

Diversity and zoogeography of marine Tubificidae (Annelida, Oligochaeta) with notes on variation in widespread species

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Abstract

The specific and generic diversities of the marine Tubificidae (Annelida, Oligochaeta) of the NE Pacific are compared to those of the NE and NW Atlantic as well as to those of Heron Island, Australia. Diversity in the NE Pacific is relatively high when compared to that of the NE Atlantic. The Tubificidae of the NW Atlantic (limited to the eastern coast of the USA) show two distinct zoogeographic regions: Florida to Cape Hatteras; Cape Hatteras to Massachusetts. Diversity, both in terms of the number of species and number of genera, is approximately the same in these two regions, and is similar to that of both the NE Pacific and Heron Island. Evidence suggests that the widespread marine species, in particular *Tubificoides pseudogaster*, have a range of morphotypes across their distributions. The apparent wide distributions of these species may be due to a taxonomy unable to resolve the differences between the morphotypes. The tubificid oligochaete fauna of the NE Atlantic appears impoverished compared to the other regions examined. The NE Pacific, NW Atlantic, and Heron Island regions are not dominated by one group of species while the NE Atlantic fauna is dominated by *Tubificoides benedeni* and *Clitellio arenarius*.

Introduction

In recent years it has become apparent that a large number of marine oligochaetes exist in the worlds oceans, mainly of the families Tubificidae and Enchytraeidae; however, the zoogeography of these groups is practically unknown. The marine tubificid faunas of three widely separated areas are compared here to the fauna of the NE Pacific. This comparison includes only those species that have been found in the intertidal zone or shallow water. This restriction was necessary as most of the investigations in the NE Pacific have been limited to the intertidal zone.

Recent work in the NE Pacific (Pt. Conception, California, USA, to Dixon Entrance, northern British Columbia, Canada), a cold temperate region (Briggs, 1974), has revealed a rich littoral marine tubificid fauna (Brinkhurst & Baker, 1979; Baker,

1981a, 1982, 1983a, 1983b, 1983c; Baker & Brinkhurst, 1981; Baker & Erséus, 1982; Erséus, 1980a; Strehlow, 1982). Most of the collections in this region have been made in British Columbia. Twelve genera with 28 species occur in B.C.; only two additional species can be added from the rest of the region.

Collections in the NE Atlantic (Ireland, N. Ireland, England, Scotland, Sweden, and Norway), also a cold temperate region (Briggs, 1974), combined with a review of the literature (including data for W. Germany) show 11 genera with 24 species (littoral and sublittoral) (Erséus, 1975a, 1975b, 1978a, 1978b, 1979a, 1979b, 1980a, 1980b, 1980c, 1982a; Erséus & Kossmagk-Stephan, 1982).

A review of the available literature for the NW Atlantic (eastern coast of the USA), a warm temperate area (Briggs, 1974), showed that 2 distinct regions could be distinguished based on the distri-

bution of tubificid species: a region along the west coast of Florida to Cape Hatteras, North Carolina (Florida region), and a region between Cape Hatteras and Massachusetts (Cape Cod region) (Baker, 1981b; Baker & Erséus, 1979; Baker & Brinkhurst, 1981; Brinkhurst & Baker, 1979; Erséus, 1978a, 1979a, 1979b, 1979c, 1979d, 1979e, 1980a, 1981a, 1981b, 1982a, 1982b, 1982c, 1983a, 1983b; Erséus & Loden, 1981). The boundary between these two areas lies at Cape Hatteras, an area long recognized as a significant zoogeographic boundary (Briggs, 1974; Hayden & Dolan, 1976). In the Florida region there are 15 genera with 30 species; in the Cape Cod region, 13 genera with 39 species.

