



Review

The potential impact of climate change on the infectious diseases of commercially important shellfish populations in the Irish Sea—a review

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The Irish Sea and surrounding regions are a rich source of shellfish production as a result of captive fishing and aquaculture. Key species produced include lobsters (*Homarus gammarus*), edible crabs (*Cancer pagurus*), langoustines (*Nephrops norvegicus*), flat oysters (*Ostrea edulis*), cockles (*Cerastoderma edule*) and blue mussels (*Mytilus edulis*). The role played by infectious disease in limiting the sustainability of the production of these species is largely neglected. This review summarizes our knowledge of the key diseases of commercially important crustaceans and bivalve molluscs and attempts to determine their role in limiting the population of animals available for food production both at present and in the future. It shows that the key diseases threatening the sustainability of shellfish production are bitter crab disease in langoustines and edible crabs, and a wide range of diseases caused by micro- and macro-parasites in some bivalve molluscs including oysters and cockles. Oceanographic models are also employed to predict how changes in climate over the next half century may affect these key diseases and their hosts as found in the Irish Sea. It is concluded that the paucity of information on the potential transfer of some disease agents in pelagic larval stages of hosts and vectors is a major hurdle in predicting how some changes in environmental conditions may influence the prevalence and severity of shellfish diseases in coming years.

Keywords: climate change, emerging infectious diseases, Irish Sea, shellfish disease.

Introduction

The food security agenda is a key concern to governments world-wide, especially as the global population of humankind may reach over 9 billion by 2050 (Godfray *et al.*, 2010; Foresight, 2011). While agriculture is of major importance in feeding this increasing population, fish and shellfish production, either by aquaculture or by capture fisheries, will play a role in achieving this goal. It is estimated that over 3 billion people are currently reliant on fish and shellfish to provide at least 15% of the protein in their diets (Smith *et al.*, 2010). Furthermore, fish and shellfish are important in providing essential amino acids and health-promoting omega

3 polyunsaturated fatty acids (Brunner *et al.*, 2008; Calder and Yaqoob, 2009). The mounting demand on food availability caused by human population growth may also be exacerbated by projected changes in our global climate. A recent review by Merino *et al.* (2012) posed the question of whether fisheries and aquaculture production will be able to meet the demands of the world’s population by 2050 within the confines set by climate change models. The authors concluded that the mounting consumption caused by increasing population may be met with improvements in aquaculture and better management of fisheries resources.

One of the major constraints in the production of shellfish is infectious disease (Stentiford *et al.*, 2012). While we have a good understanding of how disease impinges on aquaculture production, the equivalent process in populations of wild-caught shellfish is less clear as such conditions are often silent. There are, however, some well-understood examples of how disease epizootics may impact on the sustainability of crustacean fisheries (Shields, 2011, 2012).

The interplay between infectious disease agents and their hosts, and the way in which environmental factors in the marine environment including temperature, salinity and anthropogenic disturbances modulate this, is well known (Mydlarz *et al.*, 2006). Some workers in the field believe that there has been an increase in diseases in marine ecosystems as a result of a variety of anthropogenic stressors (e.g. Harvell *et al.*, 2002; Lafferty *et al.*, 2004; Ward and Lafferty, 2004), which in some cases have resulted in changes in the prevalence, geographical distribution and severity of disease. These diseases are referred to as emerging infectious diseases (Daszak *et al.*, 2000) that threaten human and animal populations globally. In aquaculture species, some diseases have emerged through pathogen exchange with wild populations and the intentional transfer of stocks for culture (Murray and Peeler, 2005; Peeler and Taylor, 2011).

Global warming is one ecological driver of these emerging infectious diseases (Ward *et al.*, 2007; Plowright *et al.*, 2008; Lafferty, 2009). Changes in climate may differ depending on the nature of the parasite/pathogen–host interaction and the geographic location in which it occurs. In northern latitudes, the higher temperatures recorded in the summer months herald the potential for increased multiplication of microbial pathogens, such as bacteria and fungi, and simultaneously stresses hosts leaving them immunocompromised (Mydlarz *et al.*, 2006). Development of disease and a relationship with increased temperature-induced stress have been demonstrated in molluscs (Bricelj *et al.*, 1992; Lee *et al.*, 1996; Friedman *et al.*, 1999; Cheney *et al.*, 2000). For example, summer mortality episodes in the Pacific oyster, *Crassostrea gigas*, have been associated with a complex association between pathogens, in particular, herpes virus, and a range of environmental stressors such as water temperature (Malham *et al.*, 2009; Cotter *et al.*, 2010). Milder winter temperatures may facilitate longer transmission periods and opportunities for reproduction or production of more cohorts of parasites. Not all diseases are likely to increase in prevalence and severity as a result of global warming. For instance, while salmon and sea trout in fish farms in Finland showed higher prevalence of some infections as a result of global warming, including bacterial columnaris caused by *Flavobacterium columnare*, other diseases such as that caused by the protozoan parasite, *Ichthyobodo necator*, actually declined in prevalence (Karvonen *et al.*, 2010). Clearly, there will be “winners” and “losers” in the climate-driven changes in the complex interaction between host and parasite.

The Irish Sea (Figure 1) is an important region for the production of shellfish including bivalve molluscs (clams, cockles, oysters, mussels) and decapod crustaceans (crabs, lobsters and langoustines), yet our knowledge of the status of disease in limiting the sustainability of these resources has been little studied until recently. This was the impetus for a recent collaborative project between oceanographers, fisheries scientists and shellfish disease experts from Ireland and Wales, which had two main goals. First, it sought to provide a “baseline” for disease prevalence in shellfish populations of commercial importance in the Irish Sea, and it also made predictions, based on oceanographic models, for how this might change by 2060. This review summarizes our main findings in relation to these

two objectives and points to where we still have deficiencies in our understanding of how infectious disease may impact on shellfisheries in the Irish Sea now and in the future.

Shellfish production in the Irish Sea and surrounding regions

The Irish Sea represents a region where marine resources provide substantial contributions to local and regional economies (Table 1). The annual economic value of the main marine sectors, including aquaculture and shellfisheries, has been estimated to be in the order of £6 billion for the Irish Sea (Vincent *et al.*, 2004). Table 1 outlines the average annual landings (tonnages and values) in Ireland and Wales for a number of shellfish species. The UK and Irish marine aquaculture industries rely heavily on such resources, particularly in Ireland and Wales where more than two-thirds of all shellfish production occurs (Callaway *et al.*, 2012). Bivalve molluscs, including predominantly mussels (*Mytilus* spp.) and Pacific oysters (*Crassostrea gigas*) but also smaller amounts of native oysters (*Ostrea edulis*), Manila clams (*Ruditapes philippinarum*) and scallops (*Aequipecten opercularis* and *Pecten maximus*), constitute the major exploited species of the region (Vincent *et al.*, 2004). In Ireland, shellfish production contributes ~€34.6 million to local economies, with mussels accounting for almost 80% of production tonnage followed by Pacific oysters, native oysters, clams and scallops (BIM, 2009). Mussels are also the major species of production in Wales, with smaller numbers of Pacific oysters also produced (Callaway *et al.*, 2012).

Shellfisheries in the Irish Sea region account for substantially higher economic returns (£43.5 million in 2002) than pelagic and demersal fin fisheries combined (£16.4 million in 2002) (Vincent *et al.*, 2004). The major commercial invertebrate species, the langoustine (*Nephrops norvegicus*), is targeted by trawl fisheries across the region and surrounding areas, whilst dredging occurs for a number of bivalve species including scallops and mussels (MMO, 2011). In 2002, langoustines accounted for the greatest economic return for Irish Sea shellfisheries (£8.2 million) followed by mussels (£3.4 million), scallops (£3.2 million) and queen scallops (£2.2 million) (Vincent *et al.*, 2004). Additionally, a number of high quality shellfish species including the European lobster (*Homarus gammarus*) and the edible (brown) crab (*Cancer pagurus*) are caught by pot and trap fisheries mainly for export to European Union countries (Anderson and Guillen, 2009; Cheung *et al.*, 2012). Between 2001 and 2006, the average UK lobster fishery annual catch was ~2500 tonnes per annum with a first sale value in 2006 of £26 million; in 2005, edible crabs had a first sale value of £30 million (SEAFISH, 2009).

