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REVIEW

Digenean trematode species in the cockle *Cerastoderma edule*: identification key and distribution along the north-eastern Atlantic shoreline

XAVIER DE MONTAUDOUIN[1], DAVID W. THIELTGES[2], MÉRIAME GAM[3], MANUELA KRAKAU[4], SUZANA PINA[5], HOCEIN BAZAIRI[3], LAURENT DABOUINEAU[6], FERNANDA RUSSELL-PINTO[5] AND K. THOMAS JENSEN[7]

[1]Université de Bordeaux, UMR EPOC 5805, Station Marine d'Arcachon, 2 rue du Pr Jolyet, F-33120 Arcachon, France, [2]Department of Zoology, University of Otago, PO Box 56, Dunedin 9054, New Zealand, [3]Université Hassan II Aïn Chock, Faculté des Sciences Aïn Chock, Départment de Biologie, Km 8 Route El Jadida, BP 5366 Maârif, 20100 Casablanca Morocco, [4]Foundation Alfred Wegener Institute for Polar and Marine Research, Wadden Sea Station Sylt, Hafenstraße 43, 25992 List/Sylt, Germany, [5]Laboratory of Aquatic Zoology, Department of Aquatic Production, ICBAS, Abel Salazar Institute for Biomedical Sciences Lg. Prof. Abel Salazar 2, 4009-003 Porto, Portugal, [6]Campus de la Tour d'Auvergne BP 90431, Université UCO Bretagne Nord, 22 204 Guingamp, France, [7]Department of Marine Ecology, Institute of Biological Sciences, University of Aarhus, Finlandsgade 14, DK-8200 Aarhus, Denmark

We describe the digenean fauna of one of the dominant intertidal hosts, the common cockle Cerastoderma edule, *in terms of biomass, off north-eastern Atlantic shores. Using published and unpublished literature we have prepared an identification key and provide an up-date of the large-scale distributional patterns of digenean species of the common cockle. At least sixteen digenean species, belonging to seven families, use cockles as intermediate host. Among these species two utilize cockles as first intermediate host only, whereas two species utilize cockles as both first and second intermediate host. The remaining eleven species have cockles as their second intermediate host. Water birds and fish are the definitive hosts to twelve and four species, respectively.*

Cockles are infected with digeneans along the latitudinal gradient from southern Morocco to the western region of the Barents Sea often with high infection levels. Whereas some of these digenean species occur along most of the latitudinal gradient others show a more restricted northern or southern distribution mostly caused by an underlying latitudinal gradient of host species.

Knowledge of digenean species and their large-scale distribution pattern may serve as a baseline for future studies dealing with the effects of climate change on parasite–host systems. For such studies the cockle and its digenean community could be an ideal model system.

Keywords: parasitism, latitudinal patterns, *Cerastoderma edule*, identification key

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INTRODUCTION

Although parasite diversity is supposed to be high (Windsor, 1998; Poulin & Morand, 2000), our knowledge of parasite diversity and latitudinal patterns is limited (Littlewood, 2005). In intertidal ecosystems, digeneans are the dominant parasite group (Mouritsen & Poulin, 2002). They play a double function being part of the living diversity, but at the same time they can also play the role as diversity indicators because their presence is linked to the occurrence of free-living fauna (their hosts) (Mouritsen & Poulin, 2002; Hechinger & Lafferty, 2005; Hudson *et al.*, 2006; Hechinger *et al.*, 2007). Knowledge of parasite diversity is thus not only

Corresponding author:
X. De Montaudouin
Email: x.de-montaudouin@epoc.u-bordeaux1.fr

valuable in itself in assessing a neglected part of biodiversity but it might also serve as a valuable and convenient proxy for ecosystem health (Hudson *et al.*, 2006). As many digeneans have been shown to affect host individuals, populations and communities (Mouritsen & Poulin, 2002) knowledge of parasite distributional patterns in host populations can contribute to an understanding of their role in shaping population dynamics in their free-living hosts. Parasite–host interactions may be influenced by climate change because parasite transmission and parasite effects on their host closely depend on temperature (Evans, 1985; Sousa & Gleason, 1989; Jensen *et al.*, 1996; Lo & Lee, 1996; Mouritsen & Jensen, 1997; Ferrell *et al.*, 2001; Mouritsen, 2002; Thieltges & Rick, 2006). Hence, climate change could disrupt equilibrium in parasite–host relationships and beget serious mortalities (Hayes *et al.*, 2001; Kutz *et al.*, 2005; Mouritsen *et al.*, 2005; Hakalahti *et al.*, 2006; Poulin, 2006; Poulin & Mouritsen, 2006). In addition, the introduction or range expansion of parasite species in the course of warming seas might increase the parasite burden for intertidal hosts. To evaluate future changes, inventories of parasite diversity over the distributional range of a particular host (parasite fauna) will be necessary to serve as a baseline. Today, no such inventories exist for hosts from intertidal systems.

The edible cockle *Cerastoderma edule* from the north-eastern Atlantic shoreline, probably harbours one of the most diverse digenean faunas of bivalve hosts in intertidal systems (Lauckner, 1983; de Montaudouin *et al.*, 2000; Thieltges *et al.*, 2006). Cockles are first or second intermediate hosts to at least 16 parasite species. These digeneans display complex life cycles involving 2–3 host species. The cockle parasites are using either water birds or fish as definitive hosts (for a general description of life cycles of digeneans see Smyth, 1994). By using reported characteristics and morphometric recordings we present an identification key to the digeneans found in cockles along its latitudinal distributional area. Their overall biogeographical distribution is described and we discuss possible causative factors for the observed patterns.

MATERIALS AND METHODS

We searched the literature for information on digeneans using the common cockle *Cerastoderma edule* as host (Table 1). From the papers on species descriptions we prepared a simple identification key. In addition, photographs of each parasite species as seen through a dissection microscope are provided as a tool for species identification. Approximately fifty publications provided data about the presence of parasite species in cockles and most of them did also report prevalence and/or abundance data for the parasites. Prevalence is the percentage of parasitized cockles and abundance is the number of parasites per cockle (Bush *et al.*, 1997). For each paper, we selected the maximum mean prevalence for species using the cockle as first intermediate host and the maximum mean abundance for species using the cockle as second intermediate host. Comparison between sites must take into account that data were obtained in many different sampling strategies (sample surface, number of replicates and sieve mesh size) and at different times of the year that were not always mentioned. The resulting database includes 45 sites ranging from Dakhla (Morocco, 23°N) to Bodø (Norway, 67°N) (Figure 1).

