UNIVERSITY OF SOUTHAMPTON

FACULTY OF NATURAL AND ENVIRONMENTAL SCIENCES

Ocean and Earth Science

In collaboration with:

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Biology and ecology of the siphonophore *Muggiaea atlantica* in the northeast Atlantic

By

Michael Blackett

Thesis for the degree of Doctor of Philosophy

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ABSTRACT

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In many regions of the world the abundance and distribution of jellyfish is increasing. These changes have important consequences for marine ecosystems and the services that they provide to humans. It is a fundamental goal of marine ecologists to develop understanding of how jellyfish populations respond to environmental change. Two key processes are involved in the regulation of jellyfish populations: local demographics (i.e. production and mortality) and dispersal (i.e. immigration and emigration). A failure to discriminate between the contributions of these two fundamental processes can obscure the specific environmental factors that drive changes in jellyfish populations, impeding understanding.

This thesis aims (1) to assess recent changes in the abundance and distribution of *Muggiaea atlantica* in the coastal waters of the United Kingdom; and to (2) investigate the influence of environmental variability on both the biological (i.e. demography) and physical (i.e. dispersal) processes that drive these changes. This study utilised data collected from a network of coastal monitoring stations, together with data on a range of local and regional hydroclimatic environmental factors.

I show that since the late 1960s, there has been a progressive northward extension of this species' distribution from its centre of population in the Bay of Biscay and Iberian Coast region. These changes involved the establishment of a resident population in the Western English Channel (WEC) and the subsequent development of transient seasonal populations on the east and west coasts of Scotland. In the WEC the *M. atlantica* population was capable of overwintering, sustaining a resident population irrespective of immigration. This population was modulated primarily by the availability of suitable local environmental conditions that influenced demography (temperature and food availability) and secondarily by changes to water circulation patterns that influenced its dispersal. In contrast, in Scotland *M. atlantica* was incapable of overwintering and its population was primarily modulated by immigration and secondarily by the availability of suitable local environmental conditions. On the west coast of Scotland, the European Slope Current (ESC) was identified as the source of immigration, whereas on the east coast the mechanism of immigration was not identified. Despite the importance of the ESC as a transport mechanism from the WEC region, a direct source-sink relationship between the WEC and Scottish coastal waters was not clearly demonstrated, suggesting the importance of a network of sources. Key environmental requirements for local *M. atlantica* production were consistent between the localities, these were: a critical limit of 10 °C for reproduction, with an optimum of 13–15°C, together with the availability of small copepod prey. Changes in the timing of this critical temperate modulated trophic phasing with copepod prey, influencing the phenology of the blooms of *M. atlantica*. This thesis provides the basis for developing a mechanistic understanding of the factors that modulate distribution in a species of jellyfish. The principles and methods used could be applied to better understand changes in the abundance and distribution of *M. atlantica* in other areas, and also for different species of jellyfish.

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Declaration of authorship

I, Michael Blackett declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

"Biology and ecology of the siphonophore *Muggiaea atlantica* in the northeast Atlantic"

I confirm that:

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2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
4. Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis is entirely my own work;
5. I have acknowledged all main sources of help;
6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
7. Parts of this work have been published as:
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    - Blackett M, Lucas CH, Harmer RA, Licandro P (2015) Population ecology of *Muggiaea atlantica* (Cnidaria, Siphonophora) in the Western English Channel. Marine Ecology Progress Series 535:129–144
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Signed:

Date: 07/01/16

List of abbreviations and definitions

ATL – *Muggiaea atlantica*

BADC – British Atmospheric Data Centre

CDF – cumulative distribution function

CI – confidence interval

CN – carbon and nitrogen

CPR – continuous plankton recorder

CTD – conductivity temperature depth (instrument)

ESC – European slope current

EVF – eigenvector filtering

GHG – greenhouse gas

G1 – group 1

G2 – group 2

G3 – group 3

G4 – group 4

HAC – heteroscedasticity and autocorrelation consistent covariance estimators

IP – informative period

IPCC – intergovernmental panel on climate change

KOC – *Muggiaea kochi*

LE – Loch Ewe

LSSW – low salinity surface water

MBA – Marine Biological Association of the United Kingdom

MD – missing data

MLD – mixed-layer depth

NAO – North Atlantic Oscillation

PASTECS – package for analysis of space-time ecological series

PC – principal component

PCA – principal component analysis

PRY – prey

QI – quantity of information

SAL – salinity

SCUBA – self-contained underwater breathing apparatus

SD – standard deviation

SH – Stonehaven

SST – sea surface temperature

STATIS – *structuration des tableaux à trois indices de la statistique* [structuring three way statistical tables]

T – temperature

WEC – Western English Channel

WP2 – working party 2

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Chapter 1

Introduction

1. Introduction

1.1 The global importance of plankton

Plankton represent a key functional group in the global marine ecosystem. Photosynthesis by phytoplankton accounts for approximately half of global primary production (Longhurst et al. 1995; Field et al. 1998) and this energy forms the basis of the oceanic food web (Sigman & Hain 2012). As the major grazers of the ocean, zooplankton provide the fundamental trophic link for the transfer of energy from primary production to consumers at higher trophic levels (Steele 1974; Cushing 1975). Ultimately, plankton production supports the diverse array of organisms within pelagic ecosystems (Pomeroy 1974; Frederiksen et al. 2006) and in turn provides the export of organic material that sustains most benthic marine communities (Turner 2002; Ruhl & Smith 2004). The energy from planktonic production propagates through ocean food webs through a variety of complex trophic interactions (Greve & Parsons 1977; Young et al. 2015). Differences in the composition of plankton communities influence these trophodynamics, modulating the structure of ocean food webs and consequently the energy transfer efficiency within them (Steele 1974; Greve & Parsons 1977). As a result, plankton community dynamics affect the structure, functioning and productivity of the global ocean ecosystem.