Diseases of bivalve molluscs

The Irish Sea is a rich source of shellfish, both in terms of abundance and species diversity (Tables 1 and 2). The shellfish species of commercial interest present in this area include the Pacific oyster, *Crassostrea gigas*, the European flat oyster, *Ostrea edulis*, the soft shell clam, *Mya arenaria*, the razor clam, *Ensis* spp., the edible cockle, *Cerastoderma edule* and the blue mussel, *Mytilus edulis*. Some of the recent work carried out in the Irish Sea indicates that many populations of shellfish, such as the soft-shelled clam, are healthy and show few pathogens (Cross *et al.*, 2012). The disease agents that have had a detrimental impact on shellfish production and sustainability in the Irish Sea commonly include haplosporidians, viruses, bacteria and digenean parasites (Table 2; Culloty and

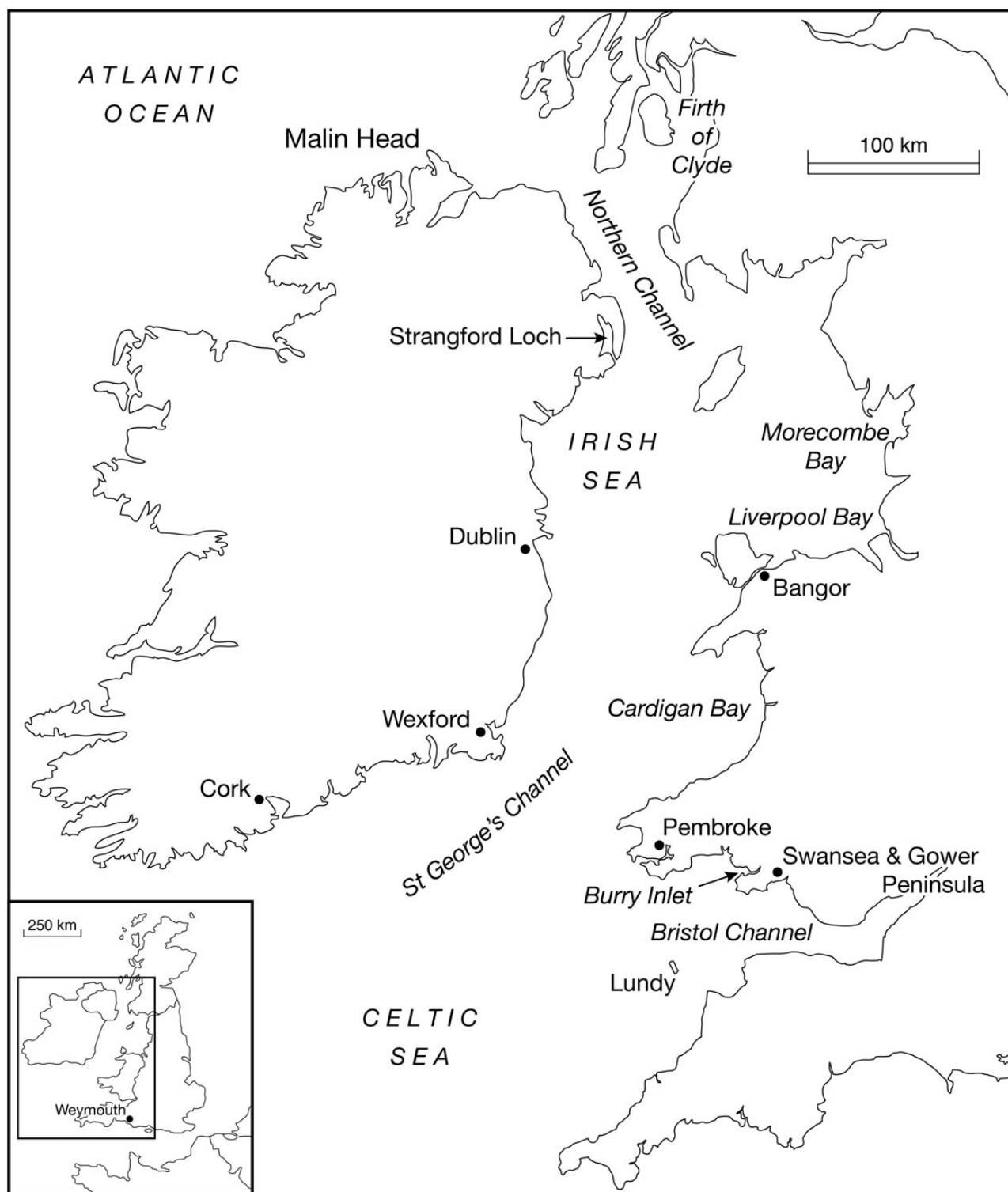


Figure 1. Map showing the Irish Sea and surrounding regions. Locations on the map are referred to in the text.

Mulcahy, 2007; Cotter *et al.*, 2010; Lynch *et al.*, 2012, 2013; Morgan *et al.*, 2012; Longshaw and Malham, 2012). Of particular significance to the shellfish populations in the Irish Sea is the emergence of previously undescribed pathogen genotypes and variants (e.g. herpes virus variant in the Pacific oyster *C. gigas*) and the first detection of known

disease agents (e.g. haplosporidian parasites in oysters) in various other shellfish species in the Irish Sea (Lynch *et al.*, 2010, 2012, 2013). The role of carriers or reservoirs for such disease agents is also of interest and contributes to a better understanding of a pathogen's life cycle (Lynch *et al.*, 2007; Lynch *et al.*, 2010).

Table 1. Principal shellfish of commercial importance in the Irish Sea and surrounding regions.

Common name	Genus/species	Type of production (capture or aquaculture)	Main areas of production	Mean annual gross value (£) 1000 ^a	Mean annual gross tonnage (mT) ^a
Edible (brown) crab	<i>Cancer pagurus</i>	Capture	South Wales and all coasts of Ireland, but the northwest coast in particular	5 523	4 559
Langoustines	<i>Nephrops norvegicus</i>	Capture	Firth of Clyde	6 524	1 856
European lobster	<i>Homarus gammarus</i>	Capture	Widespread	6 085	430
Common cockle	<i>Cerastoderma edule</i>	Capture	Burry Inlet, Dee Estuary in Wales; Dundalk Bay and Waterford Estuary in Ireland	312	685
Pacific oyster	<i>Crassostrea gigas</i>	Aquaculture	Carlingford Lough, Wexford, Waterford	5 874	2 009
Flat oyster	<i>Ostrea edulis</i>	Aquaculture	Cork Harbour, Strangford Lough in Ireland	8	3
Blue mussel	<i>Mytilus edulis</i>	Capture and aquaculture	Wexford and Wicklow in Ireland; Menai Strait in North Wales	11 282	15 868

^aBased on data from BIM (2011) and the Central Statistics Office (1994–2004) for Ireland, and MMO and DECC (2005–2011) for Wales.

Ostreid herpesvirus 1 (OsHV-1) and variants

Significant mortalities of *C. gigas* have occurred worldwide since the 1950s and have been associated with a complex aetiology including elevated temperature, nutrient and plankton levels (Malham *et al.*, 2009; Cotter *et al.*, 2010). In recent years, studies have looked at the role of ostreid herpesvirus 1 (OsHV-1) and variants as causative agents in such events (Renault *et al.*, 1994, 2000a; Arzul *et al.*, 2002; Vázquez-Yeomans *et al.*, 2004; Friedman *et al.*, 2005; Burge *et al.*, 2007; Lynch *et al.*, 2012). OsHV-1 μ var is a variant of OsHV-1 and is considered to be a more virulent strain, in particular when seawater temperatures exceed 16°C (EFSA, 2010). OsHV-1 μ var was originally associated with *C. gigas* mortalities in France in 2008 and in 2009 (Repamo, 2009; Segarra *et al.*, 2010) and has subsequently been observed in Ireland with up to 90% oyster mortalities (Table 2; www.marine.ie/home/services/operational/fishhealth/Oyster+Herpes+Virus.htm, last accessed January 2013).

Recently, an OsHV-1 μ var variant genotype was detected at two *C. gigas* cultivation sites in the Irish Sea and was associated with ongoing mortalities in both spat and market-sized adults at both sites (Lynch *et al.*, 2012). It has been reported that *C. gigas* older than 18 months can be a source of the OsHV-1 and variants (EFSA, 2010), and that the virus can persist in surviving adult *C. gigas* following primary infection. OsHV-1 variants have had a negative impact on the survival of larvae and juveniles of several other bivalve species in Europe (Arzul *et al.*, 2002; Lipart and Renault, 2002; Renault, 2008, 2011), and it is recommended that the movement and mixing of different age groups should be avoided (EFSA, 2010).

Haplosporidiosis

The phylum Haplosporidia contains obligate protozoan parasites of a number of freshwater and marine invertebrates (Burrison and Ford, 2004; Moiseeva *et al.*, 2004; Siddall and Aguado, 2006) (Figure 2a). There are four genera allocated to this phylum; *Urosporidium*, *Minchinia*, *Haplosporidium* and *Bonamia* (Reece *et al.*, 2004). Once introduced into a naïve host population, some haplosporidian species have had a significant impact on commercial shellfish species worldwide due to the mortalities that they cause (Burrison *et al.*, 2000; Burrison and Reece, 2006).