RESULTS

Identification key

In total, sixteen digenean species have been described from cockles along its north-eastern Atlantic distributional range and one new hitherto undescribed species has been observed in Dahkla (Morocco). The identification key below is based on the appearance of larval digeneans in cockles as seen through a dissection microscope. To facilitate identification of the digeneans, photographs of the individual species are presented (Figure 2). Most of the digeneans in cockles have tissue-specific (=microhabitat) infection sites (Figure 3) and hence location *in situ* can be of additional help in identification. For each species there is a reference to its distributional area.

Distributional maps of the individual digenean species are presented in Figure 4.

KEY TO LARVAL DIGENEANS IN *CERASTODERMA EDULE*

- – Isolated, spherical or oval-shaped individuals (= metacercariae), sometimes included in a cyst. Usually gathered in one or two specific tissue(s). 1
- – Proliferating individuals (×1000), entangled in most tissues when mature. Different forms can be present: small bags (sporocysts or rediae), more or less motile individuals (cercariae) and metacercariae 10

1 – No cyst, oval shaped 2
– Cyst, rather spherical. 4

2 – Occurring along the margin of the mantle or below the hinge, rather dark through transmitted light (well developed system). Body length 120–300 μm. 3
– Between adductor muscle and shell, whitish through transmitted light (small excretory system). Body length: 208–482 μm. . . . . *Gymnophallus gibberosus* (Figure 2A)

3 – Enclosed in the mantle epithelium below the shell umbo, between the shell and the flesh, body length 240–350 μm . . . . *Meiogymnophallus minutus* (Figure 2B)
– Free in the extra-pallial space, or under the hinge ligament, but also in the tissues of the mantle margins. Body length: 250–330 μm . . . . *Meiogymnophallus fossarum* (Figure 2C)

4 – Diameter < 160 μm 5
– Diameter >160 μm. 6

5 – Dark excretory vesicles across the whole cyst. Sometimes in the foot (proximal part) but more typically in the thin grey part of the mantle (in compound microscope: with 33 oral spines). Diameter 140–160 μm . . . . *Curtuteria arguinae* (Figure 2D)
– Dark excretory vesicle concentrated and looking as dark spot in a light cyst. Diameter: 140 μm . . . . *Diphterostomum brusinae* (Figure 2E)
– Light excretory vesicles across the whole cyst. Cysts often in the mantle margin opposite of the siphons (anterior end) (microscope: 29 oral spines). Diameter: 80–140 μm . . . . *Himasthla interrupta* (Figure 2F)

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Table 1. List of digenean species utilizing the cockle *Cerastoderma edule* as their first and/or second intermediate host, other hosts of the life cycle, and references to papers describing their anatomy.

	Trematode species	Synonyms	Family	1. Intermediate host	2. Intermediate host	Final host	References
Cockles 1. intermediate host	*Bucephalus minimus*	*Labratrema minimus* *Bucephalus haimeanus*	Bucephalidae	*Cerastoderma edule*	*Pomatoschistus* spp. *Mugil cephalus*	(F) *Dicentrarchus labrax*	1–3
	Monorchis parvus	*Cercaria cerastodermae* 1	Monorchiidae	*C. edule*	*C. edule*	(F) *Diplodus* spp.	3–8
	Gymnophallus choledochus	*Cercaria dichotoma*	Gymnophallidae	*C. edule*	*C. edule* or polychaetes	(B) water birds	3, 6, 9, 10
	Undescribed sp.		?	*C. edule*	?	?	
Cockles 2. intermediate host	*Asymphylodora demeli*			*Hydrobia ulvae*	*C. edule*	(F) gobiid fish	6, 11–13
	Curtuteria arguinae		Echinostomatidae	Unknown	*C. edule*	(B) water birds ?	3, 14, 15
	Diphterostum brusinae		Zoogonidae	*Nassarius reticulatus*	*C. edule*	(F) *Blennius, Symphodus, Oblata, Sargus*	3, 16, 17
	Gymnophallus gibberosus		Gymnophallidae	*Macoma balthica*	*C. edule*	(B) water birds	3, 16, 17
	Himasthla continua		Echinostomatidae	*Hydrobia* spp.	*C. edule*	(B) water birds	6, 9
	Himasthla elongata	*Himasthla secunda, Echinostomum secundum*	Echinostomatidae	*Littorina littorea*	*C. edule*	(B) water birds	3, 6, 9, 14, 18
	Himasthla interrupta		Echinostomatidae	*Hydrobia* spp.	*C. edule*	(B) water birds	3, 6, 9, 14
	Himasthla quissetensis		Echinostomatidae	*Nassarius reticulatus* *Cyclope neritea*	*C. edule*	(B) water birds (larids)	3, 7, 14, 19
	Meiogymnophallus fossarum		Gymnophallidae	*Scrobicularia plana*	*C. edule/ C. glaucum/Paphia aurea*	(B) *Haemotopus ostralegus*	20–24
	Meiogymnophallus minutus	*Distomum minutum* *Gymnophallus oedemia* *Cercaria margarita* *Cercaria cambrensis*	Gymnophallidae	*Scrobicularia plana*	*C. edule/ C. glaucum*	(B) *Haemotopus ostralegus*	6, 9, 20–26
	Psilostomum brevicolle		Psilostomatidae	*Hydrobia* spp.	*C. edule*	(B) water birds (larids)	6, 9, 27
	Renicola roscovita		Renicolidae	*Littorina littorea*	*C. edule*	(B) water birds (larids)	6, 9, 18

(F), fish host; (B), waterbird host.

