

Distribution and abundance of teredinid recruits along the Swedish coast – are shipworms invading the Baltic Sea?

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*Shipworms (teredinids) are highly specialized marine bivalves that consume terrestrially derived wood. Changes in environmental variables may result in shipworms spreading into the Baltic Sea – which would have devastating consequences for maritime cultural heritage and submerged wooden structures. We investigated the distribution and abundance of the shipworms *Teredo navalis* and *Psiloteredo megotara* along the Swedish coast in 2006–2008, and compared our findings with data collected at partly the same locations in 1971–1973. Wooden test panels were submerged in near-surface waters at 18 harbours. The presence of shipworms was determined by X-ray radiography of each panel. Sea surface temperature and salinity data were analysed to investigate whether any changes in distribution were correlated to changes in environmental variables. We found that past and present distributions of *T. navalis* were similar – indicating that no range expansion of shipworms into the Baltic Sea has taken place the last 35 years. The abundance of *T. navalis* was similar between decades at all investigated sites except two (Arild and Barsebäckshamn), where abundances were higher in 2006–2008. The abundance of *T. navalis* varied along the coast and was positively correlated to mean sea surface salinity, but not to mean sea surface temperature (2006–2008 data). The distribution and abundance of *P. megotara* were similar during the two study periods with only single observations at a few sites. In conclusion, we found no evidence of range expansion of shipworms along the Swedish coast.*

Keywords: *Teredo navalis*, spatial distribution, range expansion, Swedish coast, temperature, salinity, climate-change

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INTRODUCTION

Shipworms (family Teredinidae) are highly specialized marine bivalves that efficiently and rapidly decompose and consume terrestrially derived wood in the ocean with the aid of intracellular cellulolytic and nitrogen-fixing symbionts (Distel *et al.*, 2002). Shipworms play a major ecological role in mangrove systems and are an important link in the turnover of carbon from terrestrial ecosystems in temperate seas (Turner, 1966). This brings them into conflict with human interests because they can cause extensive damage to submerged man-made wooden structures. In the USA alone, the economic consequences of shipworm damage to ships, fishing equipment and wooden structures in marine environments have been estimated to be ~US\$ 200 million per year (Cohen & Carlton, 1995). Studies on shipworms date back to the 18th century (Clapp & Kenk, 1963), but information on the distribution of many species is still scattered (Borges *et al.*, 2014).

The geographic range of a species is determined by complex interactions among environmental and biological factors and is also affected by evolutionary processes such as adaptation (Cox & Moore, 2009). For centuries, a primary goal for biogeographers has been to identify factors that determine the distribution of species (e.g. Wallace, 1876;

MacArthur & Wilson, 1963). Among these, salinity and temperature are overridingly important abiotic determinants of species distributions, especially in estuarine and coastal ecosystems (Kinne, 1963; Bonsdorff, 2006; Ojaveer *et al.*, 2010). Previous studies have also implicated these factors in controlling the distribution of shipworms (Scheltema & Truitt, 1954; Hoestland & Brasselet, 1968; Culliney, 1970; Nair & Saraswathy, 1971; Eckelbarger & Reish, 1972; Saraswathy & Nair, 1974; Hoagland, 1986).

Of about 65 described shipworm species (Turner, 1966), the widely distributed, euryhaline species *Teredo navalis* L. is the most investigated and the most abundant teredinid in Sweden (Norman, 1976, 1977). *Teredo navalis* broods its offspring until the larvae have reached straight-hinge stage, at which time the free-swimming larvae are released to the plankton, where they grow for a further 2–5 weeks (Grave, 1928; Imai *et al.*, 1950; Loosanoff & Davis, 1963; Culliney, 1975). The species shows a wide tolerance to both temperature and salinity (reviewed in Nair & Saraswathy, 1971; Eckelbarger & Reish, 1972). Release of larvae can occur in salinities <9 PSU and temperatures <11 °C (Roch, 1940), although larvae are unable to survive at salinities less than 6–7.5 PSU (M’Gonigle, 1926; Hoagland, 1986). The second member of Teredinidae recorded in Swedish waters is the oviparous species *Psiloteredo megotara* (Hanley). Little is known about this species’ biology and ecology. However, it shows higher growth rate, is less tolerant to low salinities, and is better adapted to lower temperature than *T. navalis* (Dons, 1940; Norman, 1977).