The haplosporidian, *Bonamia ostreae*, the causative agent of bonamiosis, has had a detrimental impact on the production of

the European flat oyster, *O. edulis*, in Europe since the 1970s (Figure 2a; Comps *et al.*, 1980; Montes and Figueras, 1987; Van Banning, 1991; McArdle *et al.*, 1991; Lynch *et al.*, 2005). *Bonamia ostreae* was first detected in Cork Harbour in the 1980s (McArdle *et al.*, 1991) in close proximity to the Irish Sea and is now found at several *O. edulis* cultivation sites along the western and northern coasts of Ireland (McArdle *et al.*, 1991; Culloty and Mulcahy, 2007). *Bonamia ostreae* was first detected in mussels during routine health screening in the Menai Strait, North Wales in 2011 (<http://www.defra.gov.uk/aahm/files/Bonamia-Ostreae-CD.pdf>, last accessed January 2013). To date there are no known eradication methods and there are limited control procedures for this parasite. Close proximity of uninfected oysters to infected oysters is believed to aid transmission, and it takes 4–6 weeks for infection to develop once the oysters have been initially exposed to the parasite (Culloty and Mulcahy, 1996). Young pre-spawning *O. edulis*, from spat size up, can become infected with *B. ostreae* quite quickly following exposure and can demonstrate a high prevalence and moderate intensity of infection (Lynch *et al.*, 2005). Although infections caused by *B. ostreae* may occur throughout the year (Grizel and Tigé, 1982; Culloty and Mulcahy, 1996), prevalence and intensity of infection tend to increase during the warm season with highest prevalence occurring in spring (Engelsma *et al.*, 2010) or autumn (Montes and Meléndez, 1987). In the culture of the flat oyster, Guerra (1995) indicated that peaks of mortality during summer months are due to high metabolic and reproductive activity, making the oysters more susceptible to infection. *Bonamia ostreae* outbreaks occur at temperatures from 12–20°C, and may be limited by low temperatures. However, such conditions may also reduce an oyster's ability to fight infection (Cochennec and Auffret, 2002). In recent years, the role of other carriers or reservoirs of *B. ostreae* infection have been investigated to better understand the life cycle of this parasite and the importance of screening non-typical hosts prior to their movement from infected to uninfected shellfish culture sites. *Bonamia ostreae* DNA was confirmed to be present in several zooplankton samples and in several macroinvertebrate species (Lynch *et al.*, 2007) living in close proximity to infected oyster beds. The role of *C. gigas* as a potential carrier or reservoir of infection was also examined, and viable *B. ostreae* infections were visualized and confirmed by molecular techniques in several individuals (Lynch *et al.*, 2010).

Table 2. Status of some key diseases of bivalve molluscs in the Irish Sea and surrounding regions.

Disease	Disease-causing agent	Host range	Prevalence and severity of infection	Life stages affected	Potential effect on sustainability of fisheries	Current status of disease
Bonamiasis	<i>Bonamia ostreae</i>	European flat oyster <i>Ostrea edulis</i> , but other ostreid oysters may be affected	Prevalence is variable (0–80%)	Larvae, seed, juvenile and adult oysters	Significant, high mortalities possible	No significant mortalities have been reported in oysters at Strangford Lough since the disease was first detected in several <i>O. edulis</i> in 2008
Disseminated neoplasia	Unknown, may be viral in origin	20 species of bivalves including cockles, mussels, clams and oysters	Prevalence may increase rapidly in a short period of time	Younger cockles (around age 3) or intermediate size classes	Significant as mortality events have been associated with high prevalence	Some mortalities in 2010 and 2011 in Ireland
Vibriosis	Ostreid herpesvirus 1 (OsHV-1) and variants	Wide range of bivalves including oysters, scallops, clams and abalone	High prevalence and mortalities (up to 100%) associated with OsHV-1 μ var in the Pacific oyster	Larvae, juveniles and adults of oysters, clams and scallops	Significant, high mortalities possible	No mortalities reported in recent years due to cooler summers. Previous significant mortality events occurred in the summers of 2009 and 2010
	<i>Vibrio</i> spp.	Wide range of bivalves	Can be of high severity causing extensive mortality	All but mainly larvae	?	?
	Digenean trematodes	Extensive range of bivalves, gastropods, plus vertebrates	High prevalence; up to 100% recorded in cockles; may reduce growth rates	Juveniles and adults of bivalves e.g. cockles	May affect fisheries production during times of increased temperatures	Some mortalities during summer or in unison with neoplasia e.g. in Cork Harbour in 2009

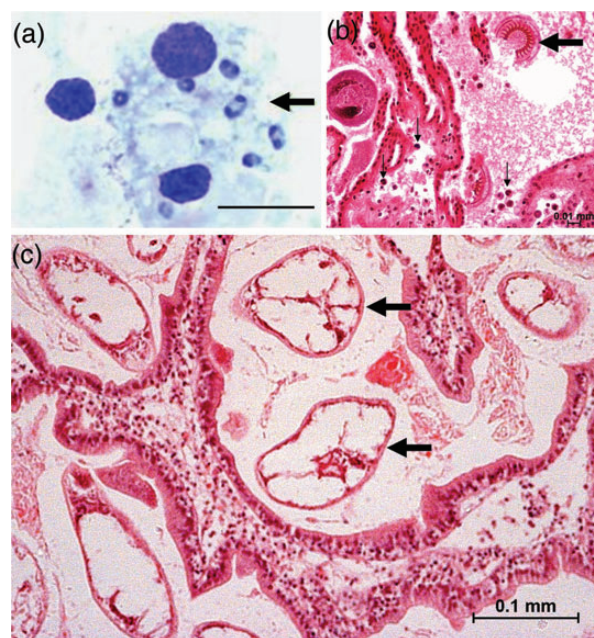


Figure 2. Examples of principal diseases of bivalve molluscs found in the Irish Sea region. (a) Uni- and bi-nucleate forms of *Bonamia ostreae* (arrow) in flat oyster (*Ostrea edulis*) haemocytes. Scale bar = 10 μ m. (b) Histological section through the gill region of *Cerastoderma edule* showing the presence of *Trichodina*-like ciliates (large arrow) and neoplastic cells (small arrows). (c) Histological section through *C. edule* showing the presence of large numbers of digenean parasites (arrows; possibly *Meiogymnophallus minutus*).

Haplosporidium nelsoni is the infectious agent of the disease Multinucleate Sphere X (MSX) (Haskin *et al.*, 1966) in the eastern oyster, *Crassostrea virginica*. *Haplosporidium nelsoni* has been detected in the USA (e.g. Haskin and Andrews, 1988), Canada (Stephenson *et al.*, 2003), Korea (Chun, 1972; Kern, 1976; Bureson *et al.*, 2000), Japan (Kamaishi and Yoshinaga, 2002) and China (Wang *et al.*, 2010). Within Europe, haplosporidian plasmodial stages were reported in Pacific oysters at a very low prevalence from the French Atlantic coast in 1993, and species-specific molecular diagnostics confirmed them as *H. nelsoni* (Renault *et al.*, 2000b). A low prevalence of *H. nelsoni* plasmodia was recently detected for the first time in populations of *C. gigas* screened from the southern coast of Ireland, in close proximity to the Irish Sea (Lynch *et al.*, 2010). Of significance was the detection at Cork Harbour of *H. nelsoni* plasmodia in a single European flat oyster, *O. edulis*, which is the first record of this haplosporidian in this species of oyster (Lynch *et al.*, 2013). It is unknown what effect *H. nelsoni* has on *O. edulis*; however, *H. nelsoni*-like plasmodia have been detected in another species of the same genus, *O. lurida* in Canada (Mix and Sprague, 1974) but no mortalities have been associated with its presence. Although unintentional introductions of *H. nelsoni* with shellfish consignments may occur, *H. nelsoni* may also be dispersed by ocean circulation and in the ship ballast water or in carrier hosts attached to ships hulls (Bureson and Ford, 2004). Lynch *et al.* (2013) concluded that the low prevalence of *H. nelsoni* in the Irish *C. gigas* and *O. edulis* indicates that these oysters are demonstrating incidental infections, which are not having a significant impact on these species. However, the environmental factors, temperature and high salinity, favoured by *H. nelsoni* are present in Ireland (Haskin and Ford, 1982; Ford, 1985).

Haplosporidium armoricum is another member of the phylum Haplosporidia. Unlike *H. nelsoni* it is not known to have had a detrimental effect on oyster populations and production. *Haplosporidium armoricum* has been reported in oysters, *O. edulis*, in mainland Europe (e.g. da Silva *et al.*, 2005) and more recently in Ireland (Lynch *et al.*, 2013). Finally, *Minchinia* sp. has been recorded in cockles from the Burry Inlet in South Wales (Elliot *et al.*, 2012), but whether it is a factor in the dramatic decline of the cockle fishery in this location is unclear.

Cercozoa

Marteilia refringens is a unicellular parasite affecting the digestive system of the flat oyster, *O. edulis* and other shellfish species (Le Roux *et al.*, 2001; Berthe *et al.*, 2004; López-Flores *et al.*, 2004). While to date *M. refringens* has not been detected in animals in the Irish Sea, this pathogen is spreading northwards, with its most recent detection being in mussels (*M. edulis*) from the Tamar estuary in Cornwall, UK in 2011 but with no evidence of morbidity or mortality in these animals (<http://www.defra.gov.uk/aahm/2011/08/25/first-detection-of-marteilia/>, last accessed January 2013).