Heron Island, Australia, which lies in a tropical region (Briggs, 1974) at the southern edge of the Great Barrier Reef, has 11 genera with 32 species (Erséus, 1979d, 1980a, 1981a, 1981c, 1982a, 1983a; Erséus & Jamieson, 1981; Jamieson, 1977). Sampling at Heron Island has covered only the Heron and Wistari reefs (Erséus, pers. commun.); the very high diversity here is amazing for such a small area.

Comparison of the regions

The number of both genera and species of marine Tubificidae in the NE Pacific is higher than that of the NE Atlantic (Tables 1, 2). Three species are common to these areas (*Tubificoides pseudogaster*, *Monopylephorus rubroniveus*, *M. parvus*). The NE Pacific fauna lacks 3 genera found in the NE Atlantic (*Spiridion*, *Clitellio*, *Adelodrilus*) but does include 5 genera (*Tectidrilus*, *Rhizodrilus*, *Nootkadrilus*, *Discordiprostatatus*, and *Vadicola*) not found in the NE Atlantic; the latter three genera are found only in the NE Pacific. The NE Atlantic fauna lacks endemic genera entirely; only 3 species occur with

Table 1. Species of the northeast Pacific and northeast Atlantic regions, asterisked species are those shared with the northeast Pacific region.

Northeast Pacific	Northeast Atlantic
PHALLODRILINAE	PHALLODRILINAE
<i>Akteredrilus locyi</i>	<i>Adelodrilus cooki</i>
<i>oregonensis</i>	<i>pusillus</i>
n.sp. 1	<i>Akteredrilus curvipenis</i>
<i>Bacescuella labeosa</i>	<i>monospermathecus</i>
<i>Bathydrius</i> n.sp. 1	<i>sphaeropenis</i>
n.sp. 2	<i>Bacescuella arctica</i>
<i>Discordiprostatatus longisetosus</i>	<i>parvithecata</i>
<i>Nootkadrilus compressus</i>	<i>Bathydrius rarisetis</i>
<i>frigidus</i>	<i>Phalodrilus parthenopaeus</i>
<i>gracilisetosus</i>	<i>posispermathecatus</i>
<i>grandisetosus</i>	<i>prostatus</i>
<i>hamatus</i>	<i>rectisetosus</i>
<i>verutus</i>	<i>Spiridion insignis</i>
<i>Phalodrilus tempestatis</i>	
RHYACODRILINAE	RHYACODRILINAE
<i>Monopylephorus cuticulatus</i>	<i>Monopylephorus parvus*</i>
<i>parvus</i>	<i>rubroniveus*</i>
<i>rubroniveus</i>	
<i>Rhizodrilus pacificus</i>	
<i>Vadicola aprostatatus</i>	
LIMNODRILOIDINAE	LIMNODRILOIDINAE
<i>Limnodriloides monotheucus</i>	<i>Limnodriloides agnes</i>
<i>victoriensis</i>	<i>scandinavicus</i>
<i>Tectidrilus diversus</i>	
<i>verrucosus</i>	
TUBIFICINAE	TUBIFICINAE
<i>Tubificoides apectinatus</i>	<i>Clitellio arenarius</i>
<i>coatesae</i>	<i>Tubificoides amplivasatus</i>
<i>nerthoides</i>	<i>benedeni</i>
<i>pseudogaster</i>	<i>heterochaetus</i>
n.sp. 1	<i>pseudogaster*</i>
n.sp. 2	<i>Tubifex costatus</i>
n.sp. 3	<i>lioralis</i>

any regularity (*Clitellio arenarius*, *Tubificoides benedeni*, and *Tubifex costatus*). These species were found in every type of habitat throughout the intertidal range. This is in distinct contrast to the NE

Table 2. Number of species and genera per subfamily for each region (genera:species).