Plankton also play a central role in the ecosystem processes that modulate biogeochemical cycling in the oceans. Phytoplankton fix ~40% of the total atmospheric carbon sequestered by the global biosphere (Falkowski 1994). As organic material is denser than water, the ultimate fate of this biogenic carbon is to sink from the surface ocean layer in the form of the aggregates of plankton, marine snow, and the faecal pellets of zooplankton. The majority of this material is remineralised by the heterotrophic bacterial component of the plankton as it descends through the water column and is recycled as regenerated primary production (Azam et al. 1983). However, a fraction of this organic material reaches the sea floor, driving the long-term sequestration of carbon from the atmosphere to deep-sea waters and sediments (Volk & Hoffert 1985). Although only <1% of this biogenic carbon reaches the ocean floor (Sigman & Hain 2012), this 'biological pump' represents the largest carbon sink in the global carbon cycle (Battle et al. 2000). The diel vertical migration of plankton also contributes to the removal of carbon from surface waters and its release in deeper waters through their respiration (Longhurst et al. 1990). Another important role of plankton in the modulation of atmospheric carbon is the effect of calcifying plankton species on the global carbonate cycle, which influences water chemistry and the capacity for the oceans to absorb atmospheric carbon (Schiebel 2002). Different types of plankton influence these processes in different ways due to the diversity of their biogeochemical roles, physiological and environmental requirements, productivity and biomass; all modulated by the trophic interactions within ocean food webs (Quéré et al. 2005).

These vital ecosystem roles make plankton of fundamental importance to Earth's climate system and the functioning of the global marine ecosystem. The marine environment provides ecosystem services of immense economic and societal value to humans – with an annual global valuation of ~21 trillion USD (Costanza et al. 1998). The abundance and composition of plankton influences the recruitment and abundance of many exploited fish species, such as cod (Beaugrand et al. 2003; Nicolas et al. 2014), which represent a vital resource for millions of people around the world (Holmlund & Hammer 1999; Kurlansky 2011). Plankton also influence the distribution and abundance of numerous charismatic marine animals, like whales (Ari et al. 2006) and turtles (Houghton et al. 2006), which offer rich aesthetic, societal and economic benefits (e.g. Wilson & Tisdell 2001). The importance of plankton in biogeochemical cycling also makes them a critical factor in our understanding of global climate change, which is what the world's population perceives as the top global threat (Carle 2015).

1.2 Plankton, climate change and the anthropocene

There is unequivocal evidence that Earth's climate system is in a state of ongoing change. Over the period 1880 to 2012 the Earth's surface has warmed by an average of 0.85 °C (Fig. 1.1A), with the last 30 year period likely to be the warmest in the Northern Hemisphere in the last 1400 years (IPCC 2014). The oceans have absorbed the majority (~93%) of this increased energy in the climate system (Rhein et al. 2013; IPCC 2014). The upper ocean (0–700 m) has warmed significantly at a rate of 0.015 °C per decade from 1971–2010, and was probably warming since 1870 (Rhein et al. 2013). The strongest warming signal has been identified in the surface waters (0–75 m), with a recorded increase of 0.11 °C per decade since 1971 (Rhein et al. 2013). This warming is thought to have also extended to deeper waters, with significant increases recorded between 700–2000 m and 3000–4500 m (Rhein et al. 2013).

A number of important hydroclimatic changes have been associated with Earth's changing climate over the last 40 years (Rhein et al. 2013). Ocean warming has caused a 4% increase in the thermal stratification of the upper ocean (0–200 m) as well as global mean sea level rises from 1901–2010. The combined effects of long-term surface warming together with changes in evaporation and precipitation ($E - P$) are likely to have caused changes in ocean water mass properties, which affect global ocean circulation. The strengthening of the subtropical gyres in the North and South Pacific since 1993 has been associated with these $E - P$ changes, although this could also be due to basin-scale changes in wind stress and mean wave height.

The global human population has increased from ~700 million at the start of the industrial revolution (Durand 1977) to ~2.5 billion in the 1950s to 7 billion by 2011 (US Census Bureau 2015). As a result of this massive increase in population "humans and our societies have become a global geophysical force" (Steffen et al. 2007), leading to the introduction of the term 'the anthropocene' to describe the current geological epoch (Crutzen & Stoermer 2000). Anthropogenic greenhouse gas (GHG) emissions have increased dramatically since the pre-industrial era (Fig. 1.1B), leading to the highest atmospheric concentrations of GHGs in at least the last 800,000 years (IPCC 2014). Approximately 50% of the anthropogenic CO_2 emissions since the industrial revolution have occurred in the last 40 years (Fig. 1.1C). The oceans have taken up approximately 30% of this anthropogenic carbon, which has caused a 26% increase in ocean acidity since the pre-industrial era. It is extremely highly likely that this rise in the atmospheric concentration of GHGs, along with other anthropogenic drivers, has been the dominant cause of the observed warming and associated oceanic changes observed over the same 40-year period (IPCC 2014). In addition to the effects of climate change (Fig. 1.2A), several other anthropogenic activities (i.e. fishing, chemical fertilisation, pollution and coastal development) have had a significant cumulative effect on the global ocean environment (Halpern et al. 2008). No area of the marine environment is unaffected by human influence (Fig. 1.2B), and a large proportion (41%) of ecosystems have been strongly affected by multiple drivers (Halpern et al. 2008; Halpern et al. 2015).