Bacteria

Vibrio is a genus of gram-negative bacteria that are ubiquitous in marine environments. Certain *Vibrio* species have been associated with significant mortalities in several shellfish species worldwide, including clams (Gómez-León *et al.*, 2005), scallops (Tubias *et al.*, 1965; Freitas *et al.*, 1993) and oysters (Le Roux *et al.*, 2005; Garnier *et al.*, 2007). The *Vibrio* taxa commonly associated with cultured bivalves include *V. alginolyticus*, *V. (Listonella) anguillarum*, *V. splendidus* and *V. tubiashii* (DiSalvo *et al.*, 1978; Lodeiros *et al.*, 1987) and are most virulent during the bivalve larval life stage (Elston and Leibovitz, 1980; Nottage and Birkbeck, 1986; Riquelme *et al.*, 1995). *Vibrio tapetis*, the causative agent of brown ring disease, has been isolated from the common cockle *C. edule*. This cockle has been described as a carrier species as it does not exhibit brown ring disease symptoms in the wild (Lassalle *et al.*, 2007). Adult oysters are known to act as reservoirs for *Vibrio* spp. that can be pathogenic to humans (e.g. *V. parahaemolyticus* and *V. vulnificus*) but non-pathogenic to the oyster (Volety *et al.*, 1999). *Rickettsia*-like bacteria have been described in cockles from Spain and Wales in the gills and digestive area (Carballal *et al.*, 2001; Elliot *et al.*, 2012).

Disseminated neoplasia

Disseminated neoplasia was first diagnosed in cockles from Bantry Bay and Cork Harbour, Ireland in November 1982 and in the same year in Brittany, France (Barber, 2004; Romalde *et al.*, 2007; Le Grand *et al.*, 2010) (Figure 2b). It has since been recorded in cockles from other locations within or adjacent to the Irish Sea including the Burry Inlet in South Wales (Figure 1; Elliot *et al.*, 2012). Also referred to as haemic, haematic, or haemopoietic neoplasia or sarcoma, it was recorded firstly in 1969 in the oysters, *C. gigas* and *C. virginica* (Barber, 2004; Romalde *et al.*, 2007; Le Grand *et al.*, 2010). Since then this pathological condition has been reported in up to 20 bivalve species worldwide (Collins and Mulcahy, 2003; Romalde *et al.*, 2007). It is a proliferative disorder of unknown origin that affects the blood cells (haemocytes) (Figure 2b), and in the majority of cases it is lethal within 3–5 months (Twomey and Mulcahy, 1988; Romalde *et al.*, 2007; Le Grand *et al.*, 2010). Remission has been observed in *M. arenaria*

and *M. edulis*, but this is rare and occurs only in the initial stages of the disease (Le Grand *et al.*, 2010; Díaz *et al.*, 2011).

Various aetiologies have been suggested for disseminated neoplasia including biotoxins, pollution, stress, genetics and viruses (Díaz *et al.*, 2011). However, there is no clear evidence for a definitive cause, and Collins and Mulcahy (2003) proposed that several species-specific aetiologies might be in effect. In addition, the prevalence of disseminated neoplasia in cockles around Ireland has not been linked to pollution (Twomey and Mulcahy, 1988; Collins and Mulcahy, 2003). In recent years more credence has been given to viral origins of neoplasia as it has been transmitted between different bivalve species. Virus-like agents have been isolated from soft-shell clams and cockles, and retroviral activity has been shown in soft-shell clams and cockles (Romalde *et al.*, 2007; Le Grand *et al.*, 2010; Díaz *et al.*, 2011).

Disseminated neoplasia has been recorded in bivalve species experiencing mass mortalities including the cockle, *C. edule*, in the Irish Sea and nearby regions including Cork (Figure 2b; Morgan *et al.*, 2012) and the Burry Inlet (Elliot *et al.*, 2012). Surfaced (moribund) cockles in Cork were shown to have significantly higher levels of disseminated neoplasia than cockles that remained buried (Le Grand *et al.*, 2010; Morgan *et al.*, 2012).

Digenean parasites

Digenean trematodes have complex life cycles involving multiple hosts (Figure 2c). Usually the first intermediate host is a gastropod or bivalve, the second (intermediate) host a bivalve, and the third and final host (definitive host) a waterbird or fish (de Montaudouin *et al.*, 2009). Perhaps reflective of its extensive range, the cockle, *C. edule*, is utilized commonly as either a first or a second intermediate host for 16 species of digenean trematode (de Montaudouin *et al.*, 2009; de Montaudouin *et al.*, 2012). The use of the cockle as a second intermediate host is more widespread than as a first intermediate host (Lassalle *et al.*, 2007; de Montaudouin *et al.*, 2009; Fermer *et al.*, 2011). Two recent studies have identified seven (de Montaudouin *et al.*, 2009) or eight species of trematodes from Ireland (Ferner *et al.*, 2011) and three in the Burry Inlet (Elliot *et al.*, 2012) within cockle tissues. Digenean trematodes from the family Echinostomatidae are the most common trematodes utilizing cockles across their range, and they have been observed to be most common in Ireland (de Montaudouin *et al.*, 2009; Ferner *et al.*, 2011).

Meiogymnophallus (*Gymnophallus*) *minutus* (Figure 2c) is a commonly recorded parasite in terms of distribution and prevalence in the Irish Sea and in Europe in general (de Montaudouin *et al.*, 2009; Ferner *et al.*, 2011; Longshaw and Malham, 2012). It uses *C. edule* as a second intermediate host (Ferner *et al.*, 2011). Its first intermediate host is the bivalve *Scrobicularia plana*, and its definitive host is the oystercatcher, *Haematopus ostralegus* (Russell-Pinto, 1990). High intensities (e.g. 1000s of metacercariae per cockle) have been reported for *M. minutus* around the British Isles (Ferner *et al.*, 2011).

Depending on its role as a first or second intermediate host, cockles may experience various ill effects. As a first intermediate host, they may be inhabited by a large number of trematode sporocysts, which can lead to castration, and mortality under stressful conditions (such as thermal stress) as cockles are sensitive to extremes of temperature (Thieltges, 2006; Baudrimont and de Montaudouin, 2007; de Montaudouin *et al.*, 2009). Mortality events associated with trematodes in cockles have been documented; e.g. in the northern Wadden Sea cockle, mass mortality in

2004 was attributed to *Gymnophallus choledochus* with 71% of surfaced compared with 7.4% of buried cockles being parasitized (Thieltges, 2006). There are conflicting studies showing higher trematode prevalence or intensity in surfaced rather than dying cockles (Longshaw and Malham, 2012), but this may be host–parasite specific as it has not been shown for *M. minutus* in Ireland (Fermer *et al.*, 2011).

Infections by multiple trematode species can be present in one cockle creating a parasite infracommunity (de Montaudouin *et al.*, 2012). This parasite infracommunity may vary by location, and some parasites are found at certain latitudes only, e.g. *Himasthla elongata* has a more northerly distribution (de Montaudouin *et al.*, 2009).

Nematopsis spp.

Nematopsis schneideri and *N. portunidarum* are protozoan parasites of the phylum Apicomplexa and have been described in cockles (Carballal *et al.*, 2001). For these parasites, decapod crustaceans are the final definitive hosts, with cockles as intermediate hosts (Tuntiwaranuruk *et al.*, 2004). In recent years, there has been a reported increase in the prevalence and intensity of *Nematopsis* sp. in cockles in Cork, Ireland (Morgan, 2012). *Nematopsis* sp. was also found to be the most commonly encountered parasite in a recent study of the Dee Estuary and of the Burry Inlet in South Wales (Elliot *et al.*, 2012).

Other parasites

A range of other parasites and their pathologies has been described in bivalve molluscs, although greater attention has been given to neoplasia, trematodes and *Nematopsis* sp. as mortalities have been associated with them. For the sake of brevity, no description is given of the many other parasites and commensals.

Diseases of crustaceans

As already described in the section entitled *Shellfish production in the Irish Sea and surrounding regions*, the key crustacean species of economic importance in the Irish Sea are the European lobster, *Homarus gammarus*, the Norway lobster, *Nephrops norvegicus* (langoustines, Dublin Bay prawns) and the edible (brown) crab, *Cancer pagurus* (Tables 3 and 4; Figures 3 and 4). While a great deal is known about the diseases of edible crabs and langoustines, little is known about the disease repertoire of European lobsters. A comparison of these species appears to show that while crabs are subject to a wide range of micro- and macro-parasites (Stentiford, 2008), European lobsters would appear to be highly resilient to such agents. For example, there are several known viral diseases of crabs including *C. pagurus* bacilliform virus (Bateman and Stentiford, 2008), but no such conditions have been reported to affect this species of lobster. Whether this is simply as a result of a lack of studies or real biological differences in susceptibility to disease is unknown.

Pink (Bitter) crab disease

This disease is of greatest importance to the sustainability of commercial populations of edible crabs (*C. pagurus*) and langoustines (*N. norvegicus*) in the Irish Sea (Figure 3a). It is commonly called either “pink crab” disease as heavily affected animals take on a pink-orange colour (e.g. Stentiford *et al.*, 2002) or “bitter crab disease” because it can taint the meat in some species leaving an unpalatable taste (Shields, 2012). The causative agent of this condition is a parasitic dinoflagellate of the genus *Hematodinium* that was first

Table 3. Status of some key diseases of crustaceans in the Irish Sea and surrounding regions.