1: Maillard, 1976; 2: Pina *et al.*, in press; 3: Russell-Pinto *et al.*, 2006; 4: Bartoli *et al.*, 2000; 5: Jonsson & André, 1992; 6: Lauckner, 1983; 7: Russell-Pinto, 1993; 8: Sannia *et al.*, 1978; 9: Lauckner, 1971; 10: Loos-Frank, 1969; 11: Markowski, 1936; 12: Reimer, 1970; 13: Reimer, 1973; 14: Desclaux, 2003; 15: Desclaux *et al.*, 2006; 16: Pina, unpublished; 17: Prévot, 1966; 18: Werding, 1969; 19: Stunkard, 1938; 20: Bowers *et al.*, 1990; 21: Bowers *et al.*, 1996; 22: Russell-Pinto & Bartoli, 1992; 23: Russell-Pinto & Bowers, 1998; 24: Russell-Pinto, 1993; 25: Bowers & James, 1967; 26: Loos-Frank, 1971; 27: Loos-Frank, 1968.

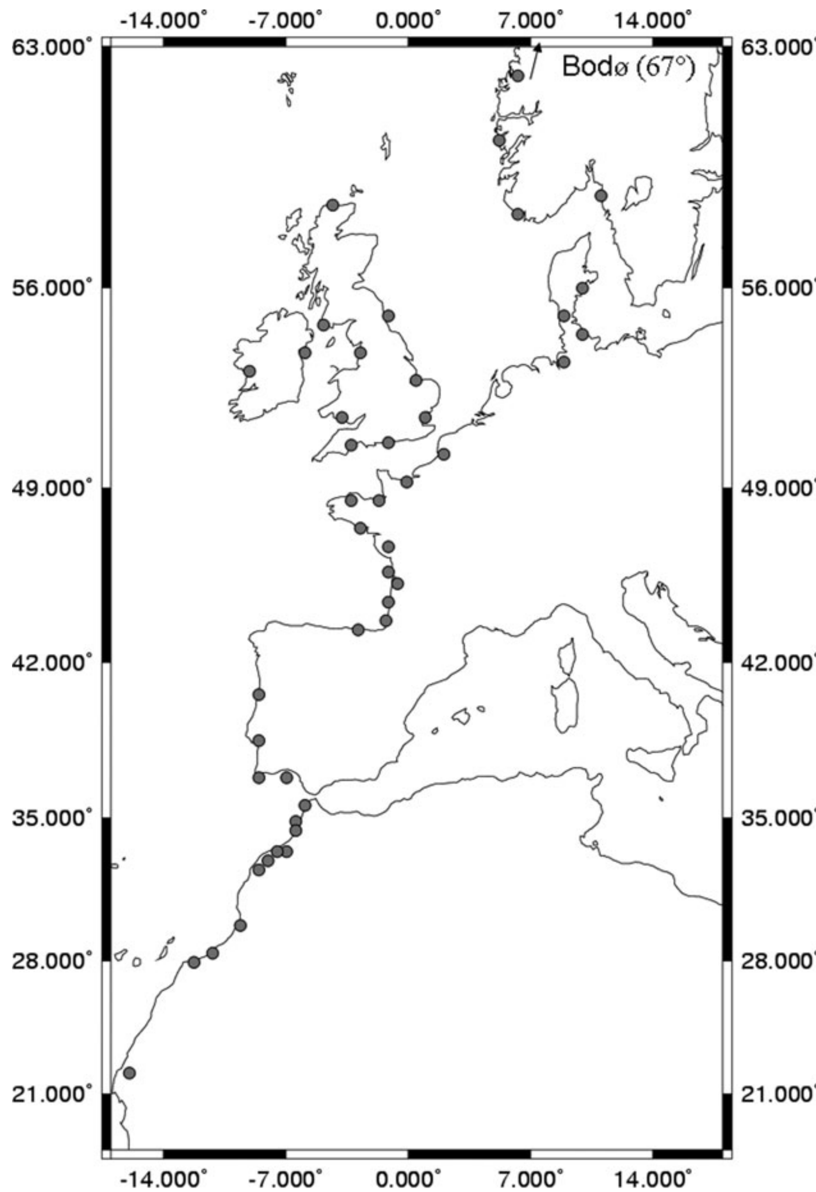

Fig. 1. Locations from where we found data on parasites in cockles *Cerastoderma edule*.

6 – Thick cyst wall (6–8 μm). Mostly in the palps. Diameter = 160–180 μm . . . . *Renicola roscovita* (Figure 2G)
– No thick cyst wall 7
7 – The whole surface of the cyst is blackish-greyish with a net-like structure of the excretory system. Often associated with the digestive gland. Diameter 200–250 μm . . . . *Psilostomum brevicolle* (Figure 2H)
– Not these characters 8
8 – Diameter > 210 μm. Mainly located in the foot, but sometimes a few in the mantle (microscope: 29 oral spines). Diameter: 210–270 μm . . . . *Himasthla elongata* (Figure 2I)
– Diameter > 290 μm. Located in digestive gland, gills, mantle. Diameter: 300–330 μm . . . . *Asymphylodora demeli* (Lauckner, 1983, p. 692)
– Diameter < 210 μm. Usually located in the foot but sometimes in the mantle. Two species that are impossible to distinguish from each other with a binocular microscope 9
9 – Diameter: 150–210 μm (microscope: 29 oral spines) . . . . *Himasthla continua* (Figure 2J)
– Diameter: 150–210 μm (microscope: 31 oral spines) . . . . . *Himasthla quissetensis* (Figure 2K)
10 – Metacercariae within or near sporocysts and cercariae 11
– Cercariae within or near sporocysts. 12
11 – Conspicuous excretory vesicle. No cyst. Ovoid (350 x 850 μm) . . . . . *Gymnophallus choledochus* (Figure 2L)
– No conspicuous excretory vesicle. Cyst. Ovoid (183 x 298 μm) . . . . *Monorchis parvus* (Figure 2M)
12 – Cercariae are ovoid with a little tail (66–81 μm). Body length: 91–120 μm . . . . *Monorchis parvus* (Figure 2 N)
– Cercariae with a conspicuous tail 13
13 – Bifurcate tail 14