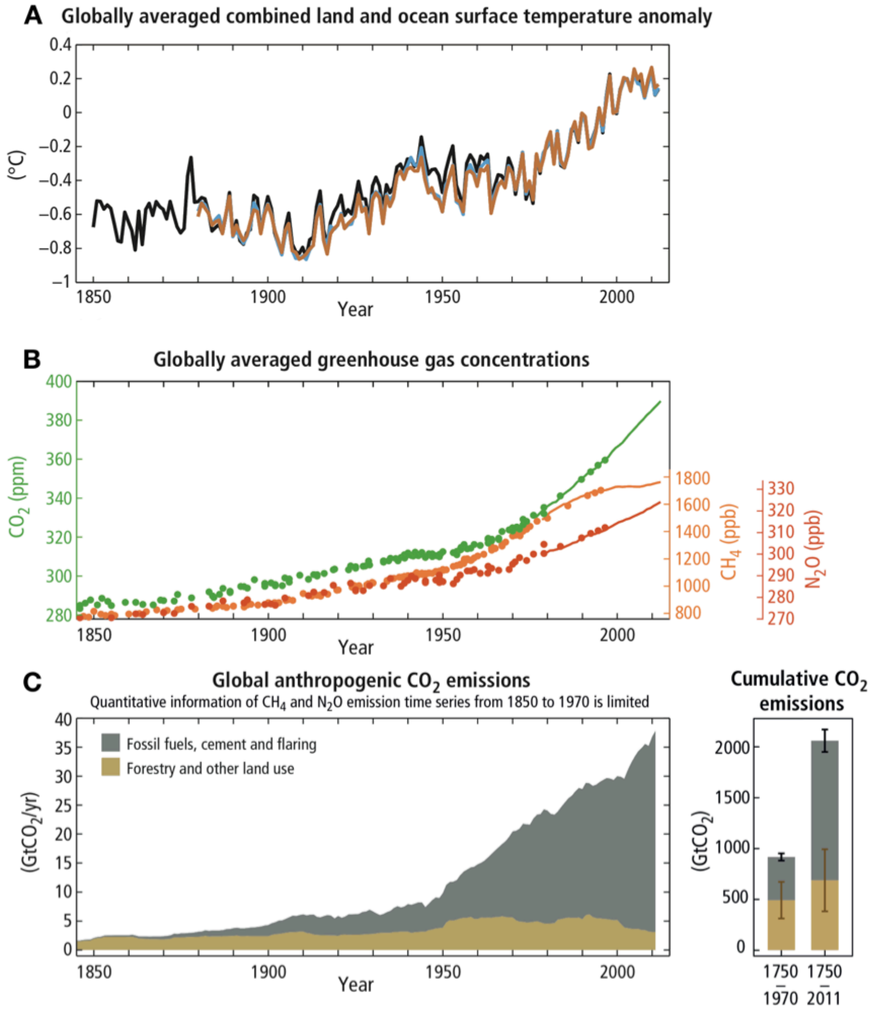

Fig. 1.1. (A) Average annual combined global land and ocean surface temperature anomalies relative to the average over the period 1986 to 2005; the different colours represent different data sets. (B) Atmospheric concentrations of the greenhouse gases carbon dioxide (CO_2, green), methane (CH_4, orange) and nitrous oxide (N_2O, red) determined from ice core data (dots) and from direct atmospheric measurements (lines). (C) Global anthropogenic CO_2 emissions from a range of sources. Cumulative CO_2 emissions are shown as bars on the right hand side (uncertainty is represented by whiskers). Adapted from IPCC (2014).

Plankton are highly sensitive to physical environmental changes. They are ectothermic organisms and consequently all aspects of their physiology are influenced by environmental temperature (e.g. Huntley & Lopez 1992). In addition, plankton have short life cycles and this results in a tight coupling with environmental conditions (e.g. Hooff & Peterson 2006). Climatic variability has well documented effects on plankton, including abundance and productivity (Hays et al. 2005; Behrenfeld et al. 2006; Costello et al. 2006), geographical distribution (Beaugrand et al. 2002; Parmesan & Yohe 2003; Hays et al. 2005), and phenology (Edwards & Richardson 2004; Ji et al. 2010). Through its effects on plankton, climate variability influences the structure and dynamics of marine ecosystems, determining the quantity and flow of energy through the oceanic food web. In summary, climate changes significantly affect plankton, while at the same time plankton influence climate. The interactions may represent complex feedback systems that act to either increase or decrease the rate of climate change (Rhein et al. 2013; IPCC 2014). In order to improve our understanding of the marine ecosystem we need to develop our knowledge of the roles of the different components and the effects of climate variability on them (e.g. Quéré et al. 2005).

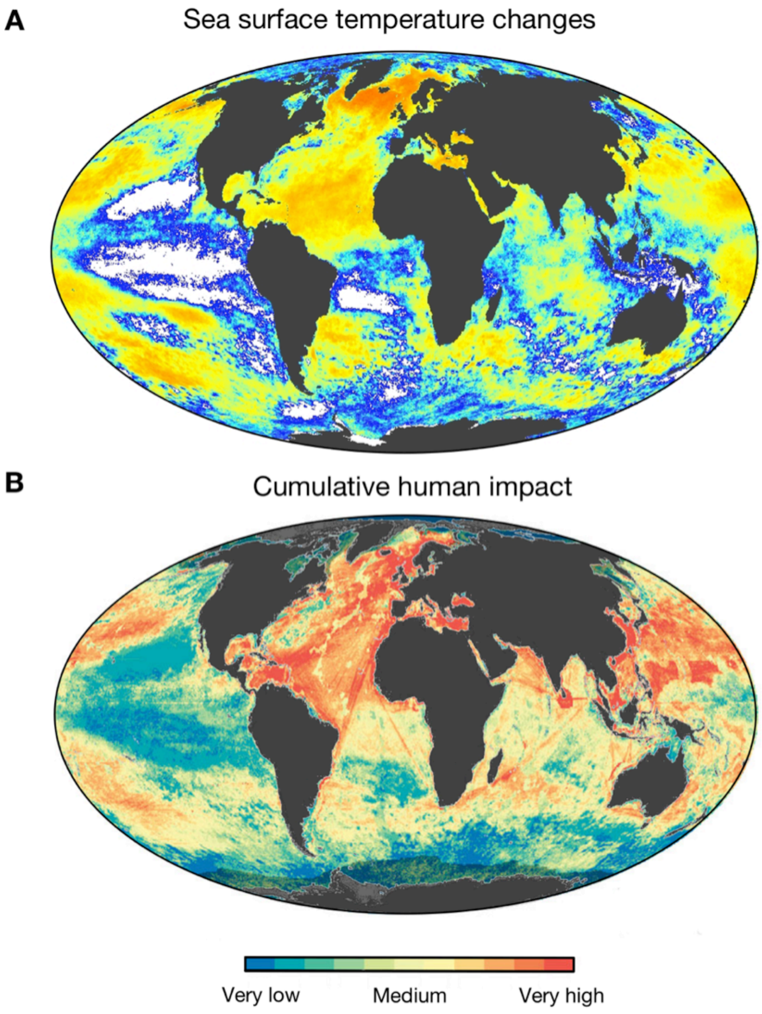

Fig. 1.2. Global maps of (A) Sea Surface Temperature changes and (B) cumulative anthropogenic impact from a range of human activities. Adapted from Halpern et al. (2008, 2015).