Disease	Disease-causing agent	Host range	Prevalence and severity of infection	Life stages affected	Potential effect on sustainability of fisheries	Current status of disease
Bitter/Pink crab disease	Dinoflagellate, <i>Hematodinium</i>	Wide range of decapod crustaceans; may be spread by other crustacean vectors including various species of zooplankton	High prevalence reported	Pre-recruits and recruits	Of key significance as the disease may be fatal and also spread to other crustaceans, hence providing a disease reservoir. Affected animals may not be marketable	Disease has probably spread across the northern hemisphere in last 50 years
Haplosporidiosis	Unidentified member of the phylum Haplosporidia	Only reported in <i>C. pagurus</i>	High prevalence	Pre-recruits and recruits	Unknown but probably fatal, no apparent loss of marketability of infected animals	Emergent disease?
Shell disease syndrome	Various chitinolytic and non-chitinolytic bacteria	Mostly affecting <i>C. pagurus</i>	Variable but mainly of significance to adults with protracted moult interval	Mainly recruits, may be more prevalent in males than females	Infection is not usually fatal but affects marketability	No indication of any major changes in prevalence and severity in Irish sea region
Vibriosis	Various species of vibrios	Wide	Low prevalence, can be high severity causing rapid mortality	Larval stages and juveniles?	Limited, but could give localized epizootics	Low prevalence in crab populations

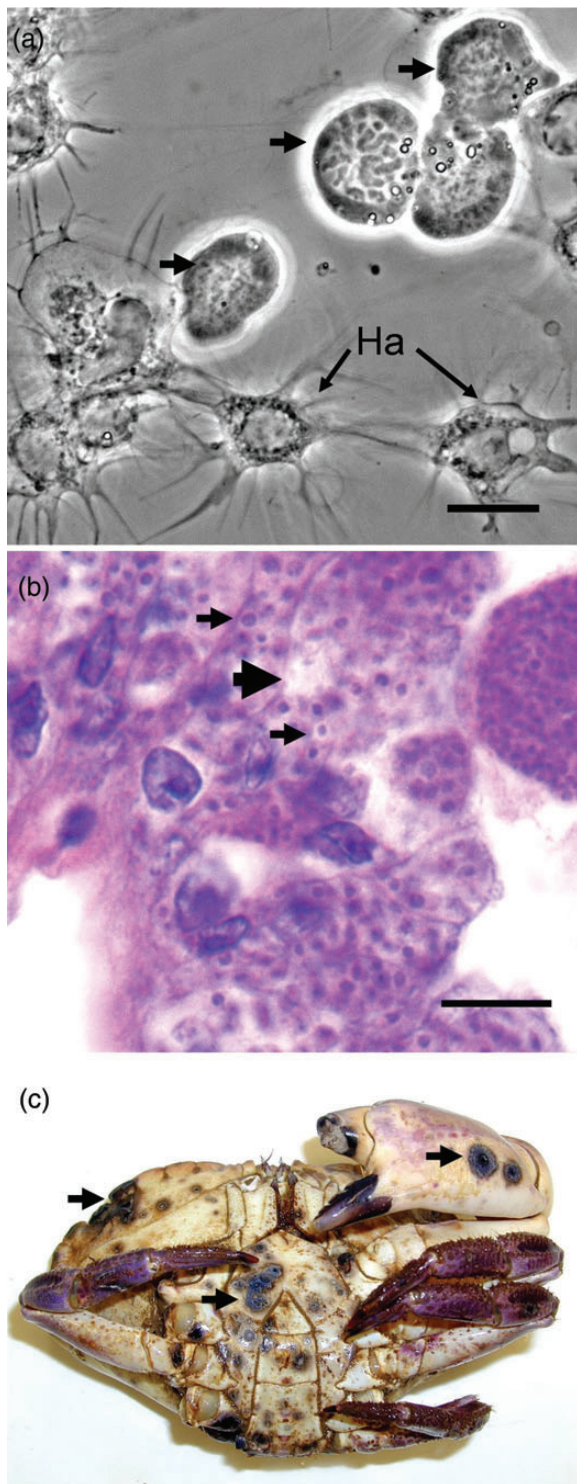


Figure 3. Examples of principal diseases of edible crabs found in the Irish Sea region. (a) Phase contrast micrograph showing the characteristic appearance of *Hematodinium* (unlabelled arrows) in the blood of an infected edible crab. The haemocytes (Ha) are easily distinguished from the parasites by their spreading behaviour. (b) Histological section through the antennal gland showing large numbers of haplosporidian-like parasites in the epithelial cells (small arrows) and apparent damage to the cells (large arrow). (c) Adult edible crab showing characteristic shell disease lesions (unlabelled arrows) on the ventral surface. Picture courtesy of Adam Powell. Scale bars = 10 μ m.

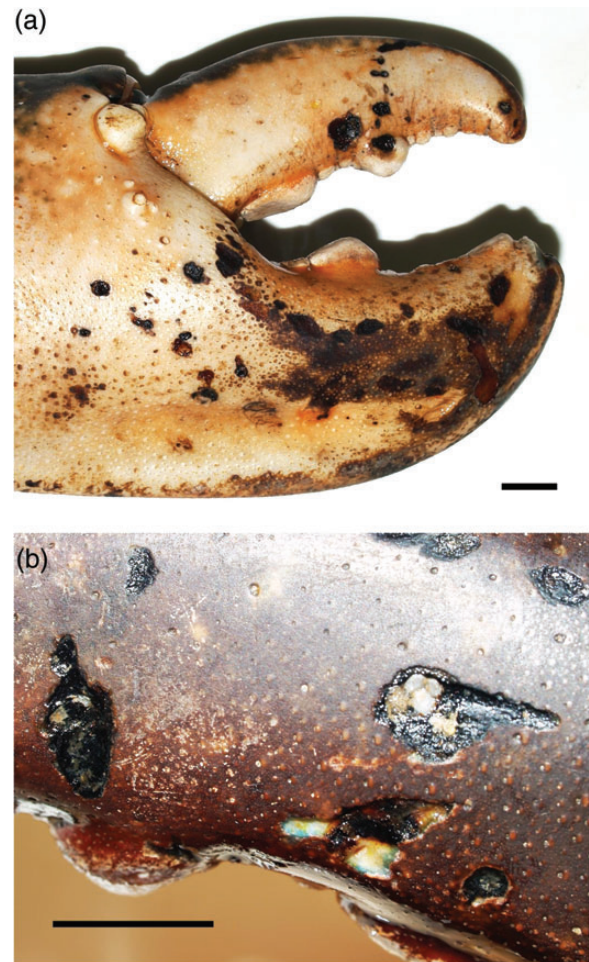


Figure 4. European lobster with superficial shell disease lesions on the claw. Scale bars = 1 cm.

reported in France by Chatton and Poisson (1931) in shore crabs (*Carcinus maenas*) but only at very low prevalence. Since that time, it has been found in over 40 different species of crustaceans and from many regions of the world (Morado, 2011; Morado *et al.*, 2012). Of significance is the observation that it causes epizootic episodes in crab and langoustine fisheries in several locations including Alaska in Tanner crabs (Meyers *et al.*, 1990), France in velvet swimmers (Wilhelm and Miahle, 1996), the USA in blue crabs (Messick and Shields, 2000; Lee and Frischer, 2004) and in the Clyde Sea (Scotland) in Norway lobsters (Field *et al.*, 1992; Tables 3 and 4). The serious effects of this disease on the sustainability of crustacean fisheries worldwide have been reviewed elsewhere (e.g. Stentiford and Shields, 2005; Morado *et al.*, 2010; Morado, 2011; Shields, 2011, 2012; Stentiford *et al.*, 2012), and readers are directed to these excellent and timely reviews. The potential importance of *Hematodinium* infections in crustaceans in the Irish Sea is less clear. As can be seen in Table 4, there are many reports showing variable prevalence levels of infection in edible crabs. The variability in the prevalence values is as a result of the seasonality of infection. For example, Ní Chualáin *et al.* (2009) found that the prevalence of infection of edible crabs surveyed in the Irish Sea was highly seasonal, with peak numbers of infected individuals found in the autumn–winter, which they concluded was driven by environmental temperature. In our surveys of pre-recruit

Table 4. The prevalence of *Hematodinium* infections in decapod crustaceans in the Irish Sea and surrounding regions.

