

Thesis for the degree of Doctor of Philosophy

Shipworm Ecology in Swedish Coastal Waters

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After all

ABSTRACT

Shipworms (Teredinidae) are marine bivalves adapted for boring into submerged wood, which they efficiently fragmentize and consume. They thereby perform a vital ecosystem service, yet simultaneously they cause extensive damage to important man-made marine structures. In Swedish waters, which this thesis focuses on, shipworms are not only a threat against marine cultural buildings, ships, bridges, and harbour structures (all made of wood), but also against the invaluable historical wrecks in the Baltic Sea. Thus, it is crucial to have knowledge about their recruitment in this region. Shipworms, as many other marine species, have changed its geographical distribution in numerous areas in concert with climate change. The first aim of my thesis was therefore to investigate the distribution and abundance of shipworms along the Swedish coast and to test the hypothesis that they had expanded their range into the Baltic Sea. Wooden test panels were submerged at 18 harbours along the coast, from Strömstad to Ystad, and around the Danish island of Bornholm. By comparing the results of this investigation to those from similar work in the 1970's, it was clear that there was no evidence for range expansion of shipworms in the surface waters in this part of the Baltic Sea the last 35 years. The second aim was then to determine the probability of spread of shipworms further into the Baltic Sea in the near-future. A simple, GIS-based, mechanistic climate envelope model was developed to predict the temporal and spatial distribution of environmental conditions that would permit reproduction and larval metamorphosis of the shipworm *Teredo navalis*. The model was parameterized with published tolerances for temperature, salinity and oxygen. In addition, a high-resolution three-dimensional hydrographic model was used to simulate the likelihood of spread of *T. navalis* larvae within the study area. The climate envelope modeling showed that projected near-future climate change is not likely to change the overall distribution of *T. navalis* in the region, but will prolong the breeding season. Dispersal simulations indicated that the majority of larvae were philopatric, but those that spread to at present uninfested areas typically spread to areas unfavourable for their survival. Consequently, there is a low probability of natural spread of *T. navalis* further into the Baltic Sea in the near-future. The predicted prolongation of the breeding season was shown in the third study, where a substantial phenological shift in the time of recruitment of *T. navalis* over the last 35 years was observed. The period of intensive recruitment during the study period (2004 – 2006) was on average one month longer than that observed in the 1970's. This extension was primarily at the end of the breeding season: intensive recruitment ended 26 days later in the 2000's than in the 1970's. These results correlated well with a highly significant increase of the sea surface temperature since the 1970's. Strong positive relationships were also found between a mean sea surface temperature of 16 °C (the reported temperature at which *T. navalis* release larvae) and the day of the year on which intensive larval recruitment began, and ended. The prolongation of the breeding season observed here increases the likelihood of successful recruitment of shipworms at the range margins, and thereby increases the risk of damage to man-made structures in the future. Finally, factors influencing substrate detection and settlement (chemical cues and small-scale turbulence and flow) of shipworm larvae were investigated. Field experiments showed, for the first time, that natural populations of shipworm larvae are attracted to wooden substrates by waterborne chemical cues. Subsequent laboratory experiments indicated, however, that small-scale hydrodynamic patterns are probably more important in determining settlement success. In the field, significantly greater numbers of competent larvae were found adjacent to plankton net bags contained wooden panels than to empty control nets. Laboratory flume experiments using ecologically relevant flow conditions showed, however, that active swimming by larvae would only influence settlement probability within a few body lengths of the substrate to reach it by altering behaviour (swimming). Thus it seems probable that chemical cues are only important for settlement when currents have advected larvae close to wooden substrata.

POPULÄRVETENSKAPLIG SAMMANFATTNING

Skeppsmaskar är, trots dess namn, musslor som är anpassade att borra i vattendränkt trä. Med sina tandade välvda skal finfördelar de effektivt trä som de transporterar till munnen för konsumtion. Inne i kroppen hyser skeppsmasken unika bakterier (symbionter) som har förmågan att omvandla cellulosa till glukos vilket ger energi åt värddjuret. Skeppsmasken kan på så vis överleva på endast trä som föda men kompletterar normalt sin diet genom att fånga plankton. Detta gör den genom ett par slangliknande organ, s.k. sifoner, som för övrigt är det enda som syns av skeppsmasken utanför en träbit. Om förhållandet i det omgivande vattnet blir ogynnsamt kan de dra in sifonerna och stänga sin gång med hjälp av två paddelliknande kalkstrukturer (paletter). Skeppsmaskar angriper trä under sitt sista frisimmande larvstadium, genomgår sedan en omvandling (metamorfoserar) och övergår till adultstadiet. De lever nu resten av sitt liv inne i sina borrhål vars väggar de klär med kalk. De sitter fast med bakdelen vid ingångshålet och tillväxer i framänden där skalen, foten och munnen är placerade. Allt efter som de tillväxer ökar gångarnas diameter men ingångshålen förblir relativt små (\varnothing 1-2 mm). En träbit kan vara näst intill uppäten inuti utan att det syns nämnvärt på dess yta. Skeppsmaskar kallas därför ibland ”havets termiter” och dess skador är svåra att upptäcka i tid. Det finns ca 66 arter av skeppsmask (Teredinidae) på jorden, varav två (*Teredo navalis* och *Psiloteredo megotara*) reproducerar sig i svenska vatten för närvarande.

Skeppsmaskar har en viktig ekologisk roll genom nedbrytning av trä som naturligt hamnar i havet, men utgör samtidigt stort hot mot mänskliga marina träkonstruktioner. Under senare år har man tyckt se en ökning i angrepp av skeppsmask på flera håll i Europa. Även längst svenska västkusten spred sig rykten i början på 2000-talet om fler och nya angrepp. Arbeten med kajer i Göteborgs hamn och utbyte av 400 träpålar under kallbadhuset Ribersborg i Malmö är ett par exempel, men även marinarkeologer var oroliga för skeppsmaskens framfart i Östersjön. Det fanns alltså behov av vetenskaplig forskning kring skeppsmaskens aktivitet och utbredning i dagsläget, samt att undersöka dess möjlighet att spridas till nya områden i framtiden i takt med potentiella klimatförändringar. För att kunna uttala sig om eventuella förändringar har skett i en arts utbredning krävs dock historiska data att jämföra med. För skeppsmaskars utbredning i svenska vatten fanns detta tillgängligt. Eva Normans omfattande studier under åren 1971 – 1973 har varit mycket användbara för jämförande studier i mitt avhandlingsarbete och liknande metoder har därför används.

Syftet med första arbetet i denna avhandling var att testa hypotesen om att skeppsmaskarten *Teredo navalis* hade ändrat sitt utbredningsområde längst svenska kusten sedan sjuttioalet. Undersökningen av skeppsmaskars utbredning och förekomst genomfördes 2006 – 2008. Varje år sattes träpaneler ut på 0,5 – 2 meters vattendjup i 18 hamnar längs svenska kusten samt runt danska ön Bornholm. Efter insamlandet skrapades marin påväxt bort vartefter panelerna röntgades. Tack vare att

de äkta skeppsmaskarna klär sina gångar med kalk går dessa, samt skal och paletter, att detektera på röntgenbilder och individer kan räknas. Genom jämförelse mellan mina resultat och Normans data från sjuttioalet, fann jag inga bevis på att *T. navalis* har spridit sig avsevärt längs svenska kusten under de senaste 35 åren. Den sydligaste platsen där träpaneler angreps av skeppsmask var i Falsterbo.