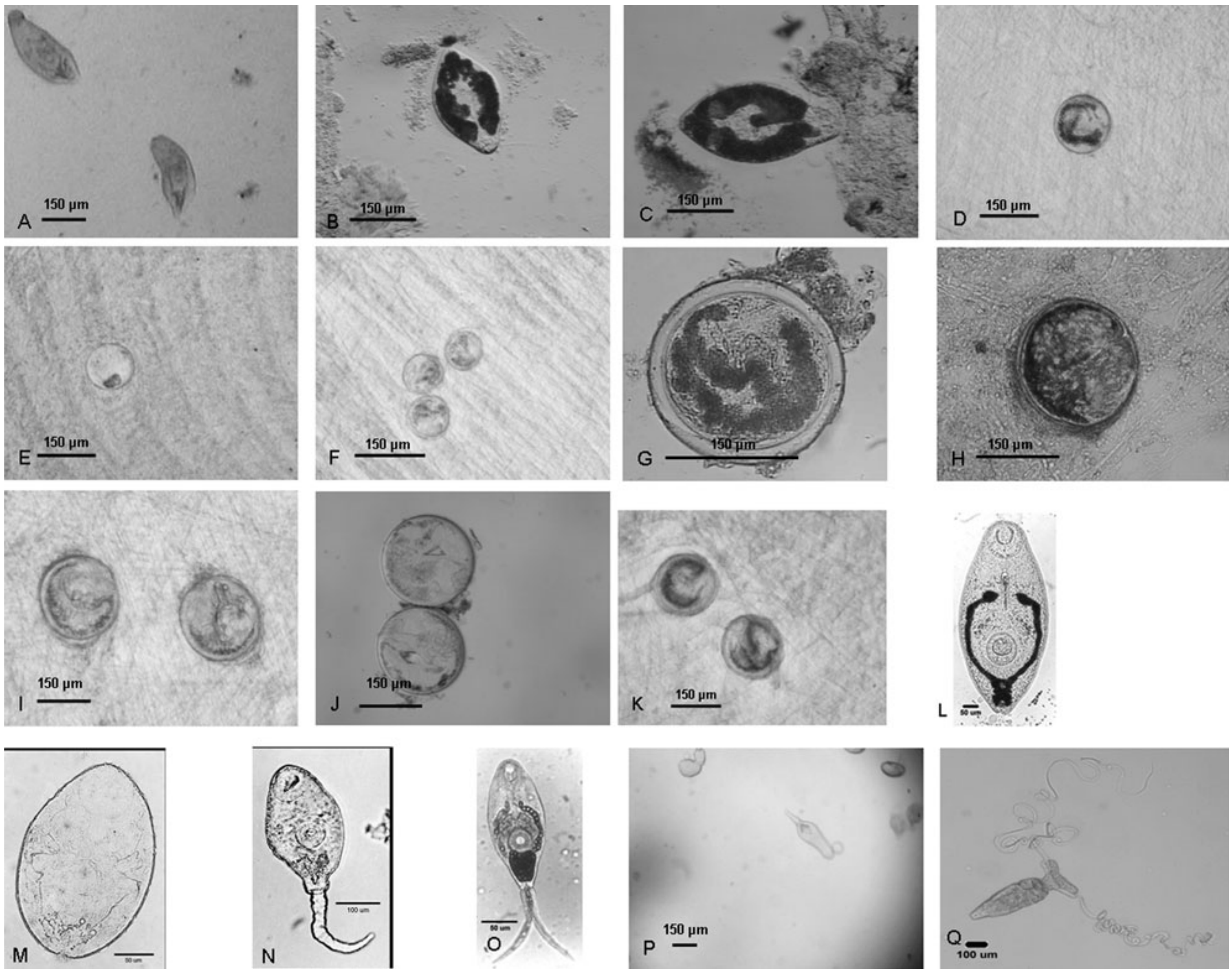

Fig. 2. Photographs of digenean larvae as they can be observed through a dissection microscope with transmitted light, within cockle tissues squeezed between two glass slides.

– Tail not bifurcate. Body length: 300–350 µm .... Unknown cercariae (Figure 2P)

14 – Tail with a muscular and glandular central stem ended by two long and thin arms. Body length: 300–350 µm .... *Bucephalus minimus* (Figure 2Q)

– Rather thick tail, bifurcate from the second half of the tail. Body length: 208–282 µm .... *Gymnophallus choledochus* (Figure 2O)

Host and microhabitat use

Sixteen digeneans, belonging to seven families, have been registered in the edible cockle *Cerastoderma edule* from the area spanning from southern Morocco to Norway (Table 1). The Echinostomatidae is represented by most species (5). Two of the parasite species utilize the cockle as first intermediate host only (including an undescribed species found in Dakhla 2007, Morocco), eleven as second intermediate host only, and two species as first and second intermediate host (Table 1). The parasites exhibit an aggregated distribution inside the cockle by showing microhabitat specific occurrences (Figure 3). Parasite species utilizing the cockle as first intermediate host usually infect the gonads but as they multiply they proliferate to other microhabitats, especially gills, digestive gland and foot. For parasite species utilizing the cockle as second intermediate hosts, most of them are tissue-specific, but some of the Echinostomatid species may infect both the mantle and the foot. As indicated in Figure 3 the different types of microhabitats are targeted by a varying number of species, the connective tissue in the foot being attractive to 5 species.

Prevalence and abundance

Cockles were infected with parasites at all sites from where data were available (Figure 1). In addition, infection levels observed at the different sites were often high, reaching more than 15% in parasites utilizing cockles as first intermediate hosts (Figure 4A–D). All parasite species using cockles as second intermediate host often have prevalence close to 100% and differ by their metacercariae abundance per host individual (Figure 4E–O). Some parasite species have generally low abundance, i.e. less than 100 metacercariae per cockle, such as *Diphterostomum brusinae, Himasthla continua, Gymnophallus gibberosus* and *Psilostomum brevicolle* (Figure 4E, 4H, 4M, 4O). Others may have, in some locations, very high abundance (>100 or 1000) such as *Himasthla elongata, H. quissetensis, H. interrupta, Curtuteria arguinae*