Genus/species	Location	Time-scale of survey	Prevalence range (mean)	Method of detection	References
<i>Cancer pagurus</i> (adult)	English Channel (Guernsey)	n.d. ^a	n.d.	Histology and TEM ^a	Stentiford <i>et al.</i> (2002)
<i>C. pagurus</i> (adult)	English Channel (Guernsey)	n.d.	> 60%	Histology and TEM	Stentiford (2008)
<i>C. pagurus</i> (pre-recruit and adult)	English Channel (Weymouth Bay)	Apr 2008 – Mar 2009 (pre-recruits) Dec 2003 – Nov 2004 (adults)	0 – 10% (pre-recruit; 3%) 0 – 47% (adult; 15%)	Histology and TEM	Bateman <i>et al.</i> (2011)
<i>C. pagurus</i> (adult)	Irish Sea (Malin Head)	Sep – Nov 2008	9 – 13%	Blood smears, histology, PCR amplification	Ni Chualáin and Robinson (2011)
<i>C. pagurus</i> (adult)	Irish Sea and surrounding regions (three locations)	Nov 2004 – Dec 2007	> 46%	Blood smears	Ni Chualáin <i>et al.</i> (2009)
<i>C. pagurus</i> (adult)	Clyde Sea	June 2004 – May 2006	0 – 50% (18%)	PCR amplification	Hamilton <i>et al.</i> (2009)
<i>C. pagurus</i> (pre-recruit)	Pembrokeshire (Freshwater East, Pembroke Ferry)	Nov 2011 – Sep 2012		Direct observation of blood and histology	TJT (unpublished observations)
<i>C. pagurus</i> (pre-recruit)	Bristol Channel – Gower Peninsula (Mumbles Head, Oxwich Bay)			Direct observation of blood and histology	ALS (unpublished observations)
<i>Nephrops norvegicus</i>	Firth of Clyde	Mar 1988 – Mar 1989	0 – 51%	Body colour, blood preparations, histology and TEM	Field <i>et al.</i> (1992)
<i>N. norvegicus</i>	Clyde Sea	Feb 1998 – Aug 2000	> 35%	Body colour and pleopod examination	Stentiford <i>et al.</i> (2001)
<i>N. norvegicus</i> (zoéal)	Clyde Sea	June 2009	18%	PCR amplification	Hamilton <i>et al.</i> (2011)
<i>N. norvegicus</i>	Irish Sea	1994 – 2001	> 18%	Body colour, parasites in blood	Briggs and McAliskrey (2002)

^an.d. = not determined, TEM = transmission electron microscopy.

(juvenile) crabs in the intertidal environment in Pembrokeshire, West Wales and Gower, South Wales, higher infection prevalences were found in the spring to autumn months (ALS and TJT, unpublished observations). The full picture of the seasonal effect is, however, revealed by examining both the prevalence and intensity (i.e. parasite load) of infection during the year. For example, although low numbers of infected crabs were found in the late autumn–early winter at Mumbles Head in the Bristol Channel, these animals were all heavily infected and probably close to death. At this late stage in the infection cycle the parasites undergo a sporulation event to produce the infective dinospores that are then released by moribund crabs into the water column to presumably infect other susceptible crustacean species (Li *et al.*, 2010). Whether all crabs affected by *Hematodinium* ultimately die is not known, and so we cannot assume that infected animals observed in the field will ultimately die. If, however, such infections are always lethal, then the peak of infection recorded in each of the surveys, as summarized in Table 4, is indicative of the mortality in the population from this one disease alone. If this is the case, this parasitic condition will represent a serious threat to the sustainability of crustacean fisheries in the Irish Sea both now and in the future.

There is a possibility that some of the papers reviewed in Table 4 underreport the level of prevalence of infection (Beevers *et al.*, 2012). The least sensitive method is that based on body colour changes alone where only those animals heavily infected are judged as positive; many infected animals are missed by this method. At the other extreme, PCR-based amplification using a variety of primers based on the ITS1 region of *Hematodinium* have proven to be highly sensitive, specific and reliable (e.g. Li *et al.*, 2010; Hamilton *et al.*, 2011; Pagenkopp Lohan *et al.*, 2013). Indeed, according to Hamilton *et al.* (2011), the nested PCR method that they employed in their studies on the presence of these parasites in the water column is capable of detecting a minimum of only 10 *Hematodinium* nuclei in 1.5 l of sample. A recent study of *Hematodinium* in pre-recruit crabs from both Pembrokeshire and Gower (ALS and TJT, unpublished observations) compared a range of detection methods ranging from colour change, histology and PCR amplification. These authors concluded that simple observation of live preparations of blood for the presence of *Hematodinium* was a rapid and reproducible method (Figure 3a).

Haplosporidiosis-like condition in edible crabs

Bateman *et al.* (2011) were the first to report the presence of an unidentified haplosporidian-like parasite in the antennal gland complex of edible crabs collected from the Weymouth Bay region of the English Channel (see Figure 1 for location and Figure 3b). The prevalence of infection was found to be greatest in recruits ranging from 0% in March to 47% in May 2004. By comparison, pre-recruits showed generally lower prevalence levels ranging from 0 to 10% in August 2008. Studies by Thrupp *et al.* (2013) showed significantly higher prevalence levels for this infection in pre-recruit crabs collected from Pembrokeshire. The peak prevalence was 70% in March 2012 from pre-recruit crabs collected from one site. Identification of the causative agent of this infection was based on histology alone (Figure 3b), as attempts to develop PCR identification methods based on a wide range of primers designed from other studies on haplosporidiosis were unsuccessful (Thrupp *et al.*, 2013). While the outcome of this disease is unclear, its extensive parasitization and damage to the epithelial cells of the antennal gland (Figure

3b) may imply that at least some animals die. Neither this nor similar infections have yet been reported in any other crustaceans of economic importance in the Irish Sea region.

Shell disease syndrome

This is a potentially serious condition in some species of crabs, as it affects their marketability because the carapace becomes covered with unsightly blackened lesions (Figures 3c and 4) and the underlying meat may be tainted. However, unlike the diseases described previously, there is no evidence that it is contagious or results in mass mortalities. The prevalence of infection in edible crabs is variable throughout the Irish Sea and surrounding regions, with recorded “hotspots” in edible crabs onshore in Gower where at one site 55% of animals have been reported to be affected by this condition (Vogan *et al.*, 1999). The causative agent(s) of this syndrome have not been elucidated, but a variety of chitinolytic and non-chitinolytic bacteria are probably key players (Vogan *et al.*, 2008). What factors cause bacteria normally found in seawater to colonize the cuticle is unclear, but abrasion injuries and fighting are probably mainly responsible as initiators of the disease (Vogan *et al.*, 1999).

The severity of shell disease in European lobsters is significantly lower than in edible crabs. Here the lesions are smaller and normally do not appear to penetrate through the carapace (Figure 4; Wootton *et al.*, 2012). The lesions do not significantly affect the marketability of lobsters and are unlikely to cause changes to the quality of the underlying muscle.

Other diseases of crustaceans

Edible crabs have been reported to harbour a wide range of parasites and pathogens, but often these infections are at low levels (Stentiford, 2008) and, therefore, at present are unlikely to have a major impact on the sustainability of fisheries. For instance, in a survey of bacterial septicaemia in pre-recruit edible crabs from the Gower coast, South Wales, although small numbers of bacteria (including vibrios) were found in the blood, very few animals had significant numbers of bacteria in this tissue (Smith *et al.*, 2014). Of some potential interest are co-infections with a variety of pathogens. For example, edible crabs collected in the English Channel, Gower and Pembrokeshire have been found to exhibit co-infections caused by *Hematodinium* together with fungi (Stentiford *et al.*, 2003; Smith *et al.*, 2013). Recent studies have shown that the fungus in such associations belongs to the *Ophiocordyceps* clade (Smith *et al.*, 2013), which include a range of entomopathogenic fungi. The relationship between these two pathogens is unclear, but both appear to benefit from the association in their ability to overwhelm the host.

As already noted, in comparison with edible crabs and langoustines, European lobsters appear to be remarkably free from pathogens and parasites. For instance, there have been no reports of such animals being infected by *Hematodinium*, and initial attempts to artificially infect them with parasites taken from edible crabs failed (CE Davies, CLV and AFR, unpublished observations) suggesting that they may be naturally resistant to this key parasite. European lobsters are, however, susceptible to gaffkaemia, a bacterial disease caused by *Aerococcus viridans* var. *homari* (Cawthorn, 2011). Stebbing *et al.* (2012) showed that there have been some occurrences of gaffkaemia in European lobsters around the UK coastline, including some in South Wales, but these appear to be limited in prevalence, distribution and severity, and therefore pose little risk to fisheries. Finally, European lobsters have often