Inga angrepp hittades i paneler som hängt längs Skånes sydkust (Skåre, Gislövsläge, Ystad) eller i fem hamnar runt Bornholm. Vid dessa platser är salthalten sällan stadigvarande över 8 PSU (dvs ca 0,8%). När det gäller antal skeppsmaskar per dm² (abundans) hittade jag en anmärkningsvärd och statistiskt signifikant ökning i Arlid jämfört med data från sjuttioalet. Även på andra platser söderut i Öresund (Ålabodarna och Barsebäckshamn) var det mer angrep under senare år. Denna ökning kan bero på att säsongen då angreppen sker har förlängts sedan sjuttioalet. Detta stöds av de tydliga resultaten från min tredje studie. I denna undersökning sänkte jag ner 3 träpaneler per lina under olika tidsintervall i vattnet vid Kristineberg och Tjärnö. Detta upprepades under tre säsonger. För att fastställa när rekryteringen (nya angrepp) av skeppsmask började på året sänkte jag ner flertalet uppsättningar, med 3 paneler på varje lina, i början på juni. En av dessa linor tog jag sedan upp var 14de dag. För att avgöra slutet på säsongen sattes en ny lina ut var 14de dag vartefter alla togs in i november. Under åren 2004 – 2006 fann jag rekryter (2mm stora individer på röntgenbilderna) från mitten på juni till slutet av oktober, och den intensiva rekryteringsperioden sträckte sig från slutet av juli till slutet av september. Dagen för starten av den intensiva perioden skilde sig inte nämnvärt åt mellan årtionden men däremot avslutningen av säsongen. Under 2004 - 2006 avslutades den intensiva rekryteringsperioden i genomsnitt 26 dagar senare än under början på sjuttioalet. Eftersom man vet att temperaturen styr flera biologiska processer hos skeppsmask, t.ex. reproduktion och tillväxt, så kan den ökade temperaturen av ytvattnet vara en möjlig anledning till denna förlängning. Förskjutningar i tid av olika återkommande biologiska händelser såsom: ankomstdatum för flyttfåglar, äggläggning, lövsprickning, algblooming, förökning av musslor mm, är påvisat för många arter på både land och i havet. Dessa skiften visar starka samband med det uppvärmda klimatet under senare tid. I denna studie fann jag även starka samband mellan första dagarna på året då medeltemperaturen var $\leq 16^{\circ}\text{C}$ i ytvattnet och dagen för start av den intensiva rekryteringen, samt sista dagarna på året då medeltemperaturen var $\leq 16^{\circ}\text{C}$ i ytvattnet och dagen för avslutning av den intensiva rekryteringen. Detta samband får stöd av andra experimentella studier där det har visat sig att 16°C verkar vara en avgörande temperatur för frisläppandet av larver hos *T. navalis*.

De här undersökningarna var jämförande studier bakåt i tiden, men vad kommer att hända i framtiden? För att försöka förutspå var, när och hur olika biologiska händelser kommer att inträffa i ett framtida klimat har olika datamodeller tagits fram. En modell för att förutspå framtida utbredning av en viss art kan vara baserad på dess nuvarande utbredning och vilka miljöförhållanden som råder inom detta område. Andra modeller kan även inkludera fysiologiska toleranser för olika miljöfaktorer som är framtagna genom laboratorieexperiment. För att avgöra sannolikheten att skeppsmasken *T. navalis* ska sprida sig till nya områden i

Östersjön i en snar framtid byggdes en enkel klimatmodell upp. Modellen baserades på artens toleransnivåer för temperatur, salthalt och syrekoncentration, då det råder gynnsamma förhållanden för reproduktion hos adulterna samt rekrytering av larver. Med hjälp av GIS-kartor kunde vi visualisera i vilka områden och när på året det fastställda gynnsamma förhållandet inträffade bakåt i tiden (1980 - 2008) och när det kommer att ske i framtiden (2009 - 2020). Denna modell kompletterades med en spridningsmodellering av *T. navalis* larver i västra delen av Östersjön. Tillsammans visade de här modellerna att sannolikheten för skeppsmask att sprida sig till nya områden där det idag inte är rapporterat några angrepp är låg. Däremot förutspår den första modellen att säsongen, för när reproduktion och rekrytering av skeppsmask kan ske, troligtvis kommer att förlängas senare in på hösten, vilket är något som redan observerats i min tredje studie (se i texten ovan).

Skeppsmaskar måste borra sig in i trämaterial för att överleva. Det är därför troligt att de kan känna av kemiska signaler som läcker ut från trä i vatten för att identifiera sitt specifika habitat. I min sista studie testade jag detta i fältexperiment. För att utesluta fysisk stimuli av trädets ytstruktur, men ändå tillåta läckage av kemiska molekyler, klädde jag in träpaneler i en nylonduk med en maskstorlek mindre än en skeppsmasklarv. Åtta stycken inklädda träpaneler och lika många tomma nätpåsar (kontroller) hängde ute i havet en vecka. Därefter hävdades det runt varje uppsättning och antal skeppsmasklarver räknades. Försöket repeterades en vecka senare. Även de naturligt förekommande strömhastigheterna uppmättes på platsen. Resultaten var påfallande. Det var nio gånger fler skeppsmasklarver runt de inklädda träbitarna jämfört med de tomma kontrollerna. Larvernans förmåga att aktivt simma mot sitt habitat är däremot förmodligen mycket begränsat. I ett strömakvarium efterliknades flödesförhållanden runt träbitarna i fältexperimentet. Här visade resultaten att flödes hastigheter som en skeppsmasklarv förmodligen kan klara av att simma i bara inträffar väldigt nära träbiten eller i lä om den. Att betydligt fler skeppsmasklarver ändå hittades nära de inklädda träbitar, jämfört med kontrollerna, kan bero på att de har en förmåga att upptäcka en eller flera attraktiva kemiska signaler när de är väldigt nära sitt habitat, samt har förmåga hålla sig kvar vid det, men att de förs dit av en slump.

De viktigaste resultaten i korthet:

- Det finns inga bevis på att skeppsmasken *Teredo navalis* har spridit sig avsevärt längs svenska kusten under de senaste 35 åren.
- Modellering visar att det är låg risk för spridning av skeppsmask till nya områden i Östersjön i en nära framtid.
- Säsongen när den intensiva rekryteringen (angrepp) av skeppsmask sker har förlängts på sensommaren med nästan en månad sedan sjuttioålet.
- Modell förutspår ytterligare förlängning av säsongen för reproduktion och rekrytering av skeppsmask senare på hösten i framtiden.
- Skeppsmasklarver attraheras av kemiska signaler som läcker ut från trä i vatten.

LIST OF PAPERS

This thesis is a summary of the following papers, which will be referred to in the text by the roman numbers below:

Paper I:

Appelqvist, C., Havenhand, J., Toth, G.B. (2014)

Distribution and abundance of teredinids along the Swedish coast - are shipworms invading the Baltic Sea? *Journal of the Marine Biological Association of the UK* *

Paper II:

Appelqvist, C., Al-Hamdani Z.K., Jonsson P.R., Havenhand, J.N. (*In Press*)

Climate envelope modeling and dispersal simulations show little risk of range extension of the shipworm, *Teredo navalis* (L.), in the Baltic Sea. *PLoS One*.

Paper III:

Appelqvist, C., Havenhand, J. (*manuscript*)

A phenological shift in the time of recruitment of the shipworm, *Teredo navalis* L., mirrors marine climate change.

Paper IV:

Toth, G.B., Appelqvist, C., Larsson, A.I., Jonsson, P.R., (*submitted manuscript*)

Natural populations of shipworm larvae are attracted to wood by waterborne chemical cues.

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RELATED WORK NOT INCLUDED IN THE THESIS

My time as a PhD student was extended 10.5 months to participate in the EU project *WreckProtect*, which was founded through the European Community's seventh Framework programme (FP7/2007–2013, Environment), grant agreement no. 226225.

Within this project the following literature has been published:

Paper

Björdal CG, Gregory D, Manders M, Al-Hamdani Z, Appelqvist C, Haverhand J, Dencker J (2012) Strategies for Protection of Wooden Underwater Cultural Heritage in the Baltic Sea Against Marine Borers. The EU Project "WreckProtect". *Conservation and management of archaeological sites*, 14, 201- 214.

Report I

Al-Hamdani ZK, Appelqvist C, Björdal CG, Gregory D, Manders M (2011a) Guidelines for predicting of decay by shipworms in the Baltic Sea.