1.3 The gelatinous zooplankton

The 'gelatinous zooplankton' is a general term used to describe the polyphyletic group of marine organisms that share the convergent features of gelatinous structure, transparency, fragility, and planktonic existence (Haddock 2004). The term encompasses medusae, siphonophores, ctenophores, radiolarians, and also planktonic representatives of the tunicates, molluscs, and worms. Throughout this thesis I only consider members of the gelatinous zooplankton belonging to the phyla Cnidaria and Ctenophora (i.e. medusae, siphonophores and ctenophores), and will use the colloquial term 'jellyfish' as a synonym.

Jellyfish have been a feature of marine ecosystems for at least the last 500 Mya (Hagadorn et al. 2002; Cartwright et al. 2007) and are ubiquitous in the contemporary global marine environment (Fig. 1.3) (Lucas et al. 2014b). Despite their ubiquity, jellyfish represent an enigmatic and poorly understood component of pelagic ecosystems. This paucity of knowledge can be attributed to a number of different factors. The fragility of jellyfish makes collection by traditional sampling methods challenging (Pugh 1989; Haddock 2004) and their identification—particularly when dealing with fragmented specimens—is challenging, often requiring specialist taxonomic knowledge (e.g. Boero 1996). Consequently, there has been a historical tendency to exclude jellyfish from most routine sampling programmes (Pugh 1989), resulting in a lack of long-term records on their abundance and distribution compared to other more robust animals such as crustacean zooplankton and fish. Their fragility poses particular problems when attempting to collect jellyfish for laboratory-based experiments (but see Raskoff et al. 2003). This has led to poor understanding of the functional biology and ecophysiology of most species of jellyfish, in contrast to other zooplankton taxa, such as the Copepoda (e.g. Mauchline 1998). Jellyfish are nutritionally poor prey due to their high water (>97%) and low carbon content (0.9–2.5%) (Lucas et al. 2011) compared to non-gelatinous zooplankton (Kiørboe 2013) and fish (Sterner & George 2000). This has resulted in a perception that they have few predators and are trophic 'dead ends' (e.g. Pauly et al. 2009). These factors historically contributed to a low recognition of their ecological importance, resulting in a low research prioritisation and their continued omission from routine zooplankton sampling (e.g. Heinle 1965 cited in Brotz, 2012).

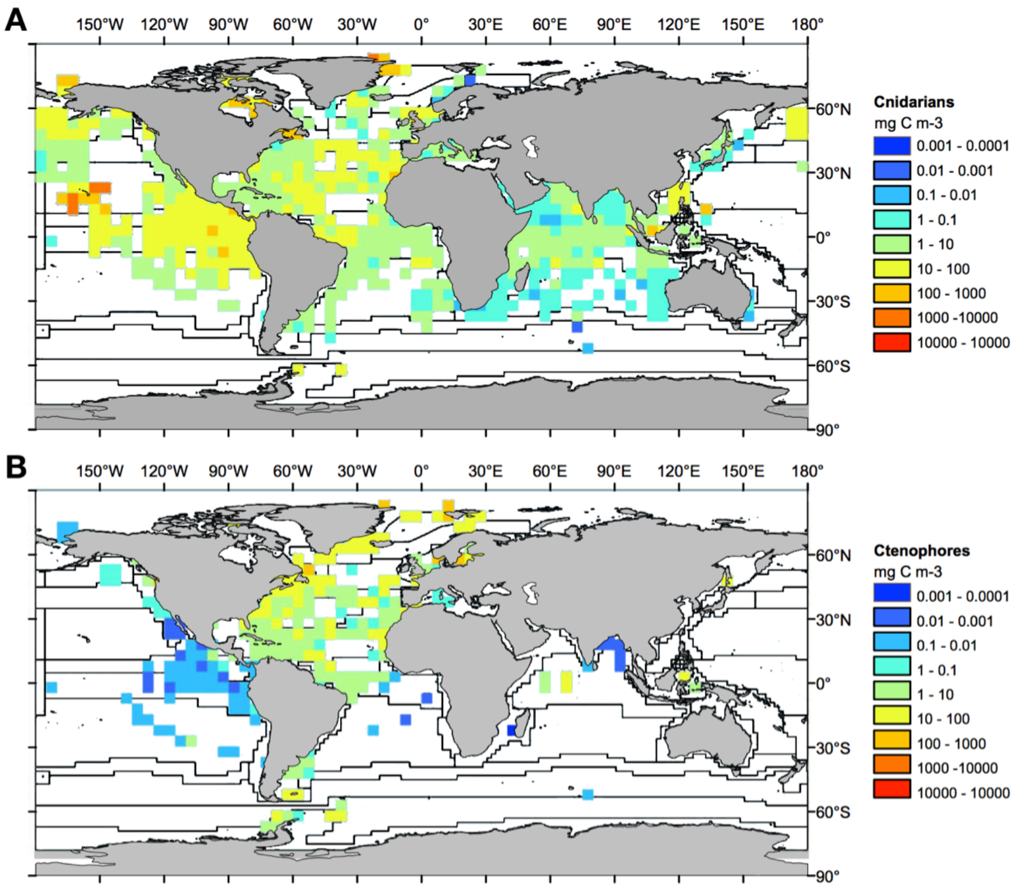

Fig. 1.3. Global maps of 5° grid cells data of the geometric mean biomass (mg C m^{-3}) of (A) Cnidaria and (B) Ctenophora. Areas where there are no observations are indicated by white. Adapted from Lucas et al. (2014b).