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There is increasing concern that climate change will lead to shifts in the geographic ranges of ecologically and economically important species. Several studies report range shifts due to climate change in terrestrial and marine species (e.g. Perry *et al.*, 2005; Harley *et al.*, 2006; Parmesan, 2006; Wernberg *et al.*, 2011), and changing distribution patterns of shipworms have also been reported recently (Sordyl *et al.*, 1998; Tuente *et al.*, 2002; Borges *et al.*, 2010, 2014). At the beginning of the 21st century rumours circulated about possible range-expansion of shipworms in Scandinavian waters: Swedish harbour authorities noticed an increased level of shipworm attacks on wooden constructions (Port of Gothenburg personal communication, Schlyter, 2009), and during the summer of 2002 shipworms were observed for the first time on the Danish island of Bornholm (Olsen, 2003). Shortly thereafter, marine archaeologists began to raise concerns over the risk of shipworms spreading into the Baltic Sea, a brackish water area with many valuable and well-preserved wooden wrecks (Olsson, 2006).

Hypotheses of range expansion are perhaps most easily tested by comparing new range records with historical distribution data. We used a 35-year-old investigation of the geographical distribution of shipworms in Swedish waters as a baseline (Norman, 1977). Norman (1977) found high frequencies of *T. navalis* along the Swedish west coast from close to the Norwegian border (Koster Islands) southwards to the entrance to the Sound at Mölle (Figure 1). Beyond

this point abundances declined and the most southern point of shipworm recruitment was observed at Klagshamn. The second species, *P. megotara*, was rare with very few specimens at some sites from the Koster islands down to Mölle. We repeated Norman's (1977) study to assess whether shipworms have changed their range over the past 35 years. Furthermore, in order to explore whether any shifts in the range of shipworms could be correlated with temporal changes in environmental variables, we compared historical and present-day sea surface temperature and sea surface salinity data.

MATERIALS AND METHODS

Study area

We investigated occurrence of teredinids from the Skagerrak to the Baltic Sea (Figure 1). This region is a transitional area with complex hydrography and strong salinity gradients between the North Sea and Baltic Sea (Gustafsson & Stigebrandt, 1996). The oceanographic system is barotropically driven mainly by differences in sea levels and wind patterns (Stigebrandt & Gustafsson, 2002). Large inflow of high saline water into the Baltic Sea through the Danish Straits and the Sound is limited by the topography and occurs only occasionally (Schinke & Matthaus, 1998). The dominant sea surface current is west along the Swedish south coast, and northbound along the Swedish west coast. However, daily variation occurs at local scales. Coastal sea surface temperature shows wide seasonal variation ($\sim -4-27\text{ }^{\circ}\text{C}$) (<http://www.smhi.se>). Sea surface salinity in the study area ranged from fully marine conditions in the Skagerrak ($>30\text{ PSU}$) down to brackish levels ($\sim 7\text{ PSU}$) along the southern coast of Sweden and around Bornholm (<http://www.smhi.se>).

Distribution and abundance of shipworms

The study was conducted along the Swedish west and south coasts and around the Danish island of Bornholm during 2006–2008. In 2006, the distribution of shipworms was investigated at 9 sites that partly followed the sites investigated in Norman (1977) (Figure 1). In order to increase spatial resolution of the investigation, and to study a possible range expansion of shipworm infestations in the Baltic Sea, five additional harbours along the Swedish coast, and four additional harbours around Bornholm, Denmark, were also included in 2007 and 2008 survey (Figure 1).

At each site, four unplanned pine (*Pinus sylvestris*) panels ($25 \times 75 \times 200\text{ mm}$) were submerged at a depth of 0.5–2 m below sea surface in the spring of each year. Holes ($\varnothing 25\text{ mm}$) were drilled in the centre of the panels, the panels attached to a polypropylene rope with cable ties, and then suspended vertically in the water. Panels were collected one year later, surface fouling organisms were removed, and the panels were stored in the freezer ($-20\text{ }^{\circ}\text{C}$). In order to estimate the shipworm abundance, panels were analysed by X-ray radiography (Siemens – Elema Mobilet II 40 kV and 14 mA). Before X-ray, panels were thawed and dried at room temperature for 48 h. The number of shells visible was counted over the whole X-ray photo area, and abundance (per dm^2) calculated for the exposed surface of the panel (4.275 dm^2 per panel).