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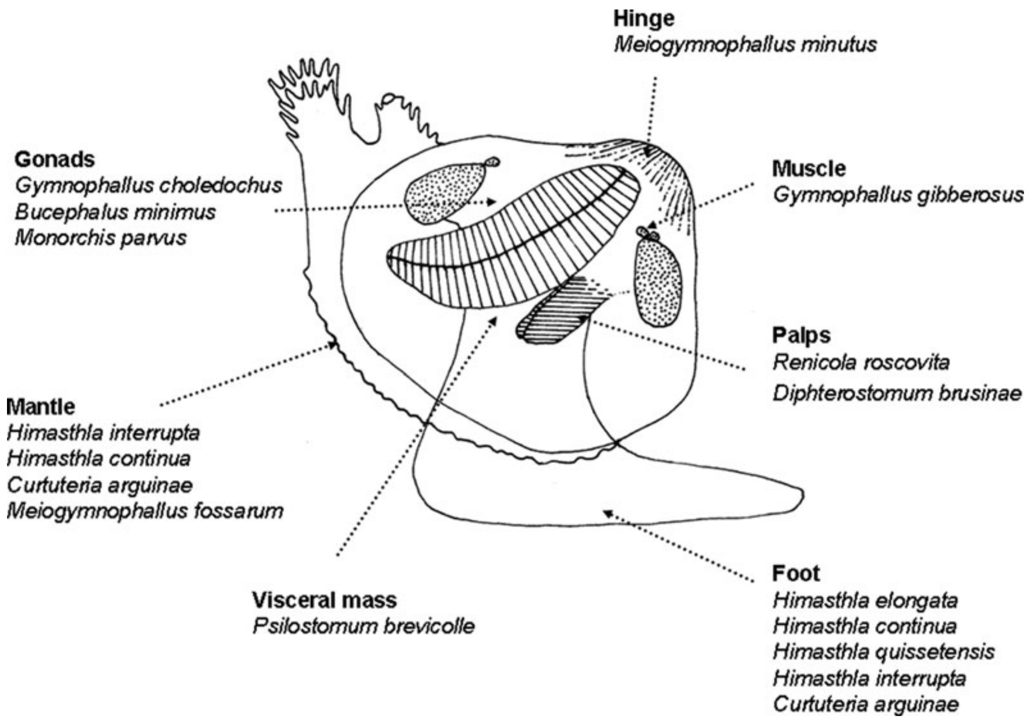


Fig. 3. *In situ* location of the parasites infecting *Cerastoderma edule*. When mature, *Gymnophallus choledochus*, *Bucephalus minimus* and *Monorchis parvus* can invade most tissues.

and *Renicola roscovita* (Figure 4F, 4G, 4I, 4J, 4N). Finally, *Meiogymnophallus minutus* appears as the most abundant and widespread parasite (Figure 4K).