Scientific interest in jellyfish has increased over recent decades as a result of observed changes in the populations of many species. Since the 1980s, increases in the abundance and distribution of jellyfish have been reported in numerous areas around the world (e.g. Brodeur et al. 2002; Link & Ford 2006; Uye 2008; Licandro et al. 2010). A recent global study (Brotz et al. 2012) showed that ~42% of the world's 66 large marine ecosystems (LMEs) showed trends of increasing jellyfish abundance (Fig. 1.4). These observations have provided the impetus for increased research on jellyfish, leading to a greater recognition of their ecological importance. Aspects of jellyfish biology enable them to exert important effects on marine ecosystems. Jellyfish have opportunistic life history characteristics (i.e. high fecundity, rapid development, both sexual and asexual reproduction, short generation times, and high feeding rates) that enable rapid population growth rates, culminating in dramatic levels of abundance, i.e. 'blooms' (Lucas & Dawson 2014). Their high water and low organic content (Lucas et al. 2011) enables them to increase their body size and achieve large capture surfaces despite low energetic investment. This capability facilitates high prey encounter rates, enabling jellyfish to exhibit high prey clearance rates and potential for growth and reproduction that allow them to compete with more complex predators such as fish (Acuña et al. 2011). Some jellyfish have been found to modify their swimming behaviour to maintain or re-locate their position to optimise feeding on patchily distributed zooplankton prey (Frost et al. 2010; Hays et al. 2011). These factors enable jellyfish to effectively exploit zooplankton prey populations and when abundant their predation can have significant structuring effects on marine pelagic ecosystems (Matsakis & Conover 1991; reviewed in Purcell 1997; Hansson et al. 2005).

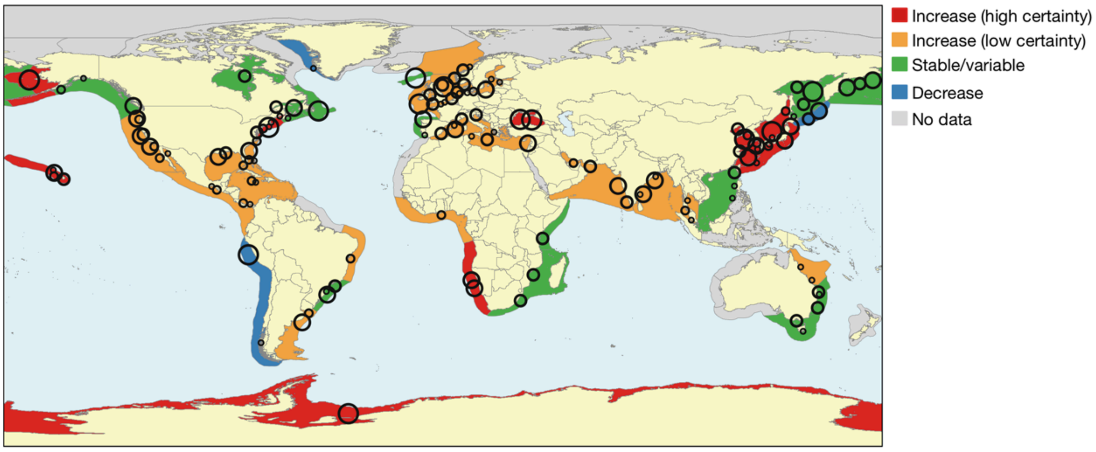

Fig. 1.4. Global map of trends in jellyfish populations after 1950. Contiguous areas represent LMEs, with the colour indicating the direction of the trend (See figure legend). The size of the circles reflects the Confidence Index, with larger circles indicating greater confidence. Adapted from Brotz et al. (2012).

Despite the low nutritional content of jellyfish, they are prey for numerous species of fish (Reviewed in Purcell & Arai 2001) and turtles (Houghton et al. 2006). However, rates of predation are typically low compared to other zooplankton taxa and available predator levels do not allow the pulsed nature of jellyfish abundance to be fully exploited. These low levels of predation limit the transfer of energy from jellyfish biomass to higher trophic levels (Greve & Parsons 1977; Jackson et al. 2001). The ultimate fate of most jellyfish blooms is to sink from the surface waters (e.g. Condon & Steinberg 2008), representing an important bentho-pelagic link, exporting energy and carbon to the deep ocean levels (Billett et al. 2006; Tinta et al. 2012; Sweetman et al. 2014). However, it has been shown that the dissolved organic matter released by jellyfish is primarily eliminated by microbial respiration, representing a diversion from the usual pathway of bacterial production, thus limiting the recycled energy available in the water column (Condon et al. 2011). Jellyfish also excrete inorganic nutrients, which represents a small but significant contribution to the nutrients required for primary production (Pitt et al. 2009). Jellyfish may also indirectly affect phytoplankton production through top-down controls by removing zooplankton grazing pressures (Greve 1994; Schneider & Behrends 1998). These findings represent a new level of understanding compared to the previous general perception that jellyfish were nuisance species of low ecological importance.

In addition to the ecological effects of jellyfish, they also impact on a wide range of human activities (Reviewed by Purcell et al. 2007; Purcell 2012). Jellyfish can directly impact fisheries by predating fish eggs and larvae (Möller 1984; Purcell & Arai 2001), and indirectly through competition for prey or by clogging nets, spoiling catches and stinging fishers (Pauly et al. 2005). Jellyfish stings also represent a significant problem for tourism, forcing beach closures and causing medical emergencies (Fenner et al. 2010). Large swarms of jellyfish can block the intake pipes of seawater coolant systems necessary for a variety of industrial operations (Jenner et al. 1998), for example leading to the closure of nuclear power plants (Associated Press 2013).