Subfamily	Region				
	Northeast Pacific	Northeast Atlantic	Cape Cod	Florida	Heron Island
Phalodrilinae	6:14	6:13	6:11	7:12	5:13
Rhyacodrilinae	3: 5	1: 2	2: 8	4: 8	4: 9
Limnodriloidinae	2: 4	1: 2	3: 8	4:10	2:10
Tubificinae	1: 7	3: 7	2:12	0: 0	0: 0
Total	12:30	11:24	13:39	15:30	11:32

Pacific where species ranges are often quite narrow and well defined (Baker, unpubl. observ.). The composition of the fauna in terms of the number of genera per subfamily is similar between these two regions (Tables 2, 3).

The Cape Cod fauna is quite diverse (Tables 2 and 4) and has more genera and species than the NE Pacific; 5 species are shared (Table 3). The Cape Cod region shares 8 species with the NE Atlantic (compare Tables 1 and 4); thus the northern regions of the Atlantic do show a slightly greater similarity to each other than do either to the NE Pacific. It is interesting to note that of the three common NE Atlantic species only *C. arenarius* and *T. benedeni* are found in the Cape Cod region; *T. costatus* is not.

There is a fundamental difference between the Cape Cod and Florida regions in that the latter is dominated by genera belonging to the Limnodriloidinae, Rhyacodrilinae, and Phallo-drilinae (Table 2) whereas the Tubificinae are an important faunal element of the Cape Cod region (12 of 39 species). There are no known members of the Tubificinae in the Florida region, although Shirley and Loden (1982) found *Tubificoides hererochaetus* and described *Tubificoides denouxi* from the Calcasieu estuary in Louisiana (Gulf of Mexico). Other species of *Tubificoides* remain to be described from the Gulf of Mexico (Baker, unpubl. observ.). Future sampling will undoubtedly show the existence of tubificine species in the Florida region. The only species common to Florida and the NE Pacific is *Limnodriloides monothecus* (Erséus, 1982a); to Florida and the NE Atlantic *Phallo-drilus rectisetosus* (two different subspecies; Erséus, 1981c).

Heron Island (Table 5) is totally distinct from the NE Pacific in terms of species but shares some of the cosmopolitan genera (see below).

Table 3. Number of species and genera shared by the northeast Pacific and the other regions relative to the total number of species or genera of the two regions being compared (shared species or genera:total species or genera).

	Northeast Atlantic	Cape Cod	Florida	Heron Island
Number of shared:total species	3:50	5:64	1:59	0:62
Number of shared:total genera	7:16	6:19	5:22	4:19

Table 4. Species and genera of the Florida and Cape Cod regions. Asterisked species are those shared with the northeast Pacific region.

Florida	Cape Cod
PHALLODRILINAE	PHALLODRILINAE
<i>Adelodrilus acochlearis</i>	<i>Adelodrilus anisetosus</i>
<i>magnithecatu</i>	<i>crisatus</i>
<i>Aktedrilus floridensis</i>	<i>magnithecatu</i>
<i>Bathydrius adriaticus</i>	<i>multispinosus</i>
<i>Inanidrilus bulbosus</i>	<i>Aktedrilus monospermathecus</i>
<i>Peosidrilus biprostatus</i>	<i>Bathydrius longus</i>
<i>Phallo-drilus caudatus</i>	<i>Peosidrilus biprostatus</i>
<i>extremus</i>	<i>Phallo-drilus coeloprostatu</i>
<i>rectisetosus</i>	<i>obscurus</i>
<i>sabulosus</i>	<i>parvatriatus</i>
<i>tenuissimus</i>	<i>Uniporodrilus granulothecat</i>
<i>Uniporodrilus granulothecat</i>	
RHYACODRILINAE	RHYACODRILINAE
<i>Heterodrilus bulbiporus</i>	<i>Heterodrilus bulbiporus</i>
<i>minisetosus</i>	<i>minisetosus</i>
<i>occidentalis</i>	<i>occidentalis</i>
<i>pentcheffi</i>	<i>pentcheffi</i>
<i>Kaketio ineri</i>	<i>Monopylephorus evertus</i>
<i>Marcusaedrilus hummelincki</i>	<i>irroratus</i>
<i>luteolus</i>	<i>parvus*</i>
<i>Parakaketio longiprostatu</i>	<i>rubroniveus*</i>
LIMNODRILOIDINAE	LIMNODRILOIDINAE
<i>Limnodriloides baculatus</i>	<i>Limnodriloides agnes</i>
<i>barnardi</i>	<i>barnardi</i>
<i>hastatus</i>	<i>medioporus</i>
<i>monothecus*</i>	<i>monothecus*</i>
<i>rubicundus</i>	<i>rubicundus</i>
<i>vespertinus</i>	<i>Smithsonidrilus marinus</i>
<i>Smithsonidrilus marinus</i>	<i>Thalassodrilides belli</i>
<i>Tectidrilus bori</i>	<i>milleri</i>
<i>squalidus</i>	
<i>Thalassodrilides gurwitschi</i>	
TUBIFICINAE	TUBIFICINAE
	<i>Clitellio arenarius</i>
	<i>Tubificoides apectinatus*</i>
	<i>benedeni</i>
	<i>brownae</i>
	<i>diazii</i>
	<i>dukei</i>
	<i>heterochaetus</i>
	<i>intermedius</i>
	<i>longipenis</i>
	<i>maueri</i>
	<i>pseudogaster*</i>
	<i>wasselli</i>

