed that in the field and with natural reproduction, populations of *Tubificoides* spp. remained fairly stable and were not depleted by predation.

Nutrition of oligochaetes

Aquatic oligochaetes, similar to their terrestrial relatives, the 'earthworms,' are usually considered as non-selective detritivores or deposit feeders. Harper et al. (1981) found bacteria to be a major food item for *Nais variabilis* (Naididae) in freshwater sediments. Given the very large populations of naidids in sediments rich in organic matter the authors extrapolated that up to 48 times the bacterial stock in the sediment were continuously ingested by the worms. Thus, bacterivory seems to be the primary feeding strategy for these oligochaetes, which confirms earlier findings on tubificids (Wavre & Brinkhurst, 1971). More detailed studies, also on marine species, are required and feasible with evolving micro-ecological techniques and the application of molecular and isotopic methods. The indiscriminate terms 'detritus feeders' or 'deposit feeders' are probably not appropriate for oligochaetes (they are useful general terms cf. carnivore or herbivore).

Another food source that should be investigated is the uptake of dissolved organic substances, particularly sugars and amino acids. All degraded organic matter, each bacterial cell and biofilm, releases or excretes rich amounts of solutes of high nutritive value. The relatively large body surface area to volume ratio of oligochaetes with their thin cuticle renders them well adapted to uptake of nutrients across the body wall. Petersen et al. (1998) found in the brackish water species *Nais elinguis* (a salinity tolerant freshwater species) that amino acids alone could contribute up to 1/4 of its food requirement. Uptake of dissolved substances is obligatory in the gutless tubificids (*Inanidrilus leukodermatus*) (Liebezeit et al., 1983). Uptake rates of glucose were comparable to those found in gutless pogonophorans where this feeding mode was estimated (Southward & Southward, 1980) to cover 30% of the metabolic needs.

Despite the absence of other detailed studies on marine oligochaetes, there is a high probability that transepidermal and transintestinal uptake of dissolved substances are significant trophic pathways especially for the smaller, meiobenthic oligochaetes.

Conclusions

The marine environment plays a dominant economic, recreational and protective role in our society. Bagheri & McLusky (1984) suggest that in estuarine waters "oligochaetes ... form an absolutely vital, sometimes dominant component of secondary production ...". This view can probably be generalized for all eutrophic littoral sediments. It has also been shown that 'oligochaetes are capable of major modifications of their physical environment' (McCann & Levin, 1989). Thus, their ecological role in eulittoral ecotones requires at least as much intense scientific attention as do polychaetes. In fact McCann and Levin (1989), who mostly work on polychaetes have suggested with reference to oligochaetes. 'Future research efforts on the ecology and biology of this ecologically relevant annelid group are seriously needed'.

The lack of new ecological and biological studies on marine oligochaeta, since the 1982 review, is disturbing. Perhaps our focus on marginal aspects, relevant to only a small group of specialists and their symposia, and published only in specialized journals of small influence, may be contributory to this lack of new research? I have tried to show in this review that it is not only specialists in marine oligochaetes who have brought this group of organisms into main stream marine research. These biologists likely see the values of these organisms in a larger context. Beyond just coastal ecology, marine oligochaetes can serve as valuable models for solving problems of general biological relevance. Topics such as tissue senescence, genetic strategies of populations, or patterns and evolution of symbioses can and should be tackled using marine Oligochaeta as convenient tools and examples.

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