Report II

Al-Hamdani ZK, Appelqvist C, Björdal CG, Gregory D, Manders M (2011b) Guidelines for protection of submerged wooden cultural heritage, including cost-benefit analysis.

Monograph

Björdal CG, Gregory D, Manders M, Al-Hamdani ZK, Appelqvist C, Dencker J (2011) *WreckProtect - Decay and protection of archaeological wooden shipwrecks.*, Oxford, UK, Archaeopress LTD, ISBN 978-1-905739-48-6.

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1. INTRODUCTION

1.1 Shipworms – wood-boring bivalves

Shipworms are, despite the name, bivalves that efficiently fragmentize and consume submerged wood. In this way they have an ecologically important roll in the turnover of organic material in the sea, yet they simultaneously cause extensive damage to economically and culturally important marine structures (Turner, 1966). The largest morphological difference between shipworms and other bivalves are the reduced shells that function primarily as a drilling tool rather than for protection. In the family Teredinidae the nearly hemispherical shells cover only the anterior part of the animal (Fig. 1), and a characteristic thin calcareous layer are deposited on the walls of the burrows to protect the rest of the worm-like body.

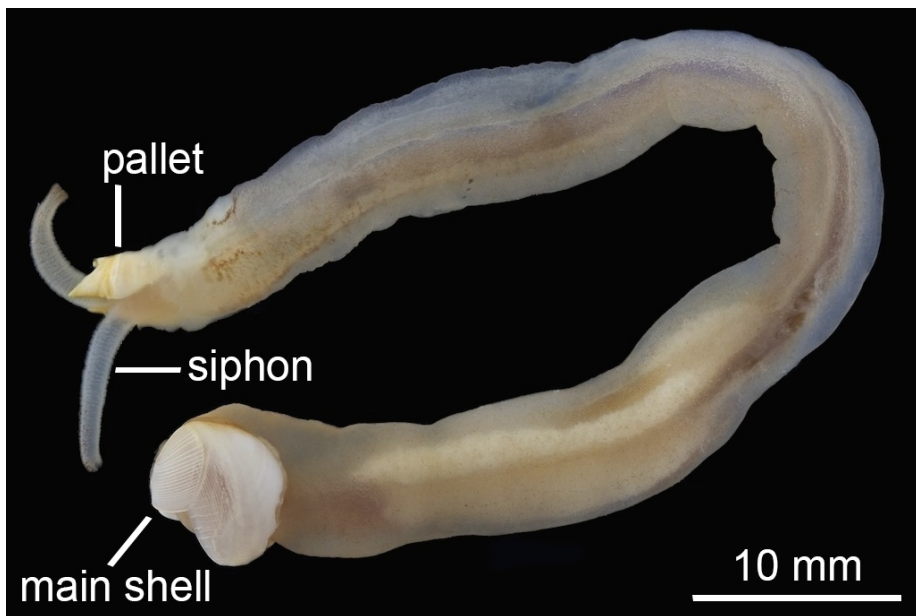


Fig. 1. Adult *Teredo navalis*. Photo credit: F. Pleijel

Of about 66 described teredinid species (Turner, 1966) only *Teredo navalis* (Linnaeus, 1758) and *Psiloteredo megotara* (Hanley, 1848) reproduce and settle onto wood in Swedish waters at present (Norman, 1976, this thesis). *Teredo navalis* is a protandric hermaphrodite with internal fertilization and a relatively short generation time (Calloway & Turner, 1988; Coe, 1933). They may become sexually mature 40 - 45 days after metamorphosis (Grave, 1942; Imai *et al.*, 1950). The offspring are brooded until larvae reach the straight-hinge veliger stage (75 x 80 μm) (Fig. 2A), after which they are released to the plankton and

develop for a further 2-3 weeks into settling mature pediveliger larvae (200-240 μm) (Fig. 2B) (Culliney, 1975). In contrast to *T. navalis*, *P. megotara* have external fertilization and a free-swimming period of about 4 weeks (Nair, 1962). After larval settlement and metamorphosis (Fig. 2C) the adult bore into wood (Fig. 2D) through repeated rasping movements by the fine serrated shells (Fig. 1). Subsequently small wood particles are transported by ciliated movement to the mouth, become ingested, and carbohydrates are assimilated with help from endosymbiotic bacteria (*Teredinibacter turnerae*) (Distel *et al.*, 2011). These unique symbionts both produce cellulolytic enzymes and are able to fix nitrogen, the latter may supplement the shipworms nitrogen deficient diet (Waterbury, 1983; Lechene *et al.*, 2011). At the posterior end of the animal a pair of retractable siphons, and two associated calcified structures (pallets) are situated (Fig. 1). By sealing their burrow with the pallets the shipworms avoid unfavourable environmental conditions and can survive upon stored glycogen (Lane *et al.*, 1952). The tube-like siphons are used for filtration of plankton and obtaining oxygen, as well as for extruding waste products and gametes/larvae into the water.

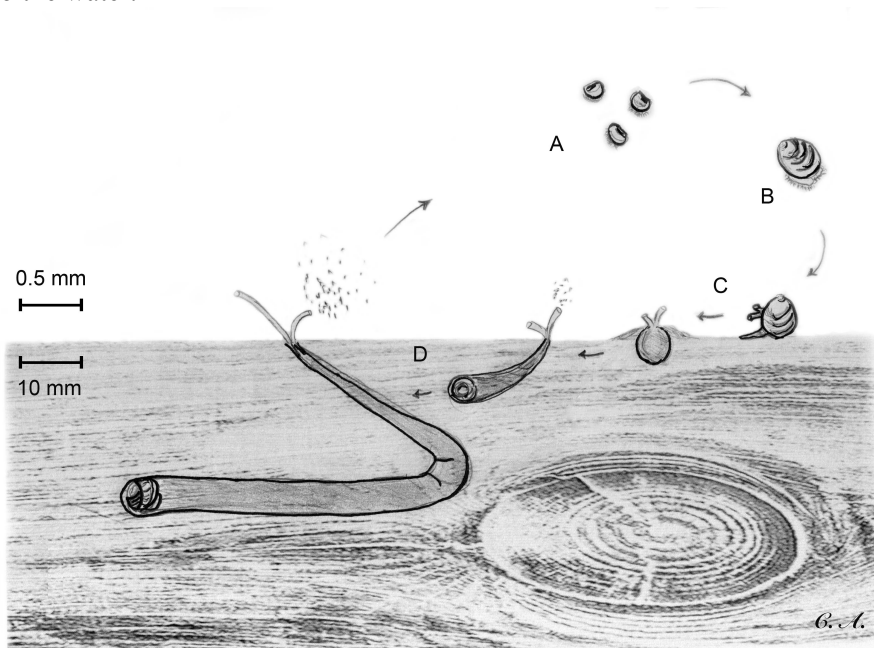


Fig. 2. Life cycle of the shipworm *Teredo navalis*. (A) straight-hinge veliger larvae, (B) pediveliger larvae, (C) settlement and metamorphosis, (D) adult wood-boring stages. Scale bars are approximates; 0.5 mm for the pelagic larval stages, and 10 mm for the wood-boring adult stages. Illustration C. Appelqvist

The physical key parameters affecting the physiological and ecological behaviours of shipworms are salinity, temperature, dissolved oxygen, ocean

currents and the availability of wooden substrate (Nair & Saraswathy, 1971). *Teredo navalis* show wide tolerance of temperature and salinity, which determine the species range and abundance, and may explain its global distribution (Turner, 1966; Borges *et al.*, 2014). It is also the species causing most economic damage and is therefore relatively well-studied (reviewed in Nair & Saraswathy, 1971; Borges *et al.*, 2014). Selection of earlier shipworm ecology research in Scandinavian waters comprises work by: Pettersson (1921), Runnström (1925), Roch (1932), Kramp (1937), Dons (1940), Thorson (1946), Nair (1962), Norman (1976, 1977), Kristensen (1969, 1979), Santhakumaran and Sneli, (1984), of which Normans investigations have been most important for the comparative studies in this thesis.