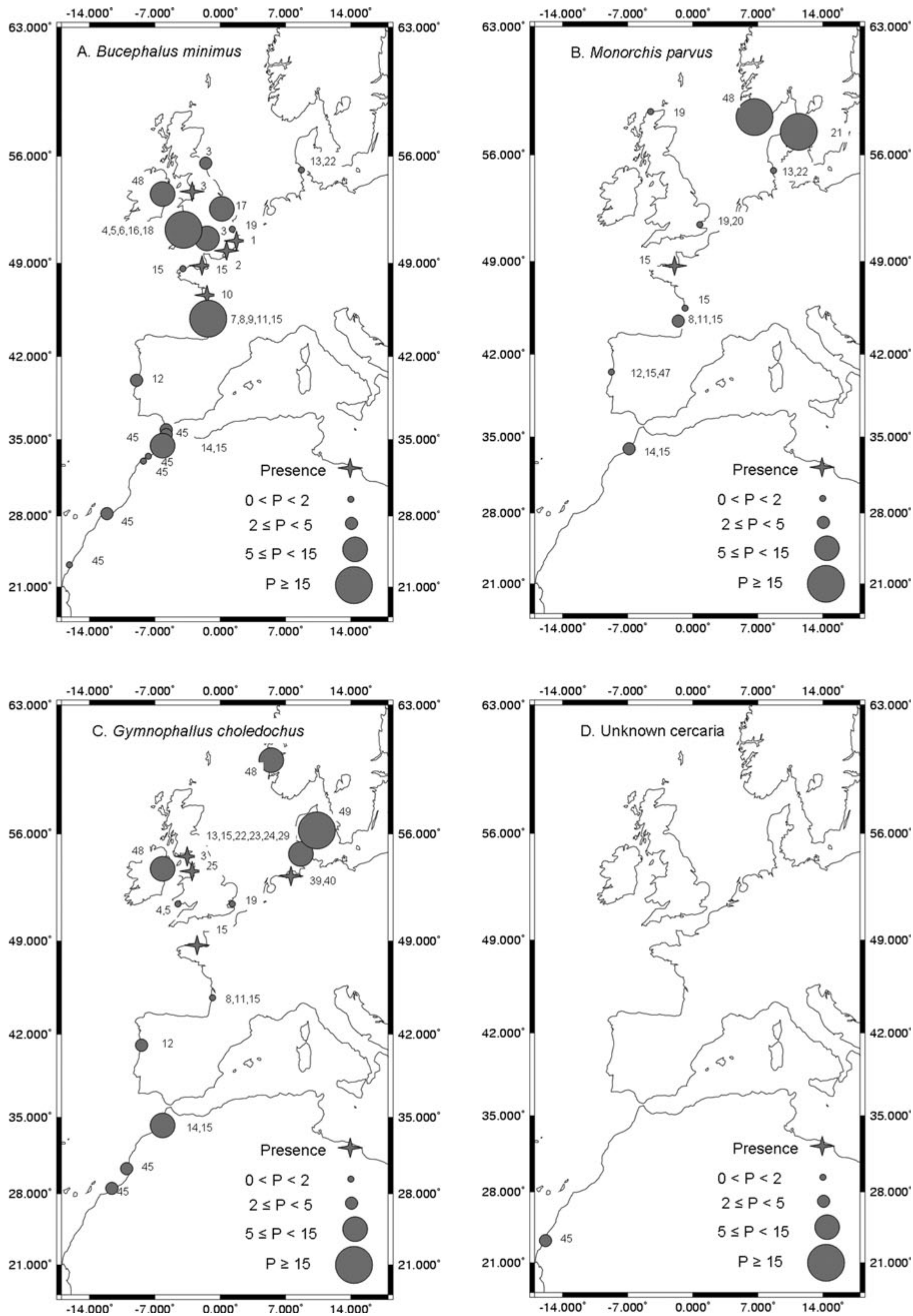
Latitudinal distribution patterns

Although cockles are infected with digeneans along their entire distributional range, the parasite communities within cockle populations are not the same everywhere. Some parasite species show restricted latitudinal distribution (Figure 4). The unknown cercariae, *Diphterostomum brusinae* and *Curtuteria arguinae* display a rather southern distribution (<50°N) while *Renicola roscovita*, *Gymnophallus gibberosus* and *Asymphylodora demeli* display a rather northern distribution (>40°N). *Meiogymnophallus minutus* and *Psilostomum brevicolle* occupy the largest latitudinal distribution (40°).

DISCUSSION

Although cockles are infected with digeneans along their entire distributional range, the parasite communities within cockle populations are not the same everywhere. Some parasite species show restricted latitudinal distribution. The latitudinal distributions of first intermediate hosts are important for understanding the patterns of digenean species in cockles. For example metacercariae of *Gymnophallus gibberosus*, *Himasthla elongata* and *Renicola roscovita* occur primarily in the northern part of the cockles' range while metacercariae of *Diphterostomum brusinae* and *Curtuteria arguinae* occur exclusively in the south (Figure 4). The northern distribution of *G. gibberosus* is correlated with the general distribution of the first intermediate host *Macoma balthica* (north of the Gironde estuary, exceptionally Arcachon Bay, France) and of the final host, the eider duck *Somateria mollissima*. For *H. elongata*, and *R. roscovita* the distribution of their first intermediate snail hosts the periwinkle *Littorina littorina* has a more northern distribution. The southern occurrence of *Diphterostomum brusinae* and *Himasthla quiessetensis* could be a result of the distribution pattern of their first intermediate host *Nassarius reticulatus*. To the north the dogwhelk is not found on intertidal flats and as a consequence it has not been observed in north where studies of parasites in cockles have been limited to intertidal areas or lagoons without *N. reticulatus*. Besides this, *H. quissetensis* may have been overlooked in the older records as it was not registered along the east Atlantic shoreline before 1990 (Russell-Pinto, 1993), unless it is an introduced parasite species (de Montaudouin

Fig. 4. [See next page for Figure 4] Distribution of digenean species along the distribution of their cockle *Cerastoderma edule* host, in the north-eastern Atlantic. P, maximum mean parasite prevalence observed; A, maximum mean parasite abundance observed. Numbers correspond to the following references: 1. Pelseneer, 1906; 2. Vaullegard, 1894; 3. Lebour, 1911; 4. James & Bowers, 1967; 5. James *et al.*, 1977; 6. Bowers, 1969; 7. Deltreil & His, 1972; 8. Desclaux *et al.*, 2002; 9. Baudrimont *et al.*, 2006; 10. Sauriau, 1992; 11. de Montaudouin *et al.*, 2000; 12. Russell-Pinto *et al.*, 2006; 13. Thieltges & Reise, 2006; 14. Gam *et al.*, 2008; 15. de Montaudouin, unpublished; 16. Hancock & Urquart, 1965; 17. Boyden, 1971; 18. Malek, 2001; 19. Sannia & James, 1978; 20. Sannia *et al.*, 1978; 21. Jonsson & André, 1992; 22. Thieltges *et al.*, 2006; 23. Thieltges, 2006; 24. Lauckner, 1971; 25. Jonstone, 1904 (in Lebour, 1911); 26. Bowers & James, 1967; 27. Bowers *et al.*, 1990; 28. Goater, 1993; 29. Krakau *et al.*, 2006; 30. Lauckner, 1984; 31. Russell-Pinto, 1990; 32. Russell-Pinto & Bartoli, 1992; 33. Desclaux *et al.*, 2004; 34. Wegeberg & Jensen, 1999; 35. Wegeberg & Jensen, 2003; 36. de Montaudouin *et al.*, 2005; 37. Desclaux *et al.*, 2006; 38. Kesting *et al.*, 1996; 39. Loos-Frank, 1971; 40. Loos-Frank, 1969; 41. Thieltges & Reise, 2007; 42. Lassalle *et al.*, 2007; 43. Goater, 1995; 44. Reimer, 1970; 45. Bazairi, unpublished; 46. Dang, unpublished 47. Bartoli *et al.*, 2000; 48. Krakau, unpublished; 49. Jensen, unpublished.