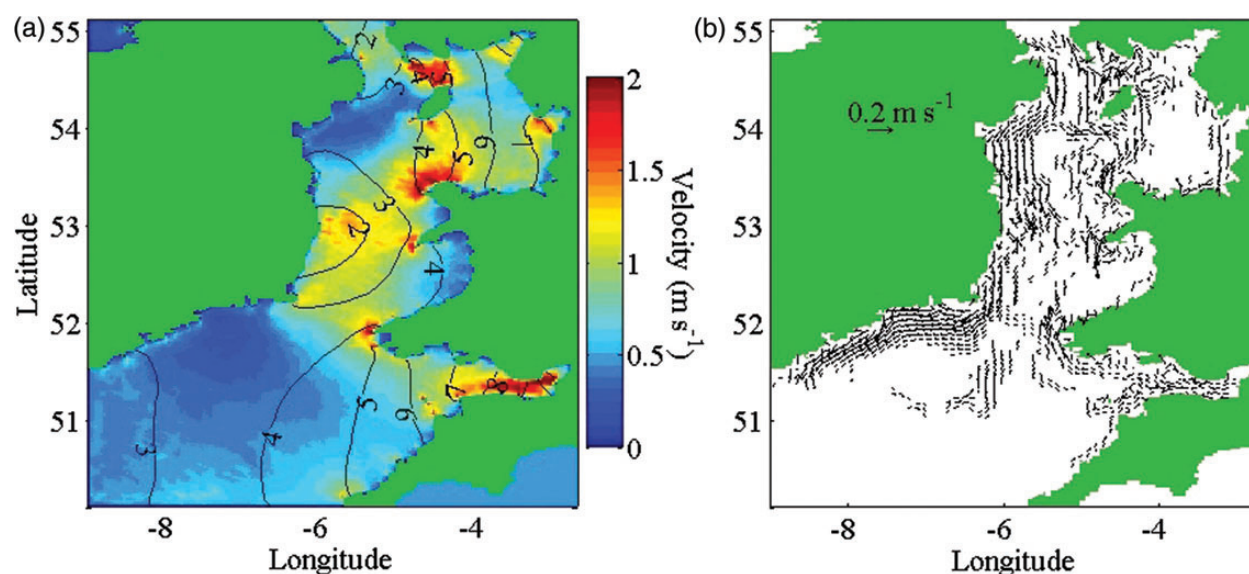


Figure 5. (a) Co-tidal contours of maximum tidal range (m), superimposed upon coloured contours of maximum depth-averaged scalar velocity (m s^{-1}) in the Irish Sea. (b) Depth-averaged residual currents over the period 01 June – 30 September 1990. Residuals less than 0.02 m s^{-1} have been removed for clearer visualization of the stronger currents. The western Irish Sea gyre, where density-driven currents flow anticlockwise between North Wales, Isle of Man and Ireland, can clearly be depicted. Other significant residuals flow west across the Celtic Sea front (St George's Channel) and clockwise around southeast Ireland towards the Celtic Sea [from Robins *et al.* (2013)]. Copyright 2014 by the Association for the Sciences of Limnology and Oceanography, Inc.

been found to harbour a copepod parasite (*Nicthoë astaci*) in their gills (Wootton *et al.*, 2011). The prevalence and severity of infection of lobsters from the Irish Sea is currently unknown, although it may damage its host by affecting the respiratory activity of the gills as a result of heavy infestation. The ectoparasite shows hematophagous feeding and thus it could also act as a vector of other diseases.

Oceanographic controls on shellfisheries and disease transmission in the Irish Sea and surrounding regions

Shellfish that are sessile as adults depend on larval-stage transport to mediate population dynamics (Knights *et al.*, 2006) and, consequently, spread of disease. As there is increasing evidence that at least some infectious diseases, including pink crab disease and vibriosis (see sections *Bacteria* and *Pink (Bitter) crab disease*), may be spread in host larvae or alternatively in a variety of mobile vector organisms, knowledge of their transport mechanisms in plankton is of importance. Lagrangian biophysical larval-tracking models have been used to identify drivers for larval dispersal within the Irish Sea. The Irish Sea is a highly energetic and hydrodynamically complex environment; atypical of other semi-enclosed mesoscale (10–1000 km) basins as a consequence of extremely large tidal ranges (exceeding 12 m in the Bristol Channel), regions of strong tidal flow (Figure 5a), and regions of strong residual flow (Figure 5b) (Simpson and Hunter, 1974; Robinson, 1979; Horsburgh and Hill, 2003).

Density-driven, residual currents (controlled by seasonal heating), as well as tidal currents, affect larval dispersal of hosts and potential vectors as much as coastal bathymetry and behaviour (e.g. spawning, swimming and settling strategies) (Hartnett *et al.*, 2007; Drake *et al.*, 2011; Coscia *et al.*, 2012; Robins *et al.*, 2013). For example, passive larvae disperse widely leading to high “wastage” off-shore; tidal-stream transport enables larvae to travel large distances, and thus potentially results in a far-reaching

spread of disease, whilst diel transport results in low dispersal and potentially low spread of disease (Fox *et al.*, 2009; Robins *et al.*, 2013). Hill *et al.* (1996) discovered that distributions of Norway lobster *N. norvegicus* larvae released in the Western Irish Sea gyre residual circulation show strong correspondence to the stratification field, with the gyre acting as a retention mechanism, therefore potentially restricting the spread of disease. Westward residual currents across St George's Channel have been shown to be important for cross-shelf transport (Hartnett *et al.*, 2007; Coscia *et al.*, 2012; Robins *et al.*, 2013). Secondary flow within estuaries (Nunes and Simpson, 1985) is also important for larval transport (Robins *et al.*, 2012) and spread of disease.

Consequently, while we can accurately predict the physical properties of the marine environment (e.g. Horsburgh and Hill, 2003; Robins *et al.*, 2013), larval dispersal models have been limited so far because species-specific migration is poorly understood (Knights *et al.*, 2006). Hence, without improved knowledge of the behaviour of individual host and disease vector species, it is difficult to model their likely spread within the Irish Sea region.

Potential changes in infectious diseases of shellfish in the Irish Sea as a result of climate change

Setting the scene—oceanographic models and disease dispersal now and in the future

Changes in global atmospheric conditions are predicted to influence the northwest European continental shelf environment (Holt *et al.*, 2010). Consequently, our present knowledge of population dynamics, movement of different species and the potential for spread of diseases within the Irish Sea, may not hold for future climatic conditions. How species adapt to a changing climate is therefore of primary concern for predicting the spread of diseases and formulating mitigation strategies.

Oceanographic changes in the Irish Sea over the next century will occur, mainly due to increasing temperatures and rising sea levels.

Table 5. Potential implications (*and confidence level of predictions*) of varying climate change scenarios on the prevalence and severity of shellfish diseases in the Irish Sea and associated regions.

Disease	Increase in sea surface temperature	Increased freshwater runoff (reduced salinity)	Acidification	Changes in zooplankton and phytoplankton populations	Temperature-induced environmental stress affecting immune reactivity
Pink crab disease in crabs and langoustines	Limited, as disease not thought to be affected by temperature increase (Morado <i>et al.</i> , 2010). <i>High confidence</i>	Limited reduction in infection based on climate change models. Infective stage of parasite inactivated in low salinities (Coffey <i>et al.</i> , 2012). <i>Limited confidence</i>	?	<i>Hematodinium</i> may be harbored in plankton (Hamilton <i>et al.</i> , 2011). <i>Limited confidence</i>	<i>Hematodinium</i> appears to evade immune recognition, and therefore temperature unlikely to be a major driver of disease susceptibility. <i>Moderate confidence</i>
Haplosporidiosis in crabs	?	Limited (Thrupp <i>et al.</i> , 2013). <i>High confidence</i>	?	?	?
Bacterial septicaemia (including vibriosis) in crabs and molluscs	Increases in numbers of vibrios in seawater resulting in elevation of prevalence and severity of disease (e.g. Vezzulli <i>et al.</i> , 2012, 2013). <i>High confidence</i>	Reduction in vibrio abundance. In estuarine conditions, vibrio numbers generally decrease with lower salinities (e.g. Hsieh <i>et al.</i> , 2008). <i>High confidence</i>	?	Elevation or reduction in infections, as some vibrios have been found to attach to the these as part of their environmental survival strategy (e.g. Colwell, 1996). <i>Limited confidence</i>	Defence against bacterial pathogens, such as vibrios, is influenced by temperature (Volety <i>et al.</i> , 1999). <i>High confidence</i>
<i>Bonamia ostreae</i> in the flat oyster <i>Ostrea edulis</i>	Mortality correlated with higher seawater temperatures (Engelsma <i>et al.</i> , 2010). <i>High confidence</i>	Mortality correlated with lower seawater salinities (Engelsma <i>et al.</i> , 2010). <i>Moderate confidence</i>	?	Oysters are more susceptible to infection in seasons with reduced food availability	?
Ostreid herpesvirus 1 (OsHV-1) and variants in molluscs	OsHV-1 μ Var is more virulent when seawater temperatures exceed 16°C. <i>Moderate confidence</i>	?	?	?	?
Digenean infections of molluscs	Increases due to increased infectivity (Poulin and Mouritsen, 2006). <i>High confidence</i>	Long-term reduced salinity may reduce the number of cercaria released (Lei and Poulin, 2011). <i>High confidence</i>	Potential reduction in transmission success (MacLeod and Poulin, 2012). <i>Limited confidence</i>	?	Temperature affects total blood cell count, which may have implications for host susceptibility (Cheng <i>et al.</i> , 2004). <i>Limited confidence</i>

Note, this table is not designed to be an exhaustive review of all potential diseases that may affect shellfish in the Irish Sea in several decades' time.