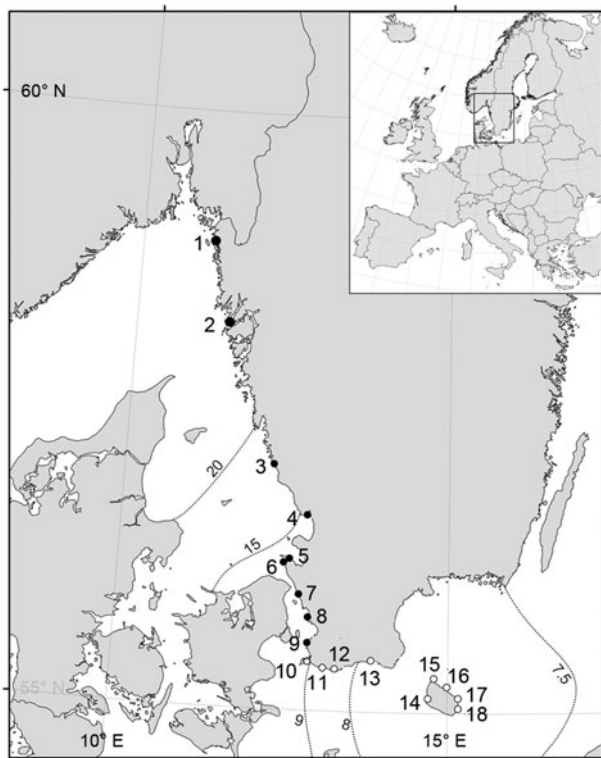


Fig. 1. Map of the sampling sites for shipworm abundance, and sea surface salinity and temperature along the Swedish coast and around the Danish island of Bornholm. Filled circles represent sites visited during the 1970s by Norman (1977). Site: (1) Tjörn, (2) Kristineberg, (3) Träslövsläge, (4) Grötvik, (5) Arild, (6) Mölle/Höganäs, (7) Ålabodarna, (8) Barsebäckshamn/Lundäkra, (9) Klagshamn, (10) Falsterbo/Höllviken, (11) Skåre, (12) Gislövsläge, (13) Ystad, (14) Ronne, (15) Sandvig, (16) Gudhjem, (17) Svaneke, (18) Nexø. Dotted lines represent the boundary of different salinity regimes.

Yearly mean values of *T. navalis* abundance (individuals dm^{-2}) at each site were calculated and analysed in a 2-way analysis of variance (ANOVA) with Decade as a 2-level, and Site as a 9-level, fixed factor. Data from 2006–2008 were analysed in two separate statistical tests due to lost wooden panels at some sites in 2006 and extension of sites in 2007 and 2008. The abundance data from 2006 were statistically analysed in a one-way ANOVA with Site as a fixed 9-level factor. The abundance data from 2007 and 2008 were statistically analysed in a two-way ANOVA with Year as a 2-level random factor and Site as a 17-level fixed factor. Means were compared using the Student-Newman-Keuls (SNK) procedure (Underwood, 1997). All data were tested for homogeneity of variances with Cochran's test (Underwood, 1997). The abundance of *P. megotara* was very low during both study periods with only a few observations of single individuals, and therefore no statistical analysis of these data was performed.

Sea surface salinity and temperature

Sea surface temperature and salinity data along the Swedish west and south coast were analysed for the summer period (May to October – the season for adult *T. navalis* reproduction and larval metamorphosis). Data were obtained from the Swedish Meteorological and Hydrological Institute (<http://www.smhi.se>). Additional salinity and temperature data were also obtained from the marine biological stations at Kristineberg and Tjärnö (<http://www.loven.gu.se>, Figure 1).

In order to investigate a possible long-term change in sea surface temperature from the 1970s to the 2000s, 3 daily averages of temperature data were extracted from Kristineberg (handwritten logbook and <http://www.loven.gu.se>) each month during the study season (May–October) from 1971–1973 and 2006–2008. Long-term high-resolution temperature data were only available for Kristineberg and therefore possible changes in sea surface temperature at this site were assumed to be representative for the whole study area. Data were analysed statistically using a mixed model ANOVA with Decade as a 2-level fixed factor, Year as a 3-level random factor nested within Decade, and Month as a 6-level fixed factor.

In order to investigate possible short-term changes in sea surface temperature and salinity along the Swedish west coast during the study period (2006–2008), data were extracted from monitoring stations (Höganäs, Lundåkra and Höllviken) close to sampling sites in the Sound (Mölle, Barsebäckshamn and Falsterbo) (<http://www.smhi.se>), as well as from Kristineberg (<http://www.loven.gu.se>) and Tjärnö (<http://130.241.163.18/BB/defaultB.html>). Data were analysed using 2-way ANOVAs with Year as a 3-level random factor and Site as a 5-level fixed factor. In order to investigate if the abundance of *T. navalis* was correlated to the environmental variables, yearly mean values for 2006–2008 at different sites (Tjärnö, Kristineberg, Mölle/Höganäs, Barsebäckshamn/Lundåkra and Falsterbo/Höllviken) were calculated, log-transformed and compared with sea surface temperature and salinity data using simple linear regression.