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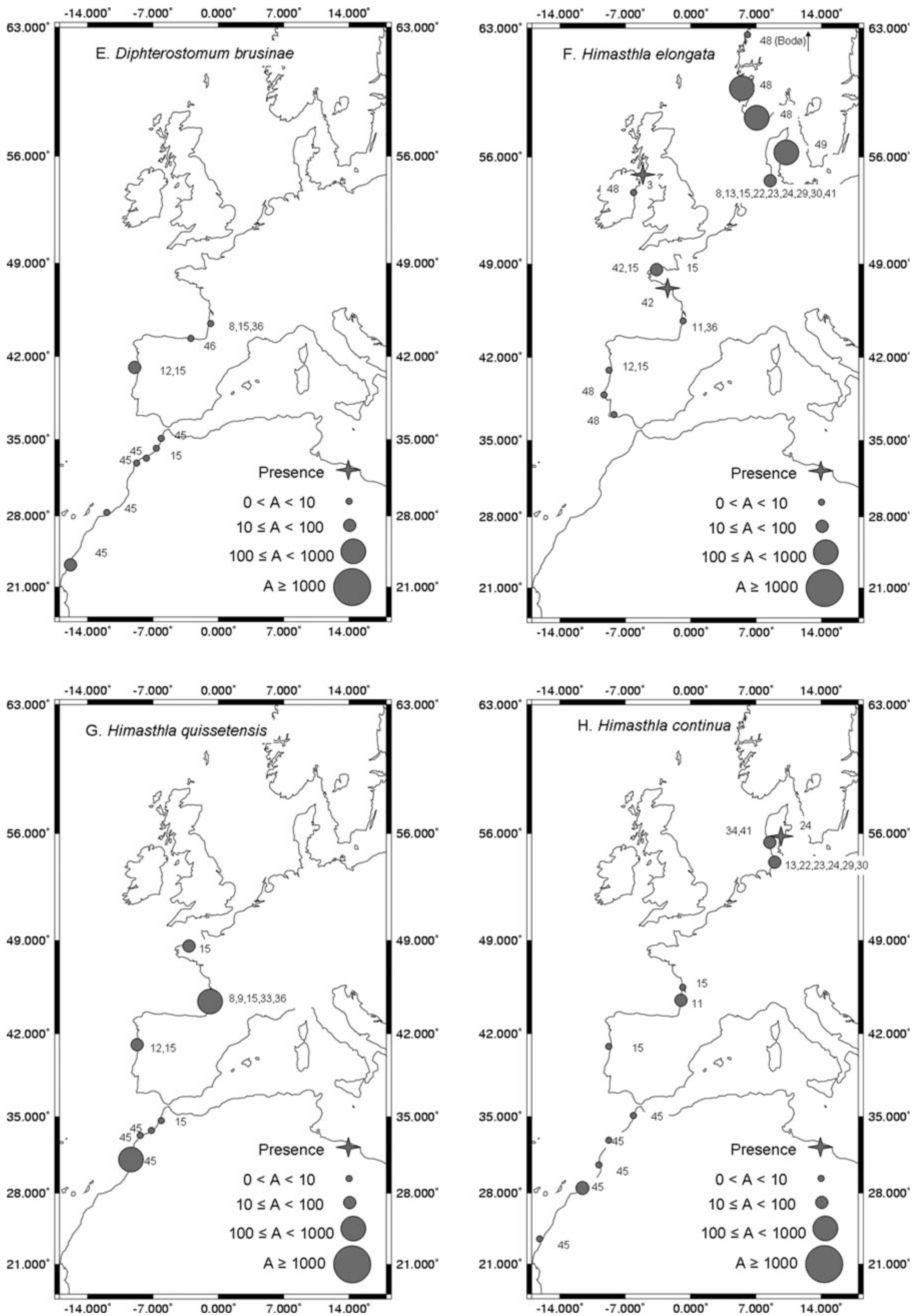

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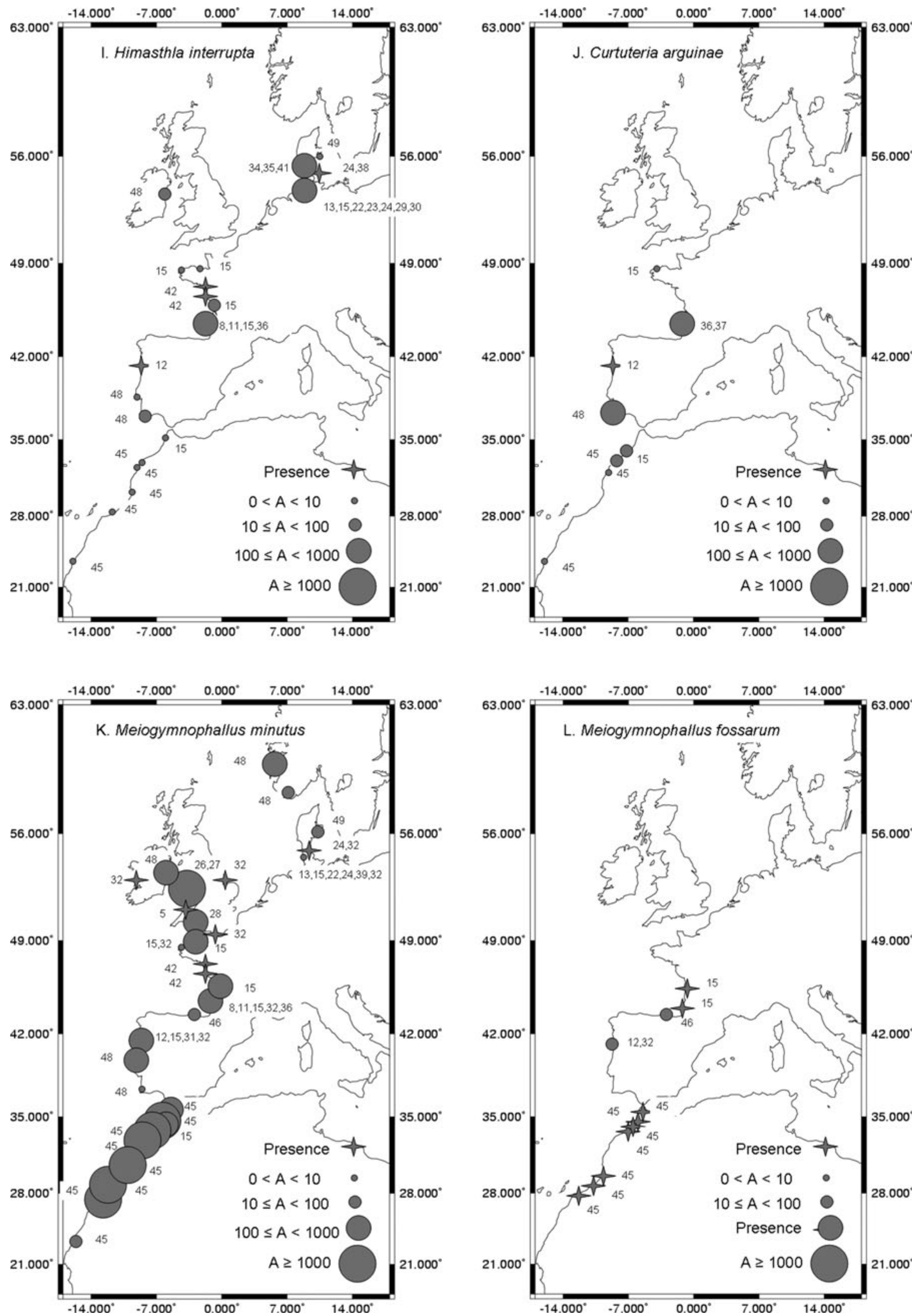