The NE Pacific shares very few species with the other regions discussed here (Table 3) but does show more affinities to the NE Atlantic and Cape Cod regions than to Heron Island and the Florida region.

As can be seen from Table 2 the NE Pacific has

Table 5. Species and genera of Heron Island.

PHALLODRILINAE

Akteredrilus parviprostatu
Bathydriulus rohdei
superiovasatus
Coralliodriulus atrio bifidus
avisceralis
oviatratus
parvigenitalis
Jamiesoniella athecata
Phalldrillus albidus
clavatus
filiitheatus
geniculatus
rectisetosus

RHYACODRILINAE

Gieredrilus inermis
Heterodriulus claviatratu
jamiesoni
keenani
queenslandicus
scitus
Heronidriulus bihamis
fastigatus
Macquaridriloides heronae

LIMNODRILOIDINAE

Limnodriloides armatus
australis
tenuiductus
uniampullatus
Marcusaedrilus capricornae
irregularis
grandiculus
minusculus
sacculatus
tuber

approximately the same number of species and genera as the Cape Cod, Florida, and Heron Island regions. All of these show a higher number of species and all except Heron Island have a higher number of genera than the NE Atlantic (Table 2); these regions are all similar in terms of latitudinal range except for Heron Island (see above).

There are only four genera common to all 5 regions; *Phalldrillus*, *Akteredrilus*, *Bathydriulus*, and *Limnodriloides*. The subfamilies Phalldrilineae, Rhyacodrilinae, and Limnodriloidinae are well represented and appear to be cosmopolitan (Table 2). The Tubificinae are best represented in the temperate latitudes but are unknown to date in Florida (see above discussion) and Heron Island.

Variation in widespread species

Most species of marine Tubificidae have quite restricted distributions. There are only 5 species that appear to be at all widespread (*Tubificoides pseudogaster*, *Monopylephorus rubroniveus*, *M. parvus*, *Limnodriloides monotheucus*, and *Phalldrillus rectisetosus*). One common characteristic of these 5 species is that the genital systems are all relatively simple as compared to the other members of their respective genera. These forms may, therefore, be classified as single species over their geographic range simply because they lack the suite of complex characters necessary to adequately express variation.

M. rubroniveus has been regarded as being composed of up to 10 synonyms two of which have now been separated as distinct taxa (*M. limosus*, *M. kermadecensis*; Baker & Brinkhurst, 1981). All of the remaining 8 synonyms differ slightly in various characters. *M. parvus* has also been described as varying in some characters between material from different localities (see Marcus, 1965; Baker & Brinkhurst, 1981). Erséus (1982a) noted several differences between material of *L. monotheucus* from different areas but declined to erect new taxa based on these differences. Erséus (1979d, 1981c) has erected three subspecies of *P. rectisetosus* from different areas (Italy and France; Florida; Heron Island) based on minor differences in the genitalia. *T. pseudogaster*, redescribed from type material by Baker (1980), also displays variation in material from different geographical areas.