RESULTS

No evidence for range expansion of *T. navalis* along the Swedish coast between the 1970s and the 2000s was detected

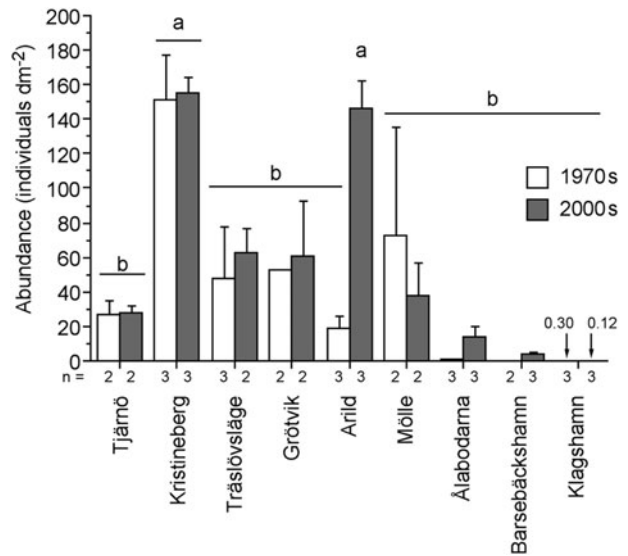


Fig. 2. Abundance of *Teredo navalis* (number of individuals per dm^2) at different sites along the Swedish west and south coasts in the 1970s and 2000s. Data from the 1970s are modified after Norman (1977). Letters above bars indicate significant differences between mean values based on the Student-Newman-Keuls multiple comparisons test (SNK, $P < 0.05$). Error bars show + SEM ($N = 2-3$, indicated by figures under bars).

(Figures 2 & 3), although we found one individual at Falsterbo, a site that was not investigated in the 1970s (Figure 3B). However, we found a statistically significant interaction between the effects of Decade and Site on shipworm abundance (Table 1). The mean abundance of *T. navalis* at one site (Arild) was significantly (SNK, $P < 0.05$) higher in samples from the 2000s (Figure 2). There were no statistically significant differences in shipworm abundances at the other sites (SNK, $P > 0.05$), although at Barsebäckshamn, *T. navalis* was only observed in the 2000s (Figure 2). The presence of *P. megotara* was similar during the two periods with observations of single individuals at Tjärnö, Kristineberg, Träslövsläge and Mölle (Table 2).

Analysis of *T. navalis* abundance in 2007 and 2008 showed no statistically significant interaction between the main factors Year and Site (Table 3, Figure 3B), however there were statistically significant effects of both of these factors independently (Table 3). Mean *T. navalis* abundance in 2007 and 2008 was 32.36 ± 7.33 and 20.94 ± 6.12 individuals per dm^2 (mean \pm SEM) respectively. Mean abundance of *T. navalis* was also greatest at Kristineberg and Arild in all years 2006–2008 (Table 3, Figure 3B). Furthermore, when means from 2007 and 2008 were compared, we found statistically ($P < 0.05$) greater abundances of *T. navalis* at Träslövsläge and Grötvik compared with the more southern sites (Figure 3B). No shipworms were found on the Swedish south coast (Skåre, Gislövsläge and Ystad), or around the Danish island of Bornholm during the years 2006–2008 (Figure 3A, B).

Sea surface temperature during the summer months at Kristineberg differed significantly between decades (Table 4). Mean temperature was 12.5% higher in the 2000s ($16.01 \pm 0.44^\circ\text{C}$, mean \pm SEM) compared with the 1970s ($14.23 \pm 0.47^\circ\text{C}$, mean \pm SEM). As expected, there was also a statistically significant difference in temperature between different months, with highest temperatures during