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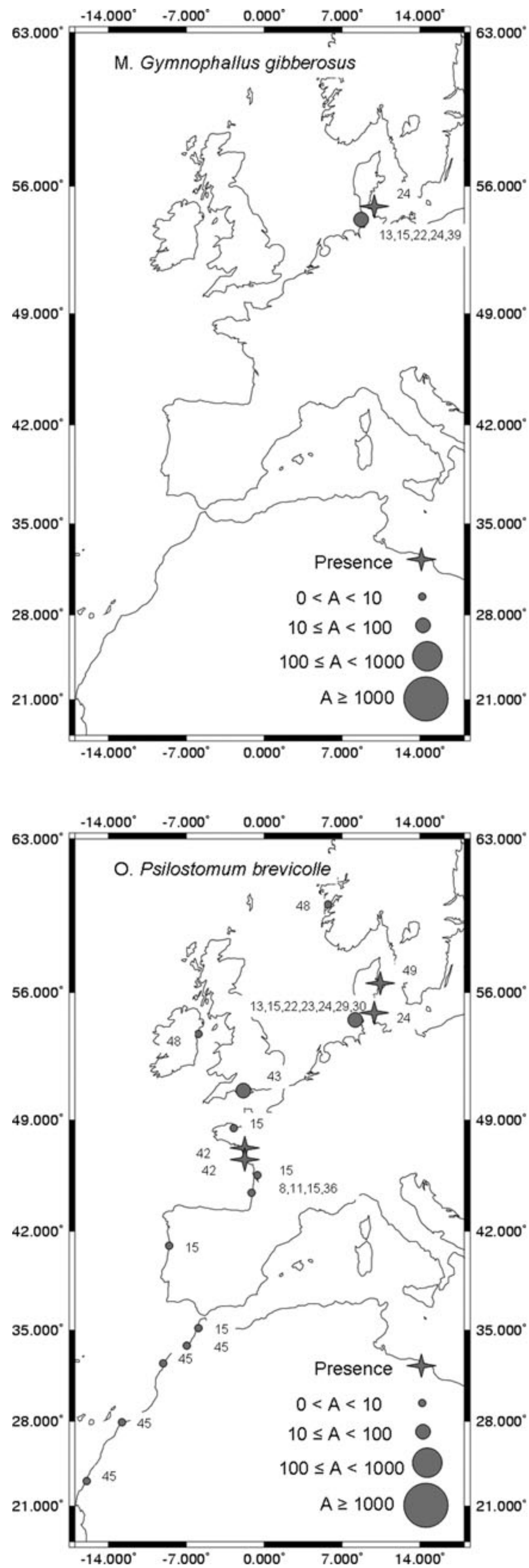

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et al., 2005). For final hosts, generally we can expect bird hosted parasites to be more widespread than fish hosted parasites considering that many waterbirds have longer annual migratory routes than fish. As an example the fish *Dicentrarchus labrax* host to *Bucephalus minimus* has expanded its northern boundary to the North Sea probably caused by increased sea temperature. In accordance *Bucephalus minimus* has now been registered in the German Wadden Sea (Thieltges *et al*., 2006, 2008).

Compared to other bivalves co-occurring with cockles within intertidal flat communities the parasite fauna in cockles is particularly diverse and abundant (de Montaudouin *et al*., 2000; Thieltges & Reise, 2006). Many of the parasites using cockles as second intermediate host may also be found in other bivalves (de Montaudouin *et al*., 2000; Krakau *et al*., 2006; Thieltges *et al*., 2006), whereas those using cockles as their first intermediate host are more host specific. The relatively large biogeographical area of cockles compared to some of the other bivalves from shallow water ecosystems along the east Atlantic shoreline could contribute to the richness of the supracommunity of digeneans in cockles. In addition cockles occur at a range of habitats within an ecosystem resulting in overlap with many potential first intermediate hosts (*Hydrobia*, *Littorina* and *Scrobicularia*). With an analogy to diversity promoters among free-living organisms, the heterogeneity of appropriate tissue types (i.e. microhabitat) is important for digenean diversity in bivalves. To what extent cockles are unique in this respect remains unresolved.

Parasites are potentially important for the dynamics of cockle populations along its entire distributional range in the north-eastern Atlantic and not just a local phenomenon. Digeneans utilizing cockles as first intermediate hosts are known to castrate their hosts and to be involved in cockle mass mortalities when additional stressors are present (Jonsson & André, 1992; Thieltges, 2006). Digeneans utilizing cockles as second intermediate host show a range of different effects such as impaired burrowing ability, reduced growth, increased mortality, and reduced tolerance of anoxia (Lauckner, 1983; Jensen *et al*., 1999; Wegeberg & Jensen, 1999, 2003). Hence, studies on cockle populations should include parasites and our identification key will hopefully facilitate inclusion of parasites in future population studies of cockles.

An understanding of the prevalence and abundance patterns requires consideration of a range of local abiotic and biotic factors determining transmission rates such as adverse environmental conditions, distance to and densities of hosts emitting parasite propagules, duration of the transmission window, age- and size-distribution of hosts, presence of ambient species interfering with the transmission of the free larval stages etc (Goater, 1993; de Montaudouin *et al*., 1998; Jensen *et al*., 1999; Wegeberg *et al*., 1999; Thieltges, 2007; Thieltges & Reise, 2007; Thieltges, 2008; Thieltges *et al*., in press). It will be a challenge to examine if climate-related factors or latitudinal patterns in temperature profiles have a superior impact on prevalence and abundance patterns and how global heating will impact such patterns. A clear understanding of this requires standardized experimental studies along latitudinal gradients to eliminate the importance of local factors. However, given the present knowledge of the common cockle and its parasite fauna along its latitudinal distributional area, this could be a convenient model for studying the impact of global changes on parasite–host systems.

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Correspondence should be addressed to:
X. de Montaudouin
Université de Bordeaux, UMR EPOC 5805
Station Marine d'Arcachon 2 rue du Pr Jolyet
F-33120 Arcachon, France
email: x.de-montaudouin@epoc.u-bordeaux1.fr