1.2 Biogeography

Questions about why species live where they live have fascinated researchers for a long time. As early as the mid 18th century Carl Linnaeus suggested that animals were structured after their physical surroundings. A range, the geographical area in which a species can be found, is determined by complex interactions among environmental and biological factors, such as physiological tolerances, predation and dispersal (Cox & Moore, 2009). In the marine environment salinity and temperature are overriding important abiotic determinants of species distributions, especially in estuarine and coastal ecosystems (Kinne, 1963; Bonsdorff, 2006; Ojaveer *et al.*, 2010). However, since life histories of most marine species include pelagic stages, additional crucial factors that affects distribution is the dispersal by ocean currents (Shanks, 1995), and the transfer of species due to human activities (Minchin *et al.*, 2009). Detailed knowledge of species' range in relation to their environment is essential for understanding many aspects of their ecology, as well as for effective conservation, management, and assessment of possible impacts of climate change.

1.3 Climate change

The Earth's climate has changed many times throughout its history. In this thesis, I use "climate change" to refer primarily to the rising temperature in the ocean. The global average warming trend in the upper 75 m of the oceans has been 0.11°C per decade from 1971 to 2010, and the recent 30-years (1983-2012) has been the warmest period during the last 1400 years (IPCC, 2013). Melting glaciers and polar ice-caps, rising sea levels, changing ocean circulation, stronger coastal winds, more precipitation and increased fresh water run-off at higher latitudes are all examples of recently changed abiotic events caused by a warmer climate (IPCC, 2013). This rapid warming has fundamentally altered the

environmental conditions of marine ecosystems (Poloczanska *et al.*, 2013). Considerable geographical heterogeneity exists in recent rates of warming and the greatest temperature shifts have been observed in the northern hemisphere, particularly in semi-enclosed seas in Northern Europe (Belkin, 2009). For example, summer sea surface temperature (SST) in the Baltic Sea and North Sea has increased 3 times faster than the global rate since 1985 (Mackenzie & Schiedek, 2009), and is predicted to continue rising during the 21st century (Meier *et al.*, 2012).

There is also evidence for increased heterogeneity in salinities of the oceans (IPCC, 2013). Since the 1950's regions of high salinity have typically become more saline while regions of low salinity have become less saline. However, no large salinity change has been observed in the brackish transit zone to the Baltic Sea during the 20th century (Madsen & Højerslev, 2009), but it is predicted to decrease in the future (Meier *et al.*, 2012).

1.4 Biological responses to climate warming

Climate warming challenges populations of species to respond in different ways. They may adapt to the new conditions, migrate to track temperature changes in space and time, or fail to do either of these and go extinct. By far, the most commonly observed biological responses to climate warming have involved shifts in species' distribution ranges (Parmesan, 2006; Philippart *et al.*, 2011), and alterations of phenological traits (McCarty, 2001; Morgan *et al.*, 2013).

Observed range shifts of marine species have generally followed the direction of changing isotherms and expanded polewards in temperate regions, although other patterns have also been seen (Sorte *et al.*, 2010). The greatest impact of climate warming is probably at the polar zones where contraction of species' ranges and declining abundances has been documented (Atkinsson *et al.*, 2004; Rode *et al.*, 2014). Effects of shifting ranges may cause changes in biodiversity, disturbance of existing ecosystem structure and function, and in the worst (rare) cases global or local extinction of species.

Perhaps, the simplest way to track responses to climate warming is to study changes in species phenologies – the timing of recurrent biological events with respect to the environment (Lieth, 1974). The effect of increased temperature on phenology has mostly been studied in terrestrial ecosystems. Several temperate taxa, such as birds (Charmantier & Gienapp, 2013), amphibians (Klaus & Loughheed, 2013) and insects (Diamond *et al.*, 2011) have changed their reproductive and migration behaviors, and numerous species of plants have changed or extended their growing season (e.g. Khanduri *et al.*, 2008). Much less is known about phenological responses of marine species to rapid warming

of the oceans (Sydeman & Bograd, 2009). Nonetheless, changes in the timing of seasonal events have been observed for plankton (Mackas *et al.*, 2007; Richardson & Poloczanska, 2008), benthic organisms such as molluscs and crustacean (Philippart *et al.*, 2003; Moore *et al.*, 2011; Richards, 2012; Morgan *et al.*, 2013), and fish (Perry *et al.*, 2005). Because temperature is an important factor controlling species' breeding seasons, a warmer climate could change the phenology of reproduction and disrupt the synchrony between trophic levels, resulting in predator–prey mismatches (Beaugrand *et al.*, 2003; Richardson, 2007; Gremillet *et al.*, 2008; Mieszkowska *et al.*, 2009).

Different life-history stages of marine organisms are differentially susceptible to environmental changes. Juveniles are often more vulnerable to stress than adults and certain planktonic larval stages are particularly sensitive to thermal effects (O'Connor *et al.*, 2007). In temperate species, elevated temperature may accelerate larval development and shorten their duration time, and thereby shorten the larval dispersal distance (O'Connor *et al.*, 2007). Thus, the number and diversity of adult species in a certain area can change in responses to climate warming.

1.5 Ecological modelling

Species distributions shift naturally due to changes of their environments or as an effect of human activities. In order to predict future ranges various species distribution models (SDM) have been developed (Elith & Leathwick, 2009). These models have become useful tools for addressing questions in biogeography, ecology, evolution, conservation biology, and climate change (Guisan *et al.*, 2013). A common approach is to correlate the current geographical distribution (usually presented as presence-absence data) of a species with corresponding climate variables in order to infer the species' environmental requirements and create an overall “climate envelope” (Guisan & Zimmermann, 2000). A drawback of many of these climate envelope models is that they aim to identify the current realized niche (Hutchinson, 1957) rather than the potential niche that a species may inhabit with in a future climate (Kearney & Porter, 2009; Robinson *et al.*, 2011; Dormann, 2012). In contrast, mechanistic models use knowledge of a species' physiological tolerances to model the future potential niche. These mechanistic models have the benefit of being independent of non-climate factors that can influence the present distribution (Kearney & Porter, 2009), but may still ignore environmentally-driven plasticity. Regardless of the type of model, SDM's seldom include factors that affect dispersal (Araujo & Peterson, 2012), and yet such factors are crucial for the majority of marine organisms whose larvae disperse through ocean currents (Gaylord & Gaines, 2000).

2. AIMS AND APPROACHES

There is increasing concern that climate change will lead to shifts in the geographic ranges of ecologically and economically important species. Recently, changing distribution patterns of shipworms have been reported in coastal European waters (Sordyl *et al.*, 1998; Tuentje *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 structures (Port of Gothenburg, pers. com.; Schlyter, 2009), and during the summer of 2002 shipworms were observed for the first time at 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; Eriksson & Ronnby, 2012). Thus it became clear that an updated scientific survey of the current distribution of shipworms, and an assessment of the potential for their spread, was required.

The **first aim** of my thesis was therefore to investigate the distribution and abundance of shipworms along the Swedish coast and to test the hypothesis that they had expanded their range. In order to determine possible range shifts historical data are needed. Fortunately, this was available for shipworms in Swedish water from the 1970's (Norman, 1977). In order to maximise comparative power I used similar methods to those of Norman (1977) in the follow-up study. Wooden panels were submerged in harbours from Strömstad to Ystad and around Bornholm (Denmark) in multiple years and shipworm abundance was subsequently determined by X-radiography. The possibility that shifts in the range or abundance of shipworms were correlated with temporal changes in environmental variables, was tested using historical and present-day sea surface temperature and sea surface salinity data.

The **second aim** was to assess the risk of spread of shipworms further into the Baltic Sea in the near future. This aim was achieved through successful collaboration within the EU-funded project WreckProtect (Björdal *et al.*, 2012). Hindcast and forecast climate data were used to build a simple mechanistic GIS-based climate envelope model based on physiological tolerances of the shipworm *Teredo navalis*. This model, together with a biophysical dispersal simulation model, was used to determine the likelihood of spread of *T. navalis* into the Baltic Sea during the period 2009 – 2020.