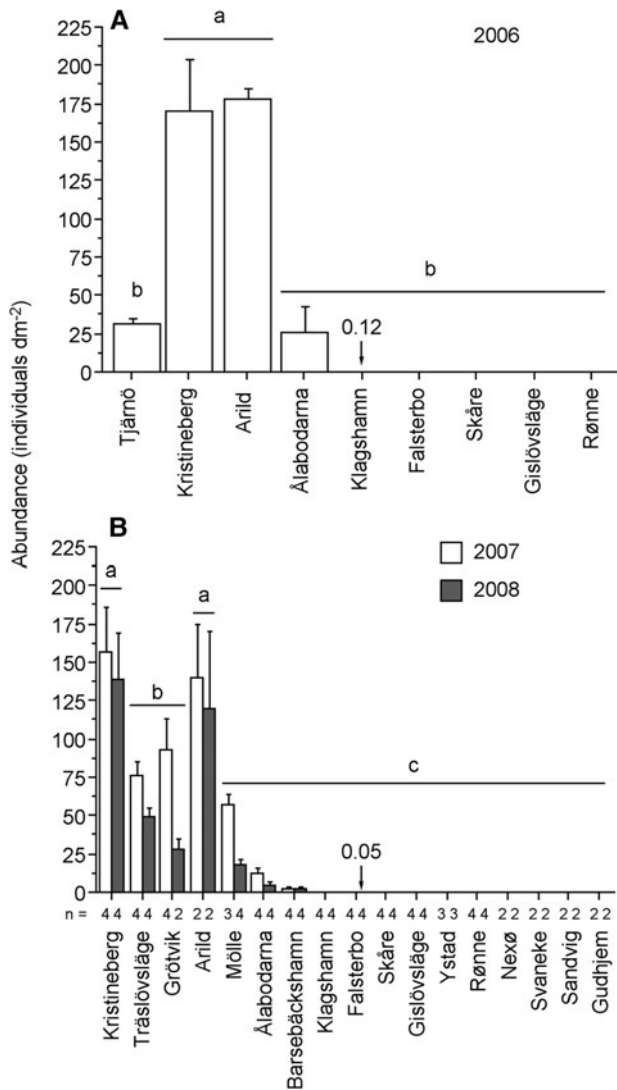


Fig. 3. Abundance of *Teredo navalis* (number of individuals per dm²) at different sites along the Swedish coast in (A) 2006 (N = 2) and (B) 2007 and 2008 (N = 2–4, indicated by figures under bars). Letters above bars indicate significant differences between mean values based on the Student-Newman-Keuls multiple comparisons test (SNK, $P < 0.05$). Error bars show + SEM.

July and August (Figure 4). There was no statistically significant short-term difference at the five sites in summer (May–October) sea surface temperature values among years or sites (Table 5A, Figure 5A). Mean sea surface temperature for 2006, 2007 and 2008 was 15.91 ± 0.63 , 15.48 ± 0.63 and $15.70 \pm 0.46^\circ\text{C}$ (mean \pm SEM) respectively.

Table 1. Analysis of variance of mean *Teredo navalis* abundance (number of individuals per dm²) at different sites along the Swedish coast during different decades (1970s and 2000s). Mean values and SEM are presented in Figure 2.

Source of variance	df	MS	F	P
Decade	1	2577.31	3.12	0.09
Site	8	13,717.77	16.62	<0.01
Decade \times Site	8	2735.54	3.31	<0.01
Residual	28	825.43		

Table 2. Mean abundance (number of individuals per dm²) of *Psiloteredo megotara* at different sites along the Swedish coast during 6 years (1971–1973 and 2006–2008) from 2 decades (the 1970s and 2000s). Data from 1970s are modified after Norman (1977). n.a. = not applicable due to lack of test panels.

Site	1970s			2000s		
	1971	1972	1973	2006	2007	2008
Tjärnö	0.05	0.09	n.a.	1.17	n.a.	1.17
Kristineberg	0.05	0.07	0	0.07	0	0.58
Träslövsåge	0.02	0	0	n.a.	0	0
Grötvik	0	0	n.a.	n.a.	0	0
Arild	0	0	0	0	0	0
Mölle	0.05	0	n.a.	n.a.	0	0.06
Ålabodarna	0	0	0	0	0	0
Barsebäckshamn-	n.a.	0	0	0	0	0
Klagshamn	0	0	0	0	0	0

Table 3. Analysis of variance of mean *Teredo navalis* abundance (number of individuals per dm²) at different sites along the Swedish coast during different years (2007 and 2008). Mean values and SEM are presented in Figure 3B.

Source of variance	df	MS	F	P	F vs
Year	1	2664.31	5.80	0.02	Residual
Site	16	14,311.98	29.06	<0.01	Year \times Site
Year \times Site	16	492.59	1.07	0.40	Residual
Residual	77	459.37			

Table 4. Analysis of variance of mean sea surface temperature data from different months (May to October) during 6 years (1971–1973 and 2006–2008) from 2 decades (the 1970s and 2000s) at Kristineberg. Mean values and SEM are presented in Figure 4.