I have recently examined additional specimens of *T. pseudogaster* from Sweden (Tjärnö), Germany (Schlei Fjord), England (Hull River estuary), Canada (Frobisher Bay, Northwest Territories), and USA (Friday Harbour, Washington). Penis sheath lengths of material from the above localities are shown in Fig. 1. The new material examined showed significant variation with regard to penis sheath lengths ($P \leq 0.05$) of the above material belonging to the same population; Baker, unpubl. data) and appears to be different than the material from the type locality of *pseudogaster* (Kysing Fjord, Denmark; Dahl, 1960; Baker, 1980). There is a definite cline in the penis sheath lengths of the new material (Fig. 1). Length and width of the atria and vasa deferentia also show significant variations between the above populations. However, while these differ-

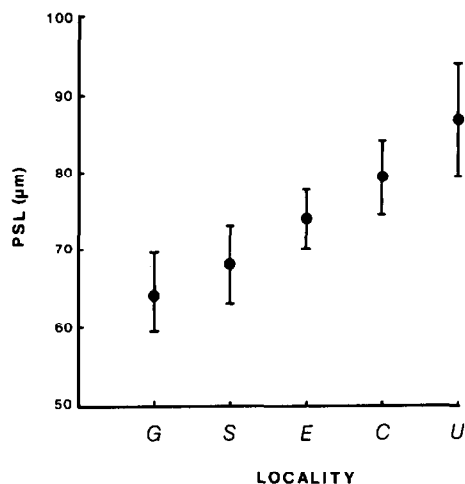


Fig. 1. 95% confidence intervals about the means of penis sheath lengths (PSL) of *T. pseudogaster* material from Schlei Fjord, Germany (G); Tjärnö, Sweden (S); Hull River estuary, England (E); Frobisher Bay, Canada (C); and San Juan Island, USA (U). Localities arranged in order of increasing geographical distance from the type locality of *T. pseudogaster*.

ences do exist, it is not known if they are genotypic or phenotypic in nature; the differences are not pronounced enough to warrant specific or subspecific separation of the various populations.

This problem is one of the main failings of the primarily morphological taxonomy in use today; in simple forms, with few distinctive characters, it becomes almost impossible to distinguish phenotypic from genotypic variation. This situation is aggravated by the lack of modern studies on intra-specific variation in more complex, easily distinguishable species. Until the scope of variation within distinct species in a limited geographical range is known, it will be impossible to determine if the variation in widespread species represents intra- or inter-specific variation. Thus, given the very high number of endemic marine species, these so-called widespread species may in fact reflect the results of an inadequate taxonomy rather than truly cosmopolitan species.

Conclusions

It would appear that there is a fundamental difference between the tubificid faunas of the NE Atlantic and the other regions studied. In all 4 of the other regions the littoral tubificid fauna is rich and in the

NE Pacific (Baker, unpubl. observ.) and NW Atlantic (Florida and Cape Cod regions) there is a distinct change in species composition with latitudinal change. In the NE Atlantic the littoral tubificid fauna is not as rich and is dominated by *Tubificoides benedeni* and *Clitellio arenarius* (Baker, pers. observ.) over the whole region.

The NE Pacific, Cape Cod, Florida, and Heron Island regions have littoral tubificid faunas with high diversity, definite species ranges, and no dominant group of species. The NE Atlantic fauna usually has a relatively low diversity with broad species ranges, and is dominated by *Tubificoides benedeni* and *Clitellio arenarius*.

The very few widespread marine tubificid species are all simple forms; their apparent wide distributions may be a taxonomical artifact.

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