Climate change not only affects species' distribution patterns but may also alter phenology – the timing of recurring biological events in relation to the environment. Generally, biological impacts of warming are seen in advancement

of spring phenologies (e.g. earlier onset of seasonal reproduction; Poloczanska et al., 2013), but delayed completion of reproductive seasons have also been reported in marine ecosystems (Richards, 2012). In Swedish waters, *T. navalis* occurs close to its northern range-margin, where the sea surface temperature has increased significantly the last decades (Philippart *et al.*, 2011, and refs. therein). As temperature is known to be a key driver of reproductive cycles (Nair & Saraswathy, 1971), this raises the possibility that the species may have changed its breeding season. Consequently, the **third aim** was to investigate the phenology of recruitment of *T. navalis* in western Sweden, and to assess whether any changes were related to warming in the region. Again using the same methodology as a study of Norman (1976) allowed for temporal comparisons of shipworm recruitment. The onset and end of the shipworm recruitment season was determined and analysed by X-radiography of wooden panels, which had been submerged in near surface waters at different times.

Shipworm larvae are very effective in localizing and settle onto wood, but how do these tiny larvae detect this ephemeral habitat in the vast ocean? The **fourth**, and last, **aim** of this thesis was to examine the potential for remote detection of suitable settling substrate in shipworms. First, I investigated whether natural populations of shipworm larvae were able to sense chemical cues released from wooden structures. This was done by comparing the numbers of larvae collected around submerged wooden panels enclosed in plankton net bags in the field with numbers of larvae collected around net bags only (no wood). Secondly, instantaneous flow velocities and the dispersion of chemical cues around wooden panels were measured in flume experiments using ecologically relevant hydrodynamic conditions. Together with estimations of the swimming speed of shipworm larvae in culture, these data were used to calculate theoretical distances from which shipworm larvae should be able to respond to cues released from submerged wooden substrates in the field.

3. METHODS

3.1 The coast of Sweden

The Skagerrak - Baltic Sea region is a transitional area between the North Sea and Baltic Sea with complex hydrography and strong salinity gradients (Gustafsson & Stigebrandt, 1996). The oceanographic system is barotropically driven mainly by differences in sea levels and wind patterns (Stigebrandt & Gustafsson, 2002). Large inflow of water with high salinity into the Baltic Sea through the Danish Straits and the Sound is limited by topography and occurs only occasionally (Schinke & Matthaus, 1998). The dominant sea surface current is westerly 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 (approx. $-4 - 27\text{ C}^\circ$), and sea surface salinity in the area range 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 (SMHI, 2014).

Hydrological data for sea surface temperature and salinity included in this thesis were obtained from the Swedish Meteorological and Hydrological Institute (SMHI, 2014) (**paper I**) and from logbooks/databases available at the marine biological stations Kristineberg and Tjärnö (GU, 2014) (**paper I, III**). The sites used for the studies of spatial (**paper I**) and temporal (**paper III**) variation in shipworm recruitment are shown in figure 3.

3.2 Sampling shipworms

A common and easy procedure to collect shipworms in the field is by submerging wooden test panels (Cragg *et al.*, 2009; Paalvast & van der Velde, 2011; MacIntoch *et al.*, 2014). In the comparative studies (**Paper I, III**) similar methods to the surveys of Norman (1976, 1977) were used. Untreated pine (*Pinus sylvestris*) panels (20 x 75 x 200 mm) were submerged in near surface waters under different time periods (for details see **Paper I and III**). A hole ($\varnothing 25\text{ mm}$) was drilled at the centre of each panel through which cable ties attached the panels to polypropylene ropes. Ropes with 2 - 3 wooden panels and a weight were suspended from floating jetties at the different study sites. At the time of collection macroscopic fouling on the surface of the panels was removed and the panels were brought back to the laboratory and stored at -20°C for later analysis.

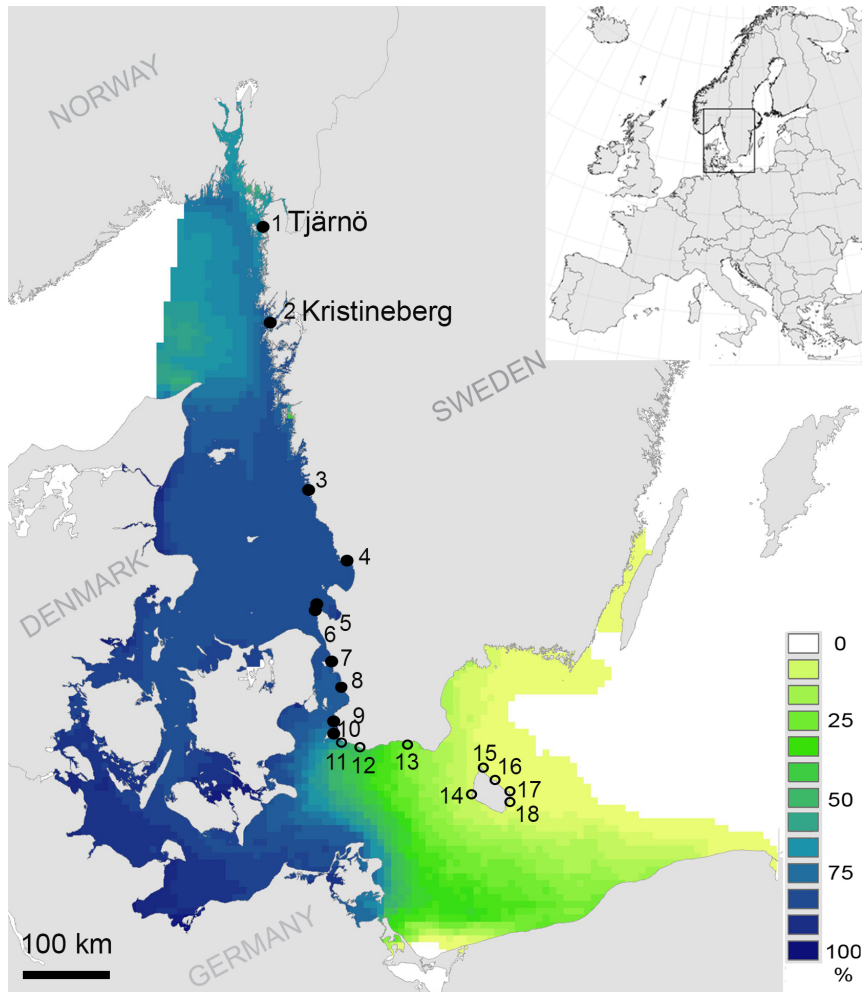


Fig. 3. Map of the sampling sites for shipworm recruitment. (1) Tjärnö, (2) Kristineberg, (3) Träslövsläge, (4) Grötvik, (5) Arild, (6) Mölle, (7) Ålabodarna, (8) Barsebäckshamn, (9) Klagshamn, (10) Falsterbo, (11) Skåre, (12) Gislövsläge, (13) Ystad, (14) Rønne, (15) Sandvig, (16) Gudhjem, (17) Svaneke, (18) Neksø. Filled circles represents sites of recruitment, empty circles represents sites of no recruitment (**paper I**). The colour gradient shows frequency of occurrence of favourable condition for *Teredo navalis* adult reproduction and larval metamorphosis (**paper II**).

3.3 Detection of recruitment

Visual detection of shipworm recruitment is extremely problematic as the entrance hole at the wooden surface is just a millimetre or so large and does not reveal the extent of underlying burrows. A convenient technique for this purpose

is the use of X-radiography (Norman, 1976). Two different kinds of equipment have been used for the analyses in this thesis: a portable Andrex BV 155 machine and a Siemens Elema Mobilett II. Exposure values used on these two machines were 30 kV/3 mA and 40kV/14 mA respectively. A Kodak X-omat 1000 Processor developing machine was used for development of the X-ray negatives (AGFA developer G1381 and fix G 3341). X-ray negatives were digitalized photographically (Canon EOS 350D) with the aid of a light table. Shipworm recruitment intensity was defined as the number of visible individual (or pairs of) shells ≥ 2 mm on the whole X-ray photo, per unit area (overall panel area = 0.015 m²; **paper I, III**) (Fig. 4).