It is somewhat ironic that anthropogenic impacts on the marine environment may act to benefit jellyfish populations (reviewed in Purcell et al. 2007; Purcell 2012). Overfishing (Jackson et al. 2001) and 'fishing down the food web' (Pauly et al. 1998) may act to promote jellyfish abundance by relaxing competitive pressure for prey resources. The explosion of fertiliser use since the 1960s (Boesch, 2002 cited in Purcell 2012) has led to the eutrophication of many coastal areas. This nutrient enrichment promotes phytoplankton growth and the abundance of zooplankton grazers that are prey for jellyfish and other zooplanktivores; it also results in increased turbidity and oxygen depletion, conditions which may allow jellyfish to outcompete other predators such as fish, which rely on visual predation (Eiane et al. 1999) and have higher oxygen demands than jellyfish (Grove & Breitburg 2005). Due to their rapid growth rates and short generation times (<1 year) jellyfish populations may be able to more rapidly exploit pulses of prey abundance than fish that are restricted by their comparatively long life cycles. Ocean warming associated with global climate change may result in increased reproductive output and the expansion of the distributional range of some species of jellyfish (reviewed in Purcell 2005; Purcell et al. 2007). The increased stratification of the ocean surface layer caused by ocean warming promotes food webs that are dominated by small phytoplankton, small primary consumers and jellyfish (e.g. Greve & Parsons 1977; Parsons & Lalli 2002).

These observations have generated concern that increases in jellyfish abundance may be an indicator of the anthropogenic degradation of the global marine ecosystem (Mills 2001; Purcell et al. 2007; Richardson et al. 2009). Some marine ecologists (e.g. Richardson et al. 2009) have speculated that the increased prevalence of jellyfish may be indicative of a systemic global increase, representing a paradigm shift in which the global ocean ecosystem is transitioning from ecosystems previously dominated by fish to an alternate stable state dominated by jellyfish. Such a transition is theorised to occur through a 'self–enhancing feedback system' (Richardson et al. 2009) whereby jellyfish progressively outcompete fish, monopolise resources and inhibit the re-establishment of fish (Parsons & Lalli 2002; Uye 2008). In some areas evidence exists that jellyfish have already overtaken fish in heavily overfished areas (e.g. the Benguela upwelling, Lynam et al. 2006).

However, whilst it is irrefutable that jellyfish populations have increased in certain regions of the world, there is insufficient evidence to substantiate the paradigm of an emerging shift to jellyfish dominated pelagic ecosystems throughout the world's oceans (Condon et al. 2012). Some regions that have experienced dramatic increases have subsequently experienced dramatic declines (e.g. Brodeur et al. 2008) and in many areas population trends have remained stable or exhibit no trends (Brotz et al. 2012). Many jellyfish populations exhibit long-term fluctuations in response to climate variability (reviewed in Purcell 2005; Kogovšek et al. 2010). These observations have led to the development of an alternate hypothesis whereby the observed increase in jellyfish abundance may instead represent one phase of long-term cyclical variation (e.g. Goy et al. 1989; Kogovšek et al. 2010). The most recent global analysis of the available long-term jellyfish data series supports this hypothesis, revealing that most jellyfish populations fluctuate with periodicities of ~20 years (Condon et al. 2013). Analysis of these periodic trends requires data sets with a minimum of twice the length of the periodicity (Legendre & Legendre 2012), but unfortunately there are few ~40 year time series available. This lack of historic data also results in the absence of a firm baseline against which to compare the contemporary levels of abundance, raising the possibility that current concerns regarding jellyfish population changes are a product of our frame of reference (Condon et al. 2013).

Irrespective of whether jellyfish are increasing on a global scale, or indeed whether they are increasing at all, there has been substantial improvement in understanding the ecological importance of jellyfish. However, this improvement has been hindered by a tendency to treat the taxonomically, biologically and ecologically diverse jellyfish species as a collective functional group, limiting our understanding of how individual species and populations function and respond to change (Condon et al. 2012). Furthermore, jellyfish blooms occur both as a direct result of growth and reproduction and also as an indirect effect of physical translocation and aggregation (Graham et al. 2001; Hamner & Dawson 2009). A failure to discriminate between these two fundamental processes can obscure our understanding of the specific factors that drive changes in jellyfish populations. An improved understanding of these mechanisms requires investigation of the biology and ecology of jellyfish and how they interact with their environment at the species level (e.g. Mills 2001; Kiørboe 2008).

1.4 Study organism: *Muggiaea atlantica* (Cunningham 1892)

This thesis is based on the analysis of time-series data on the abundance of the neritic siphonophore *Muggiaea atlantica*; however, it is necessary to have an understanding of the individual-level biology and ecology to be able to effectively interpret data at the population level (Kiørboe 2008). In the following sections of this chapter, I provide a brief overview of the morphology, functional biology and ecology of *M. atlantica*. This overview is based on a review of the published scientific literature, supplemented by laboratory-based observations conducted during the course of this PhD project (Methodological details for siphonophore collection and maintenance are provided in section A1).

"In biology, . . . the first essential is to know what you are talking about." (Pantin 1963 cited in Totton 1965)

1.4.1 Morphology

The Siphonophora are an order of colonial marine hydrozoans (Cnidaria) that posses the most complex colony-level organisation of all animals (Dunn 2009). Their colonies are composed of a collection of individual multicellular zooids—each homologous to a free-living, solitary cnidarian animal—that develop into an integrated unit from a single egg (Totton 1965; Carré & Carré 1995; Dunn & Wagner 2006). These medusoid and polypoid zooids are arranged along a central tube (the siphosome) in a systematic and polarized pattern, with high polymorphy between species (Totton 1965; Mackie et al. 1987). Throughout the life of the colony, these highly specialised zooids remain attached and physiologically integrated to one another, each performing discrete functional roles akin to the organs of conventional unitary multicellular animals (Mackie et al. 1987; Dunn 2009). This strict division of labour enables the modular colonies of siphonophores to function as tightly integrated units that superficially resemble other unitary pelagic cnidarians (Totton 1965; Mackie et al. 1987; Mapstone 2014).