Source of variance	df	MS	F	P	F vs
Decade	1	85.69	16.47	0.02	Year (Decade)
Year (Decade)	4	5.20	2.18	0.08	Residual
Month	5	181.76	52.48	<0.01	Year (Decade) \times Month
Decade \times Month	5	1.70	0.49	0.78	Year (Decade) \times Month
Year (Decade) \times Month	20	3.46	1.45	0.13	Residual
Residual	72	2.39			

Sea surface salinity values did not differ statistically among years (2006–2008) (Table 3B). The mean salinities for 2006, 2007 and 2008 were 15.63 ± 1.44 , 16.35 ± 1.32 and 16.58 ± 1.15 PSU (mean \pm SEM) respectively. As expected, mean summer salinity varied significantly among study sites (Table 5B), with significantly (SNK, $P < 0.05$) higher values at the northern sites Tjärnö and Kristineberg, and significantly (SNK, $P < 0.05$) lower values at the southern sites Lundåkra and Höllviken compared with Höganäs (Figure 5B). No major Baltic inflows of high salinity water from the Skagerrak area occurred during the study period. However, a maximum salinity value of 18.3 PSU was measured at Höllviken in June 2008, which correlates with the only year that shipworms were found at Falsterbo (Figure 3B). The log-transformed yearly mean abundance of *T. navalis* at different

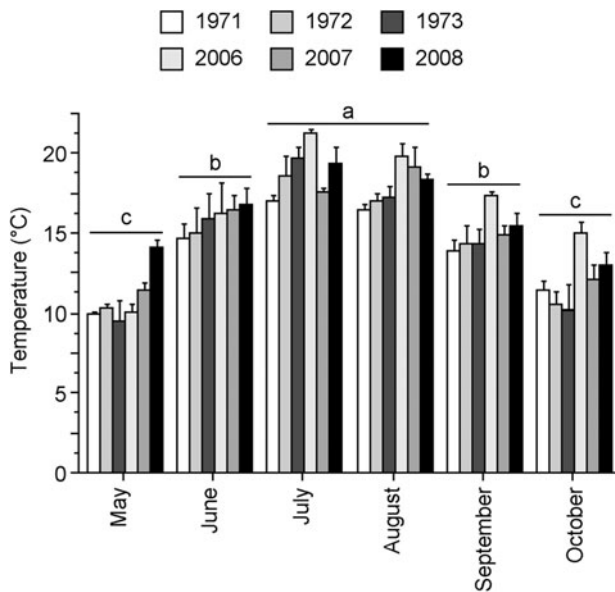


Fig. 4. Mean sea surface temperature data from different months (May to October) during 6 years (1971–1973 and 2006–2008) from 2 decades (the 1970s and 2000s) at Kristineberg. Letters above bars indicate significant differences between mean values based on the Student-Newman-Keuls multiple comparisons test (SNK, $P < 0.05$). Error bars show + SEM ($N = 3$).

sites did not correlate significantly to the sea surface temperature during the study periods ($\log(\text{abundance} + 0.001) = 2.06 \times -31.79$, $R^2 = 0.154$, $P = 0.19$, Figure 6A), but was significantly positively correlated to salinity ($\log(\text{abundance} + 0.001) = 0.21 \times -2.72$, $R^2 = 0.526$, $P = 0.02$, Figure 6B). Sea surface salinity measurements at stations close to sites where shipworms were absent (Skåre, Gislövsläge, Ystad and around Bornholm) were frequently lower than 8 PSU (data available at <http://www.smhi.se>).

DISCUSSION

The aim of the present study was to investigate a possible range expansion of teredinids in Swedish coastal waters using data from a previous study by Norman (1977) as a baseline, and to correlate the changes in *T. navalis* distribution and abundance to changing environmental variables (salinity and temperature). We found no strong evidence for range expansion of teredinids into the Baltic Sea during the 2000s, although single specimens of *T. navalis* were observed in Barsebäckshamn and Falsterbo; sites where this species either was not found or not investigated in the 1970s

(Norman, 1977). We assume that these differences are due to small seasonal changes rather than any systematic range expansion of *T. navalis*. No *T. navalis* were observed east of Falsterbo, but the absolute distribution of teredinids along the Swedish south coast and around Bornholm may be underestimated in the present study. For example, teredinids may degrade wood deeper than 0.5–2 m, which was the deployment depth for the test panels. However, the presence of many well-preserved wooden wrecks around Falsterbo and further east in the Baltic Sea (<http://www.raa.se>) suggests low (or no) presence of shipworms in this area for some time.

The abundance of *T. navalis* at different sites along the Swedish coast was similar during the two study periods (Norman, 1977). The only site where a statistically significant increase in *T. navalis* abundance was found in the 2000s compared with the 1970s was at Arild. The abundance of *T. navalis* in our samples varied along the Swedish coast and was positively correlated to sea surface salinity, but not to temperature. Sea surface temperature was significantly higher in the 2000s compared with the 1970s, but no short-term temporal differences in either salinity or temperature were found in the present study. Furthermore, the similar distribution ranges of *T. navalis* between past (Norman, 1977) and present investigations are in accordance with unchanged salinity levels in the Sound (Madsen & Højerslev, 2009).