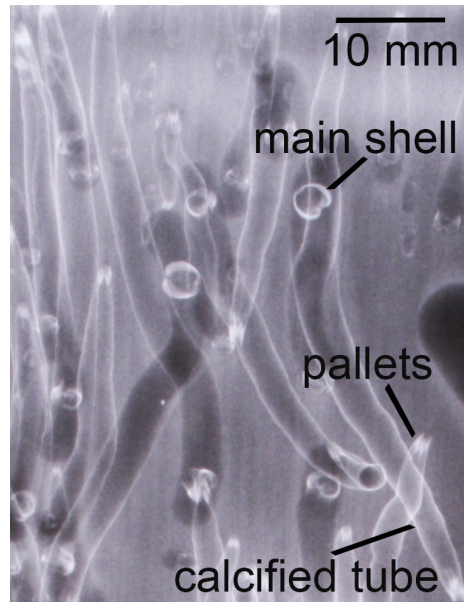


Fig. 4. X-ray photo of recruits of the shipworm *Teredo navalis*.

3.4 Time of recruitment

In order to determine the breeding season for shipworms in Swedish waters, wooden panels were submerged in two locations (Kristineberg and Tjärnö, Fig. 3), at three depths (0.5, 1.5, and 2.5 m) over three successive years; 2004, 2005 and 2006. The beginning of the recruitment season was assessed by submerging multiple sets of panels early in the summer, one set of which was retrieved every 14-days thereafter. The end of the breeding period was determined by submerging equivalent sets of panels every 14 days, and leaving these panels in the water until collection in November. About 200 panels were processed and analysed as outlined above. However, historical data from the 1970's (Norman, 1976) were only available from Kristineberg and therefore data from this site only were compared to historical records, and correlated to changes in sea surface temperature (**paper III**).

The beginning and end of the recruitment period was defined in two ways. First, I estimated the onset (and end) of intense recruitment using statistical fits of logistic growth models to cumulative recruitment data. Relevant parameters of best-fit models were obtained using the package *grofit* within the R statistical environment (Kahm *et al.*, 2010, R Development Core Team 2011). These parameters are equivalent to the “arrival intensity” measures of Denny *et al.*

(2014). These same models were also used to estimate the rates of increase, and decline, in recruitment at the beginning and end of the recruitment periods. Secondly, I recorded the first (and last) day on which new recruits were observed in panels. The day of first observation is equivalent to “first arrival date”, (FAD; Tryjanowski & Sparks, 2001). The corresponding last observation was therefore termed last arrival date “LAD”.

3.5 Assessing the likelihood of spread

Two different approaches were used to model the likelihood of shipworms spreading further into the Baltic Sea:

i) A simple GIS-based climate envelope model was built on results from a regional climate model (MIKE 3) obtained from the Danish Hydrological Institute (Uhrenholdt, 2010). The climate envelope model was parameterised with data on temperature, salinity, and oxygen saturation tolerances for the shipworm *Teredo navalis* obtained from the literature (see **paper II** for details). The model output covered two temporal periods: a "hindcast" period (1980-2008) and a "predicted" period (2009-2020), for each of two water layers: a "Surface layer" comprising the upper 9 m of the water column, and a "Bottom layer" comprising the lowest 2m of the water column. The climate envelope for the "Surface layer" was created by classifying each grid in each time-step as either "favourable" or "unfavourable" for adult reproduction and larval metamorphosis according to the environmental tolerances of these processes. An equivalent model for reproduction (only) of adults was constructed for the "Bottom layer". Maps of the temporal and spatial frequency of occurrence of the favourable conditions were produced in GIS ModelBuilder (ESRI ArcMap[®]).

ii) Dispersal of *T. navalis* larvae was simulated using a biophysical model based on velocity fields from the regional ocean circulation model BaltiX (Hordoir *et al.*, 2013), using a particle-tracking routine to generate dispersal trajectories for the period May - October (**paper II**). Dispersal from selected grid cells to waters in the Baltic Sea, Danish Straits and Kattegat was simulated by releasing particles between 0-12 m depth. Particle trajectories lasted for 30 days, and all particles that dispersed to waters deeper than 100m were excluded from the model. Dispersal probability from 4 release areas to all cells of the model was then calculated (see **paper II**). Two of these areas, Klagshamn and Hiddensee, were chosen because they are (respectively) the most southerly site of shipworm infestation in Sweden (**paper I**), and the most easterly site of infestation in Germany (Sordyl *et al.*, 1998). In addition we included two release areas further east into the Baltic Sea as reference areas, one on the Swedish coast (Sydsåne) and one on the German coast (Rügen). Finally, the sources of particles that recruited to the selected areas – i.e. the putative spawning sites of simulated

larvae that metamorphosed within the target areas – were identified using analogous methods.

3.6 Attraction to chemical cues from submerged wood

The majority of teredinid shipworm species are obligate wood-feeders (Distel *et al.*, 2011). Therefore, it is easy to hypothesise that shipworm larvae are attracted to their specific habitat by wood-associated waterborne chemical cues. To test this hypothesis, shipworm larvae were prevented from direct contact with, and to settle onto, wooden test panels by a physical barrier in form of plankton net. Eight wooden panels placed in bags made of plankton net (50 µm mesh dimension) and 8 control net bags (of similar shape but without wooden panels) were attached to weighted lines. The lines were suspended 3 m apart along a floating jetty outside the laboratory at Tjärnö. After 8 and 16 days vertical tows were made randomly around each net bag using a plankton-net (90 µm mesh dimension). The collected plankton were fixed in ethanol (96%) and analyzed under a stereo-microscope (magnification $\leq 50\times$) in the laboratory. Shipworm pediveliger larvae in the samples were identified through their characteristic oval shape (i.e. greater height than length, Fig. 2), yellowish colour, and lack of "eyespot", which distinguish them from other bivalve larvae (Chanley & Andrews, 1971; Hendriks *et al.*, 2005).

3.7 Hydrodynamics around wooden panels

Apart from functioning as dispersal vector of shipworm propagules (gametes, larvae), hydrodynamic turbulence and advection affects the spread of waterborne chemicals that act as settlement cues to competent larvae. To better understand the scope for shipworm larvae to detect potentially attractive chemical cues leaching from waterlogged wood, as well as the likelihood that larvae can encounter wooden panels in the dynamic marine environment, a series of hydrodynamic studies were performed (**paper IV**).

Initially, natural hydrodynamic conditions were measured in the field close to the jetty where plankton samples were taken (**paper IV**) using an Acoustic Doppler Current Profiler (ADCP, Nortek AS). The ADCP transmits acoustic pulses, which are scattered by small particles in the water, and the receiver collects the echoes. Flow velocities measured at a cell size of 0.3 m at 1.0 m beneath the surface (the depth of the experimental bags) were extracted and used to guide the velocities selected for subsequent flume experiments. Flow patterns around wooden panels, and transport of chemical substances released from these panels, were studied in a laboratory flume (Jonsson *et al.*, 2006). The recirculating flume, 7 m long and 0.5 m wide, was filled with seawater (33.5 PSU, 18° C), which was circulated at different speeds. Hydrodynamic behaviour

around a wooden panel was observed with the aid of Particle Image Velocimetry. Velocity patterns in three different ecologically relevant speeds (1, 3 and 5 cm sec⁻¹) were recorded and analysed. Diffusion patterns of a chemical cue were subsequently investigated using Laser Induced Fluorescence at the same velocities as above. The leaching, diffusion, and advection of small water-soluble chemical compounds away from the surface of wood panels was simulated using the pink dye Rhodamine.