In the sub-order Calycophorae, the family Diphyidae contains a large number of epipelagic (0– c. 300 m) representatives of the Siphonophorae (Mackie et al. 1987). These small (approx. <15 cm polygastric colony length), typically active species are holoplanktonic, carnivorous jellyfish that have a cosmopolitan distribution, inhabiting all oceans (Alvariño 1971; Mapstone 2014). A few genera of the family are neritic, in that they are typically distributed in coastal waters (Mackie et al. 1987; Mapstone 2014). Of these, three of the four species of the genus *Muggiaea* are almost exclusively neritic (Mackie et al. 1987). In the northeast Atlantic region these are represented by the two species *Muggiaea atlantica* and *Muggiaea kochi* (Mackie et al. 1987). The following sections of this chapter focuses on these two species, but also draws from information on other, predominantly diphyid, siphonophores that have similar physiological and ecological characteristics.

1.4.1.1 Colony structure

Haddock et al. (2005) provide a standardised system of nomenclature for the terms used to specify the axes and orientation of the colonies of siphonophores, and in this thesis I adhere to this scheme.

Calycophoran siphonophores have a metagenic life history comprising an alternation of generations between an asexual polygastric colony and a sexual monogastric colony, referred to as the eudoxid. There are two short-lived intermediate larval stages: the planula and calyconula (Carré & Carré 1991; 1995). It should be noted that Rottini (Rottini 1974) suggested the existence of a benthic stage in the life cycle of *M. kochi*; however Carré and Carré (Carré & Carré 1991) found no evidence of this stage when rearing the species through its complete life cycle. I take the view of the Carré's and consider the life cycle of the genus *Muggiaea* as strictly holoplanktonic.

The polygastric colony is divided into two visually and functionally discrete regions – the nectosome and siphosome (Fig. 1.5A). The nectosome compromises the anterior portion of the colony and is composed exclusively of locomotory medusoid zooids, referred to as the nectophores. In the majority of Diphyid species the nectosome is comprised of two dissimilar nectophores. However, within the genus *Muggiaea* the nectosome is comprised of only a single nectophore (Totton 1965; Mackie et al. 1987). Trailing from the nectosome is the siphosome, the posterior region of the polygastric colony that bears the remaining zooids; these are polypoid nutritive gastrozooids, medusoid reproductive gonophores, and defensive/buoyant bracts of an indeterminate structure (Dunn & Wagner 2006). The siphosomal zooids are grouped together in iterative units, referred to as cormidia, which are arranged along the ventral surface of the long extensible siphosome. Each cormidium is composed of one of each of the siphosomal zooids, i.e. a bract, a gastrozooid, and a gonophore. Where the siphosome connects to the nectosome there is a growth zone responsible for elongation of the siphosome and the production of successive cormidia (Dunn & Wagner 2006). This results in a linear chain of cormidia that are progressively more well developed toward the distal terminus of the siphosome. When mature, the terminal cormidium is released as an autonomous sexually reproducing eudoxid (Carré & Carré 1991; 1995).