Salinity is often claimed to be the factor limiting marine species spread into the Baltic Sea, and several studies have demonstrated negative effects of low salinity on the distribution of shipworms in estuarine environments (Sellius, 1733; Blum, 1922; M'Gonigle, 1926; Miller, 1926; White, 1929; Scheltema & Truitt, 1954; Culliney, 1970). Other studies, however, (Hoagland, 1986; Rayner, 1979; Jungueira *et al.*, 1989) have shown that shipworms in laboratory culture can tolerate salinities outside the range in which natural populations are found, suggesting that factors other than salinity may also be important for their distribution. In the present study, we found a clear positive correlation between salinity and the distribution and abundance of *T. navalis*. Nonetheless, abundances of *T. navalis* in salinities ranging from 9–30 PSU were high (> 30 individuals dm^{-2}), which confirms previous reports of wide salinity tolerance of this cosmopolitan species (Nair & Saraswathy, 1971). No shipworms were found at sites where test panels were exposed to salinities lower than 8.6 PSU (i.e. along the southern Swedish coast and at the island of Bornholm). These results indicate that shipworm recruitment in Swedish waters occurs at ≥ 9 PSU. Considering that local salinity fluctuations are large, and test panels were inspected only once a year, it is not possible to determine salinity at the time of larval settlement. The occasional settlement we observed at Falsterbo in

Table 5. Analysis of variance of mean (A) sea surface temperature (°C) and (B) salinity (PSU) during summer (May to October) 2007 and 2008 at five different sites (Tjärnö, Kristineberg, Höganäs, Lundåkra and Höllviken) along the Swedish west and south coasts. Mean values and SEM are presented in Figure 5A, B.

Source of variance	df	MS	(A) Temperature			(B) Salinity			F vs
			F	P	MS	F	P		
Year	2	1.39	0.12	0.89	7.39	0.53	0.55	Residual	
Site	4	0.73	1.65	0.25	853.49	61.51	<0.01	Year × Site	
Year × Site	8	0.44	0.04	1.00	13.88	1.12	0.36	Residual	
Residual	75	11.52			12.41				

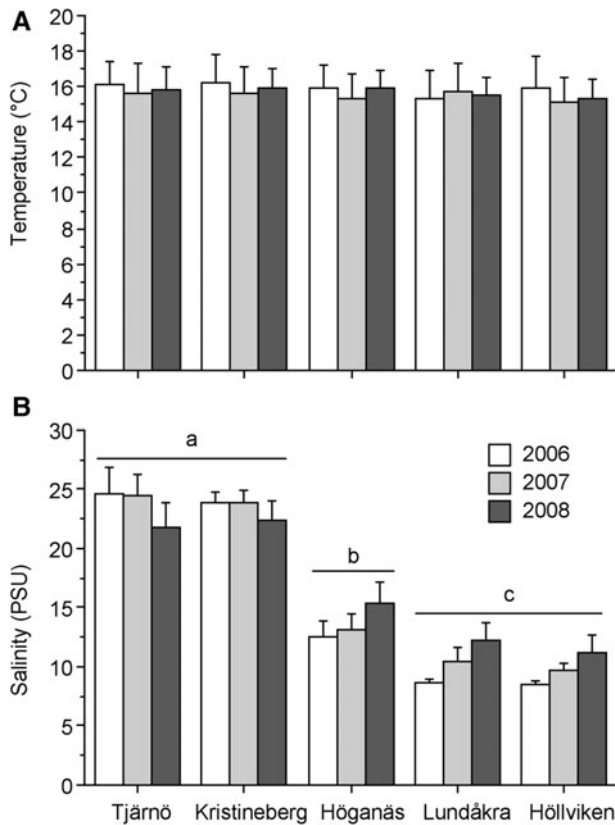


Fig. 5. Sea surface (A) temperature (°C) and (B) salinity (PSU) at different sites along the Swedish coast during 2006–2007. Letters above bars indicate significant differences between mean values based on the Student-Newman-Keuls multiple comparisons test (SNK, $P < 0.05$). Error bars show + SEM ($N = 6$).

2008 corresponded with extremely high salinity values for the area in June the same year (data not shown). However, whether this was a cause, or if settlement was due to other contributing factors (e.g. infrequent larval supply) is not known.