4. MAIN RESULTS AND DISCUSSION

4.1 The geographical distribution – present and future

Recruitment of shipworms in the near surface water occurs all along the Swedish west coast, although abundances generally decrease southwards (**paper I**) (Fig. 3) No strong evidence was found to support the hypothesis of range expansion of shipworms in this area during the last 35 years - although single specimens of *Teredo navalis* were observed in Barsebäckshamn and Falsterbo; sites where this species either was not found or not investigated in the 1970s (Norman, 1977). These later differences were probably caused by small seasonal changes rather than any systematic range expansion of *T. navalis*. The similar distribution patterns observed between decades were in accordance with unchanged salinity levels in the Sound (Madsen & Højerslev, 2009). No shipworms were found along the southern Swedish coast 2006 – 2008 or around the Danish island of Bornholm 2006 - 2012, but the absolute distribution of shipworms may have been underestimated by the present study. For example, shipworms 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 (RAA, 2014) suggests low (or no) presence of shipworms in this area. The results from this empirical field survey were in accordance with results from climate envelope modeling (CEM) (**paper II**). Although the CEM was parameterized using tolerance levels obtained from literature, the correspondence between model results (**paper II**) and observed distributions (**paper I**) suggest that these tolerances were realistic for Swedish populations of *T. navalis*: the spatial distribution of “favourable conditions” for reproduction of adults and metamorphosis of larvae occurred in high frequency at locations where shipworms actually recruit (Fig. 3; **paper I, II**). The modelled spatial area was primarily determined by the distribution of waters with salinity ≥ 8 PSU. The climate data used in this model (Uhrenholdt, 2010) projected no substantive change in salinity in this region within the modelled period and consequently; no substantial range shift of *T. navalis* is predicted in the near future (**paper II**). This prediction is supported by the results of dispersal simulations, which showed low probability of spread of *T. navalis* larvae to areas not already infested at present (**paper II**). In a longer perspective, Meier *et al.* (2012) suggest that salinity in the Baltic Sea will decrease due to increased precipitation and freshwater run-off during this century. Therefore, it seems more likely that Swedish *T. navalis* will contract, rather than expand, its geographic range in the near-future.

4.2 Time of recruitment and abundance

No significant difference was found in timing of recruitment between the two study sites (Kristineberg, Tjärnö), neither with regard to the onset ($P = 0.70$) nor the end ($P = 0.38$) of the intensive recruitment season. The data from Kristineberg 2004 - 2006 were compared with similar data from 1971 - 1973 (Norman, 1976) and related to changes in sea surface temperature (SST). Two different methods were used to define the recruitment period (see **paper III** for details), however results described and discussed here are primarily from statistical estimates of onset and end of the intensive recruitment phase. Intensive recruitment began in end of July and was completed by the end of September (Fig. 5). The recruitment period in recent years was ~30 days longer than that observed in the 1970's (Fig. 5).

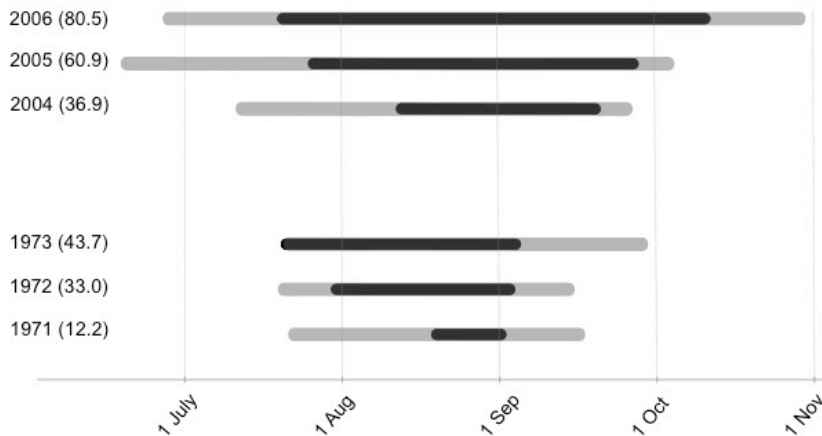


Fig. 5. Recruitment season of *Teredo navalis*. Black bars show duration of intensive recruitment based on statistical analysis, and grey bars show the total period of observed recruitment. Numbers within brackets are total days of intensive recruitment period. Data from the 1970's are modified after Norman (1976).

In contrast to many other phenological studies of terrestrial and marine species (Poloczanska *et al.*, 2013; McCarty, 2014), there was no significant change in the timing of onset of intense shipworm recruitment at the Swedish west coast, despite increased SST over this 35-year period (**paper III**). These results suggest that the phenology of gonad maturation and spawning of the majority of individuals within the populations which supply the Swedish west coast with shipworm larvae, have not changed substantively over this period. Single individuals were observed to recruit 3 weeks earlier in the 2000's than in the 1970's, although the significance of this result is difficult to assess. In contrast to

the onset of intensive recruitment, the end of intensive recruitment was ~26 days later in recent years. During this period mean late summer (Aug - Oct) SST increased by 2.2 °C. This finding that shipworms are now recruiting later into the autumn is consistent with the climate envelope modeling (**paper II**). The CEM showed clearly that the prevalence of conditions favourable for reproduction and larval metamorphosis extended over time (Fig. 6). These changes were driven by increased SST, which is projected to continue rising in the near future (to the year 2020). Although salinity is likely to constrain the geographical range of shipworms (see above), this projected increase in temperatures will likely prolong the breeding season further and thereby increase the risk of greater establishment of *T. navalis* at the margins of its present range.

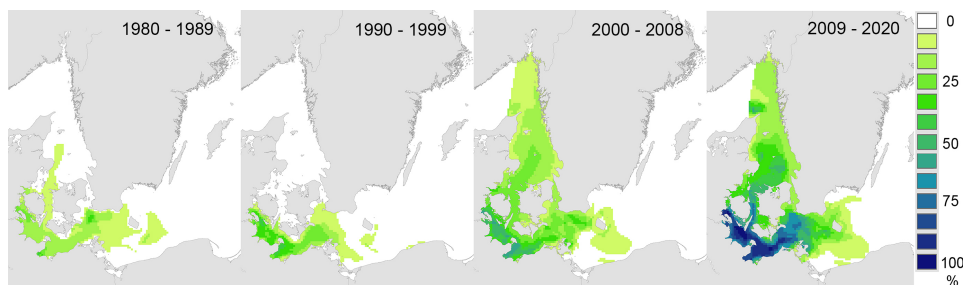


Fig. 6. Decadal patterns of occurrence of environmental conditions favourable for *Teredo navalis* adult reproduction and larval metamorphosis in the Surface layer in October.

The abundance of shipworm recruits at different sites along the Swedish coast was similar during the 1970's and 2000's, and correlated positively with sea surface salinity (**paper I**). The only site at which a statistically significant increase of *T. navalis* abundances over the 35-year period was Arild, even though higher abundances also were observed for example at Ålabodarna and Barsebäckshamn in recent years (Fig. 3). An increase of shipworm abundances in the Sound region might be a result of climate warming, as temperature is a determining factor controlling growth, reproduction and larval survival of *T. navalis* (Nair & Saraswathy, 1971; Hoagland, 1986). Increased abundance and the extension of recruitment later into autumn may have been caused by prolonged reproductive period of established adults, and/or by rapid maturation and reproduction of shipworms that recruited earlier that same summer. The latter possibility is supported by the observations of Imai *et al.* (1950) that newly settled *T. navalis* could become sexually mature within 45 days. In the 1970's, the duration of intense larval recruitment was ~ 30 days – barely sufficient for the earliest settlers to grow to maturity and then reproduce. In 2004 - 2006, however, this period was twice as long (~ 60 d), providing more than enough time for early recruits to reproduce, and for their larvae to recruit successfully. More rapid juvenile growth and maturation under the warmer summers of recent years may have amplified this effect.