Sea temperatures will warm substantially (21st century trend: $\sim 0.3^{\circ}\text{C}$ per decade; Holt *et al.*, 2010), generating larger frontal density gradients and strengthening associated baroclinic currents. It is not clear whether strengthening gyre circulation will increase retention (e.g. Hill *et al.*, 1996) and reduce potential disease spread, or cause increased dispersal and increased spread of disease. It may ultimately depend on the migration of the specific species. Where baroclinic currents, such as the Celtic Sea front, act as conduits for larval transport (Coscia *et al.*, 2012), strengthening flows will extend dispersal distances (within the residual pathway), leading to an increased risk of spread of diseases. However, for passive species, diseased individuals may become more entrained within the current and, hence, spread out less. Another effect of increased temperatures relates to egg development, spawning season, pelagic larval duration, and dispersal patterns, all of which potentially affect the spread of diseases within an area or species. For example, non-native species from warmer climates, such as Pacific oysters, may colonize waters of northern Europe (Hellmann *et al.*, 2008) and bring with them new disease conditions.

Sea levels are predicted to rise by 1 m in the next 100 years (Defra, 2006), which may reduce tidal ranges slightly and reduce coastal velocities to a greater extent (Robins and Davies, 2010). However, away from the coast, velocities will not change significantly due to sea-level rise; hence patterns of larval dispersal and potential spread of disease are unlikely to change dramatically.

Other processes will affect future circulations less. For instance, interannual variability in the timing and strength of stratification in the Irish Sea is relatively small when compared with seasonal change (Young and Holt, 2007); negligible change in wind stress is predicted (Lowe *et al.*, 2009; Holt *et al.*, 2010), and freshwater input into the Irish Sea is low (Hill *et al.*, 1996), implying that the effects of changing rainfall on shelf circulation will be small. Robins *et al.* (2013) believe that energy within the Irish Sea will increase, mainly as a consequence of warming sea temperatures, which will on the whole increase larval dispersal distances, leading to the potential for increased spread of disease. However, it is unknown how climate change will specifically affect larval dispersal for different species and different environments.

Climate change and disease

This section aims to review the potential changes of disease agents in shellfish in the Irish Sea in response to the climate change scenarios already reviewed. Table 5 summarizes the likely outcomes of the predicted changes in the oceanographic and biological parameters for each of the main diseases of crustaceans and bivalve molluscs already reviewed in sections *Diseases of crustaceans* and *Oceanographic controls on shellfisheries and disease transmission in the Irish Sea and surrounding regions*. It also attempts to give a “confidence level” for each conclusion drawn using the approach of the Marine Climate Change Impacts Partnership Report Cards (MCCIP, 2012). For some diseases, such as haplosporidiosis in crabs and molluscs, it is impossible to make any predictions because we still have little data on the relationship between the causative agents and environmental variables. For others, including *Hematodinium*, *Vibrio* spp. and some viral infections, where more baseline data are available, predictions can be made with variable levels of confidence. It should be pointed out that although the diseases currently affecting shellfish populations are reviewed in Table 5, climate change may cause the influx of either diseases not present in the Irish Sea or of those currently at low prevalence and of low severity.

In the case of pink crab disease, caused by *Hematodinium*, a recent review by Shields (2011) summarized the environmental conditions likely to favour the successful development and transmission of the parasite to its hosts. The main environmental driver for successful parasitization appears to be reduced exposure to ocean circulation leaving the parasites and their hosts in close proximity. This explains why many outbreaks of this disease have been found in fjords or shallow, poorly drained bays. The recent finding, that *Hematodinium* may be associated with free-swimming larval stages of its host or other members of the plankton community (Hamilton *et al.*, 2011; Pitula *et al.*, 2012), has implications for transmission of disease. Models for changes in larval distribution in response to climate change scenarios, such as those already described, are therefore of key importance in the understanding of likely changes in ocean circulation. In the intertidal zone, where pre-recruit crabs may first come into contact with *Hematodinium*, the predicted limited increase in freshwater runoff (resulting from an unstable climate with higher rainfall) is unlikely to dramatically reduce the impact of the disease as a consequence of rapid inactivation of infective dinospores in lower salinity conditions (Coffey *et al.*, 2012).

Vibriosis is one of the diseases that may be profoundly affected by climate change (Table 5). There are over 30 species of vibrios found in the aquatic environment, including human and shellfish pathogens. Vibrios grow preferentially in warm waters ($>15^{\circ}\text{C}$) and at low salinity (<25 ppt NaCl) (Baker-Austin *et al.*, 2010; Vezzulli *et al.*, 2013). The predicted warming and reduced salinity of coastal waters in temperate regions will provide new areas for the natural occurrence of pathogenic strains. Warming patterns have been related to the emergence of *Vibrio* outbreaks in molluscs in temperate and cold regions, such as in Chile (Gonzalez-Escalona *et al.*, 2005), Peru (Martinez-Urtaza *et al.*, 2008), Israel (Paz *et al.*, 2007), the US Pacific Northwest (CDC, 2008) and northwest Spain (Baker-Austin *et al.*, 2010), but to our knowledge there are no such reports in the Irish Sea region.

Colwell and co-workers over the last two decades have brought to light the role of plankton (mainly copepods) as reservoirs of *V. cholerae* in the aquatic environment (e.g. Colwell, 1996; Stauder *et al.*, 2012). Therefore, changes in plankton communities, such as those already reported in the UK and Ireland (e.g. Kennington and Rowlands, 2006; Silke *et al.*, 2012), may have implications for the number of types of vibrios in these environments (Vezzulli *et al.*, 2013). However, our understanding of the potential relationship between vibrios associated with outbreaks of shellfish diseases (including *V. harveyi*, *V. (Listonella) anguillarum*, and *V. pectenica*) and the wide range of phyto- and zoo-plankton present is poorly understood. A much greater understanding is required if we are to develop an appreciation of how plankton changes driven by climate change might influence the dynamics of vibrio populations. The studies of Vezzulli and colleagues in the Mediterranean (Vezzulli *et al.*, 2010) and the North Sea (Vezzulli *et al.*, 2012, 2013) have explored the effects of elevated sea surface temperatures on the distribution and pathogenicity of vibrios. In the North Sea they were able to use formalin-preserved plankton samples from the last 40 years collected by continuous plankton recorders as a source of genomic DNA from vibrios and other bacteria. They found increases in vibrios that were at least partially linked to the increase in sea surface temperature. Small increases in seawater temperature in coastal regions may tip the balance in favour of vibrios such that they can overwhelm their compromised hosts as a result of increased bacterial growth and an upregulation of virulence

genes (Kimes *et al.*, 2012). This may lead to periodic epizootics of vibriosis in summer months, especially in shallow water, estuaries and the intertidal environment. The shellfish most likely to be at risk are cockles, pre-recruit crabs and oyster spat, and the adult oysters that inhabit this environment.

In general, mortalities associated with viruses in the marine ecosystem are expected to arise sporadically when conditions become less favourable for the host. Physiological stress induced by significant increases in temperature may cause the host to become immune-compromised and unable to suppress an infection (Suttle, 2007). In the case of OsHV-1 and variants, such mortality events, occurring in an intensively cultured commercial bivalve, have become more regular and widespread, and may become a greater problem with climate change impacts, particularly those associated with temperature (Repamo, 2009; Segarra *et al.*, 2010; Cotter *et al.*, 2010; EFSA, 2010).

The emission and transmission of trematode cercariae between molluscan hosts is temperature dependent (Desclaux *et al.*, 2004; Gam *et al.*, 2008). In temperate areas such as the Irish Sea region, cercariae may be transmitted to new hosts throughout the spring to autumn (Thieltges, 2008). It has been suggested that the annual period for production of cercariae is correlated with temperatures $>12^{\circ}\text{C}$ (Gam *et al.*, 2008). Shedding of infective stages and the success of transmission is more fruitful as temperatures increase, until a species-dependent threshold is reached (Jensen *et al.*, 1999; Thieltges, 2008). However, the period of viability of cercariae declines with increasing temperatures (Jensen *et al.*, 1999; Gam *et al.*, 2008). Increasing temperatures may lead to habitat range expansions of trematodes. For example *Labratrema minimus* is now being found further north within the North Sea area (Gam *et al.*, 2008). In addition to trematode burden, cockle mortalities may be exacerbated by environmental stress (Thieltges, 2006). For instance, in the case of cockle summer mortality syndrome, documented in the Wadden Sea, temperature was suggested as a factor that may have contributed to stress (Thieltges, 2006).

Concluding remarks

This review has summarized the current status of diseases in a number of commercially important bivalve molluscs and crustaceans in the Irish Sea and adjacent regions. While many of the shellfish have been found to harbour co-infections by both parasites and pathogens, only in a few cases is there evidence of host mortality likely to result in significant economic losses. Some infectious conditions, including pink (bitter) crab disease in crustaceans and infection caused by ostreid herpesvirus 1, are likely to represent serious threats to the sustainability of shellfish production in this region now and in the future. Our knowledge of the importance of co-infections caused by a wide range of micro- and macro-parasites in some species (such as edible crabs and cockles) is extremely limited. While there are good models predicting how climate change will affect both physical and chemical oceanographic processes, our lack of understanding of how infectious diseases can be transferred by pelagic invertebrates, either as reservoirs or hosts, hampers our ability to make confident predictions of how the diseases currently observed in shellfish populations in the Irish Sea will change in during this century.

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