Apart from salinity, other environmental or biological factors may influence the distribution and abundance of tereidids. For example, reproduction, as well as larval survival and metamorphosis, of shipworms have all been shown to be temperature dependent (Nair & Saraswathy, 1971; Eckelbarger & Reish, 1972; Hoagland, 1986). *Teredo navalis* is tremendously prolific and becomes sexually mature 3 weeks after settlement (Culliney, 1970). Therefore, an increase in temperature would likely result in a longer breeding season, more offspring, and subsequent increased propagule pressure – perhaps leading to increased adult abundance. However, although we found a large increase (1.78°C) in summer sea surface temperature at Kristineberg between the 1970s and 2000s, there was no significant difference in the abundance of *T. navalis* at this or other sites (except at Arild). Furthermore, no significant correlation was found between present *T. navalis* abundance and temperature, indicating that temperature is not a determining factor for Swedish *T. navalis* distribution and abundance. Kristensen (1969) concluded that the distribution of *T. navalis* in Danish waters was salinity dependent, but that the activity was primarily influenced by temperature. Whether this is also the case for Swedish *T. navalis* remains to be investigated.

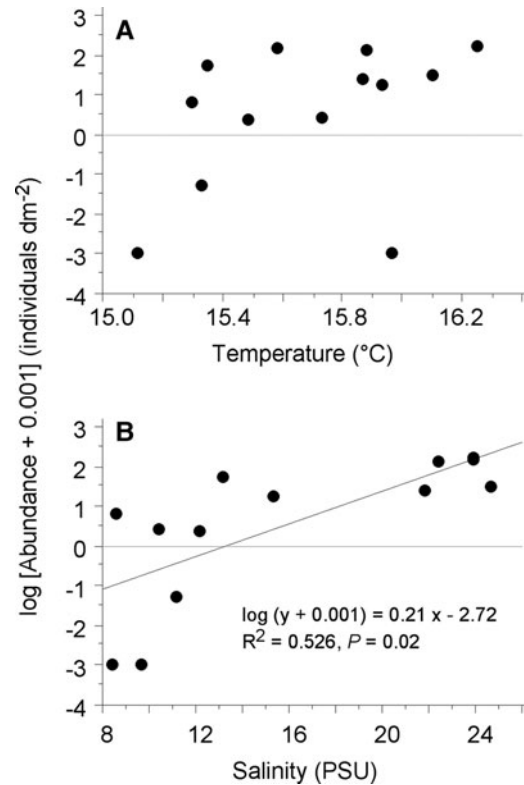


Fig. 6. Relationship between log (abundance + 0.001) of *Teredo navalis* (individuals per dm²) and sea surface (A) temperature (°C) and (B) salinity (PSU). Circles represent mean values for different sites (Tjämnö, Kristineberg, Mölle/Höganäs, Barsebäckshamn/Lundåkra and Falsterbo/Höllviken) and years (2006–2008).

Small-scale variation in larval recruitment along irregular and estuarine coastlines, such as the Swedish coast, may be explained by the regional variation in water transport (Gaines & Bertness, 1992). For example, the large differences in tereidid abundance we observed between two adjacent coastal ocean circulation patterns. Abundance patterns may also be driven by competition with fouling organisms. For example, the large difference in abundance of *T. navalis* between Tjämnö and Kristineberg may be related to the dense coverage of the tunicate *Ciona intestinalis* on Tjämnö panels, whereas at Kristineberg the fouling community composition was less dense and more diverse. Previous studies show that filter-feeding fouling invertebrates can inhibit settlement of shipworms either by constituting a physical barrier or by consuming incoming larvae (reviewed by Nair & Saraswathy).

In conclusion, we found no indication that a range shift of shipworms has occurred along the Swedish coast in the last 35 years. Specimens of *T. navalis* were found at high densities in wooden test panels at 0.5–2 m water depth north of Barsebäckshamn and sporadically at more southerly sites (Klagshamn and Falsterbo). The distribution and abundance of *T. navalis* was positively correlated to sea surface salinity, but not to temperature, and 9 PSU appears to be the lower limit for Swedish *T. navalis* establishment in natural populations. Furthermore, recent hydrographical and climate envelope modelling show low probability of change of the overall

distribution of *T. navalis* in the Baltic Sea in the coming decade (Appelqvist *et al.*, unpublished). In a longer perspective, global (Stocker *et al.*, 2013) and local (Meier *et al.*, 2012; Gräve *et al.*, 2013) climate models project decreased salinity in coastal marine environments due to increased precipitation and freshwater run-off. Therefore, it seems more likely that Swedish *T. navalis* will contract, rather than expand, their geographic range in the future.

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