Further interesting results of correlation analysis between SST and time of recruitment were found (**paper III**). The onset of intensive recruitment was significantly correlated with the date on which mean sea surface temperature (SST) first rose above 16°C, and the end of intensive recruitment was similarly significantly correlated with the last day on which mean SST was above 16°C. Tests of these correlations were based on the observation that adult *T. navalis* release larvae at temperatures above 16 °C (Loosanoff & Davis, 1963). The time between estimated day of onset of intense recruitment and the date on which mean SST rose above 16°C was about 5 weeks, a period long enough for newly released larvae to mature, settle and become visible on x-ray photos (Imai *et al.*, 1950; Culliney, 1975).

4.3 Attraction to chemical cues from submerged wood

Analysis of the number of teredinid larvae collected in the field around plankton bags with and without wooden panels revealed highly significant difference between treatments (**paper IV**). The natural presences of larvae were nine times higher around wooden filled bags compared to the controls. These results clearly show that shipworm larvae are attracted to their habitat by waterborne chemical cues. However, the ability for teredinid larvae to sense attractive cues and to encounter its habitat is probably only likely at very short distances to wood. In turbulent flow the concentration field of the cue was complex and offered limited directional information (**paper IV**). Is it then possible for tiny shipworm larvae to remain and encounter the source of the cue? Our second laboratory flume experiments, using ecological relevant current velocities, showed that only within the thin boundary layer or in wakes behind protruding structures may larvae be able to control their movement towards the substrate. Therefore, the capacity of shipworm larvae to encounter their habitat by active swimming behavior seems unlikely, and the higher abundance of larvae around the enclosed wooden panels may be a response to a waterborne chemical cue during or after settlement or very near the substrate.

4.4 Observations of other wood-boring species

Most of the results in this thesis concern the teredinid shipworm *T. navalis*. However, the species *Psiloteredo megotara* was also found in test panels. Individuals of *P. megotara* were larger than *T. navalis* of comparable age, but occurred in such low densities that further analysis was not possible. No other shipworms, wood-boring crustaceans, or traces thereof, were found on the panels.

5. CONCLUSIONS AND FURTHER PERSPECTIVES

- Two shipworm species: *Teredo navalis* (L.) and *Psiloteredo megotara* (H.) recruit in the near surface coastal waters of western Sweden.
- A substantial phenological shift in the time of recruitment of shipworms has occurred in concert with climate warming since the early seventies.
- No significant range expansion of *T. navalis* has taken place along the Swedish coast the last 35 years.
- The most southerly shipworm recruitment was found at Falsterbo (55.41° N, 12.93° E).
- No shipworm recruitment was found at sites with sea surface salinity frequently lower than 8 PSU (Skåre, Gislövsläge, Ystad, and around Bornholm).
- A climate envelope modeling and dispersal simulation suggests there is a low risk of spread of shipworms further into the Baltic Sea in the near future.
- Shipworm abundance has increased markedly at Arild, but also at Ålabodarna and Barsebäckshamn since the 1970's.
- Summer sea surface temperatures in western Sweden have increased significantly the last 35 years.
- Over the last 35 years the end of the intensive recruitment period has been delayed by ~26 days into the autumn.
- Intense recruitment of shipworms occurs in July – September, but first and last recruits settle in early June and late October respectively.
- The timing of recruitment correlated significantly and strongly with mean sea surface temperature ≥ 16 °C.
- A climate envelope model predict extended breeding season for *T. navalis* in the near future (2020).
- Salinity and ocean currents seem to determine the geographical distribution of shipworms in Swedish waters, whereas temperature controls the time of recruitment – other factors may also be involved.
- Shipworm pediveliger larvae are attracted to wood by waterborne chemical cues.
- The likelihood that shipworm larvae will encounter wooden substrata by active swimming is very low: encounter rates with suitable settlement substrata is probably mainly determined by advection.

No range expansion was shown for shipworms in the near surface waters along the Swedish coast over the recent ~35 years (1971-2008). Nor was any recruitment found in wooden test panels around the Danish island of Bornholm 2006 – 2012. These results, together with results of climate envelope modeling (that predicted no shift in the spatial distribution of the favourable conditions for reproduction and settlement of *Teredo navalis*), and results of dispersal modeling (that showed low probability of spread to uninfested areas), indicate that the risk for range extension of shipworms in Swedish coastal waters in the near future is low. However, continuous monitoring is recommended since intensive shipworm recruitment often occurs periodically (Nair & Saraswathy, 1971), and it is possible that the investigated periods (1971 – 1973 and 2006 – 2008) were years of low spatial and temporal recruitment.

Another reason to be particularly aware of shipworm recruitment, especially in the Sound, is the recent supply of several hundreds of fresh untreated oak piles in the water at Malmö (Schlyter, 2009). This region has few wooden structures (pers. obs.) into which shipworms could recruit, and therefore the addition of these piles might facilitate establishment of a stronger sub-population of *T. navalis* in a region of natural low abundance. If the shipworm population size increase in this area, the risk of recruitment in the future may be higher: dispersal simulations showed that a high proportion of the larvae released at Klagshamn, close to Malmö, recruit locally. Therefore, regular inspection of these piles and other maritime wooden structures in the region is recommended.

Although, the climate envelope model predicted low probability for spread of shipworms in the near future, there may be motive to be vigilant. The observation of increased recruitment of shipworms along the coast of Mecklenburg-Western Pomerania in Germany in 1993 coincide with a major inflow of saline water into the Baltic Sea (Sordyl *et al.*, 1998; Matthaus & Schinke, 1999). The Major Baltic Inflow (MBI) in 1993 was strongest (~300 km³) MBI for over 40 years, and since the 1970's the MBI occasions have been rare (Matthaus & Schinke, 1999). However, in December 2014 approximately 198 km³ of saline water were added to the Baltic Sea over a period of ~14 days (IDW, 2015). Consequently, it would be highly interesting to investigate whether this MBI will affect the distribution and abundance of *T. navalis* at the margin of its range the coming years.

Prolongation of the breeding season – as observed, and predicted, in this thesis – also gives reason to pay attention to shipworms in the future. An extension of the intensive recruitment period by approximately one month might explain the recent increased abundance of shipworms in The Sound and the extensive attacks by shipworms onto wooden structures in the harbour of Gothenburg, (two examples of regions where shipworm growth and abundance are not density limited; paper I, pers. obs.). More offspring recruited successfully in the

mid 2000's compared to the early 1970's (paper III), which was correlated with increased sea surface temperature (SST). This may be due not only to extended reproductive periods, but also to higher winter survival and greater yearly growth rates of adult shipworms, both of which are reported to be highly temperature dependent (reviewed in Eckelbarger & Reish, 1972). Additional possible explanation for increased abundances at some locations could be that *T. navalis* larvae, and adults, are less susceptible to low salinities in warmer temperatures. To test that hypothesis, and to obtain better data for possible future modeling of the effects of projected lower salinities in the Baltic, laboratory experiments of shipworm tolerance are needed.

Most observed range shifts of marine species have occurred northward in the northern hemisphere, following shifting isotherms (Poloczanska *et al.*, 2013). Since the known northern margin in the eastern Atlantic of the shipworm *T. navalis* is close to the northern study site in this thesis (Borges *et al.*, 2014, (the references therein; Nair, 1962 and Santhakumaran & Sneli, 1984 concerns another species)) it would be interesting to investigate the possibility of a range shift northward along the Norwegian coast.

The evidence presented in this thesis that shipworm larvae react to waterborne chemical cues is compelling. This information is of value not only for advancing fundamental knowledge in shipworm research but also for the development of new specific preventatives against infestation. A next step should be to identify the behavioural mechanisms by which larvae locate and settle onto wood and to characterize the attractive waterborne chemical molecules involved. This could be done using bioassay guided fractionation of extracts from wood leachate to study the response of shipworm larvae. The (currently unknown) stimulatory compounds could then be further analysed and separated using chromatographic and spectrometric methods (e.g. HPLC, GC-MS). Future research on shipworms should therefore focus on the early life-history stages, where knowledge is lacking and the potential for valuable results and applicable outcomes is high.

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