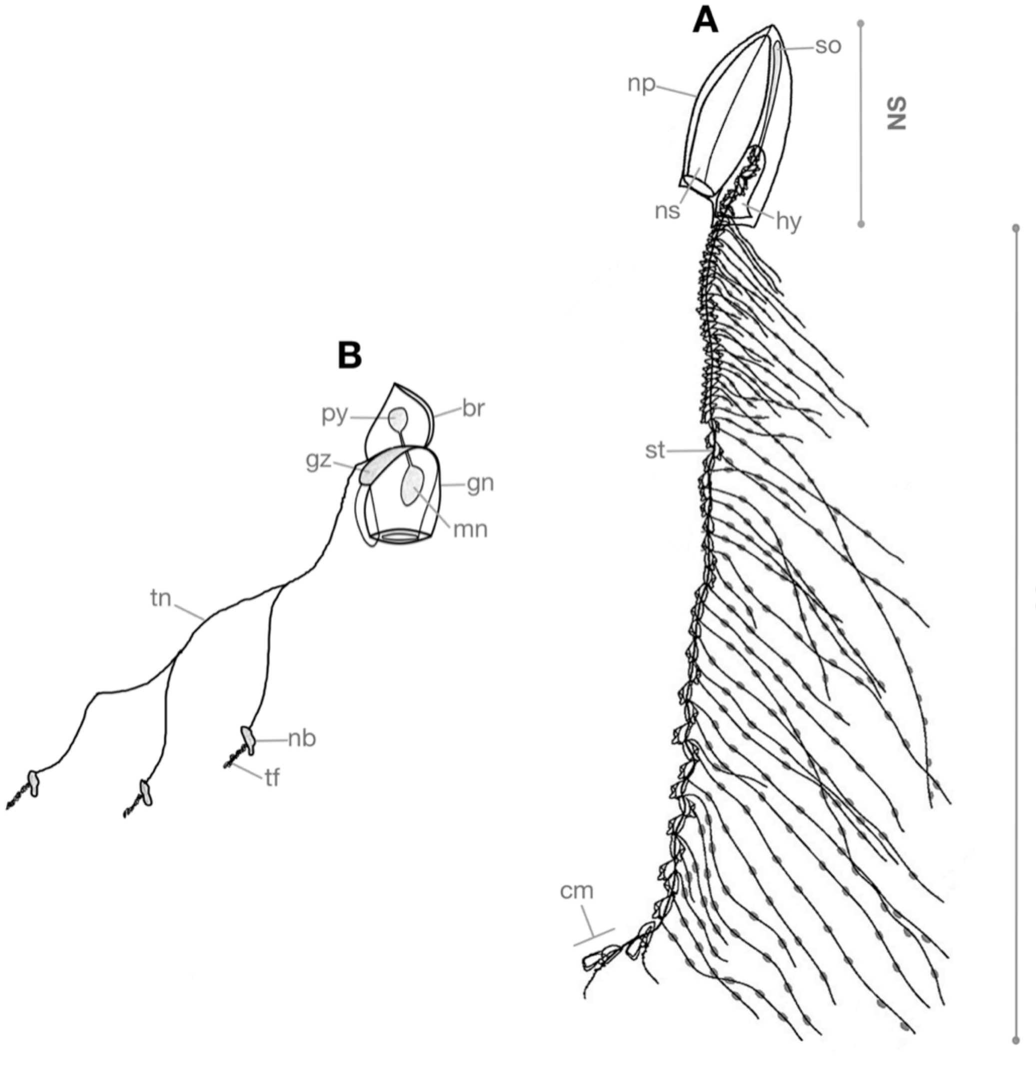

Fig. 1.5. Body plan of the main life cycle stages of *Muggiaea atlantica.* (A) Polygastric colony (adapted from Mapstone [2014] and photo image by M Blackett); (B) eudoxid colony (derived from photo image by M Blackett). NS: nectosomal region; SS: siphosomal region; br: bract; cm: cormidium; gn: gonophore; gz: gastrozooid; hy: hydroecium; mn: manubrium; nb: nematocyst battery; np: nectophore; so: somatocyst; st: stem (siphosome); tf: terminal filament; tn: tentacle.

1.4.1.2 Zooid morphology

Nectophores. The nectophores of the genus *Muggiaea* are streamlined, pyramidal medusoid zooids with a sharply pointed apex and an extensive basal cavity, referred to as the nectosac (Fig. 1.5A). The nectosac is lined with a dense layer of striated musculature, and a muscular collar equipped with a thin membrane (the velum) that encircles its opening (the ostium) (Carré & Carré 1995). Although clearly homologous to the swimming bells of unitary pelagic cnidarians, nectophores lack most of the structures that are characteristic of medusae. They have no manubrium, tentacles or sensory organs, which means that they are unable to independently feed or reproduce (Carré & Carré 1995). The sole functional purpose of the nectophore is the locomtory unit of the colony. A smaller ventral cavity, the hydroecium, houses the siphosomal growth zone and the gastrovascular junction (pedicular canal) that connects the nectophore to the rest of the colony (Fig. 1.5A). A diverticulum of the pedicular canal—the somatocyst— forms a reserve organ that extends to the apex of the nectosac (Fig. 1.5A). The somatocyst typically contains oil droplets (olleocysts) at its distal end that are thought to aid buoyancy and maintain the vertical orientation of the nectophore (Mackie et al. 1987).

Gastrozooids. The gastrozooids are elongate, muscular polypoid zooids with a terminal pore, which functions as both the mouth and the anus. The internal cavity of the gastrozooid is divided into two sub-cavities: a slender oral buccal cavity and a bulbous basal basigaster (Mackie et al. 1987). Unlike most cnidarian polyps, gastrozooids are devoid of an oral ring of tentacles (corona), but are equipped with a single highly contractile tentacle with numerous side-branching tentilla (Fig. 1.5B). Each tentillum has a sub-terminal bulbous swelling—the cnidoband—that is densely populated with highly organised batteries of nematocysts (Purcell 1984). The cnidoband terminates with a uniramous stretch sensitive elastic filament – the terminal filament, which is tightly coiled (Mackie et al. 1987).

Bracts. The bracts of *Muggiaea* have an asymmetric cone shape, with a broad flattened facet and a dense layer of mesoglea (Fig. 1.5B). The eudoxid bract possesses a club-shaped reserve organ, the phyllocyst (Kirkpatrick & Pugh 1984). In a similar way to the somatocyst, this typically contains olleocysts and is thought to aid buoyancy and maintain a vertical orientation.

Gonophores. The gonophores are simple, truncated cone-shaped, atentaculate sexual medusoid zooids. In contrast to the nectophore, the gonophoral cavity contains an astomous manubrium, formed of a short stalk (peduncle) and a distal bulbous swelling where the gametes are produced and stored (Fig. 1.5B). The ostium of the gonophore is equipped with a smooth dorsal process, referred to as a mouthplate (Kirkpatrick & Pugh 1984). The gonophores also serve as the locomotory unit of the eudoxid.

1.4.2 Identification

Both *M. atlantica* and the congeneric *M. kochi* occur in the northeast Atlantic (Mackie et al. 1987; Mapstone 2014). A brief description of the two species follows, after Kirkpatrick and Pugh (1984):

1.4.2.1 *Muggiaea atlantica* (Cunningham 1892)

Nectophore: up to 7 mm in height with five complete, relatively straight longitudinal ridges. The hydroecium extends to about one third the height of the nectophore. The long slender somatocyst has a slight distal thickening and extends to the apex of the nectosac (Fig. 1.6A).

Eudoxid: The bract has an asymmetric cone shape with a flattened ventral facet and a basal process on the opposite side; the club shaped phyllocyst is centrally placed. The gonophore is cylindrical with four longitudinal ridges with a ventrad spiral twist; there is a short, curved mouthplate (Fig. 1.6C).

1.4.2.2 *Muggiaea kochi* (Will 1844)

Nectophore: similar in size to that of *M. atlantica*, with five complete longitudinal ridges that bend ventrally as they approach the ostium. The hydroecium is shallower than in *M. atlantica*, with the somatocyst extending to half the height of the nectophore (Fig. 1.6B).

Eudoxid: The eudoxid stage is morphologically indistinguishable from *M. atlantica* (See Fig. 1.6C)

It should be noted that an additional species, *Muggiaea cantabrica* Alcazar, 1982, was described from samples collected in the Bay of Biscay, off the coast of Gijon, Spain. However, this species is currently considered to be 'probably invalid' as it "is a very doubtful species, which has never been found since its original description, and that was probably based on a few atypical specimens." (Schuchert & Mapstone 2015).

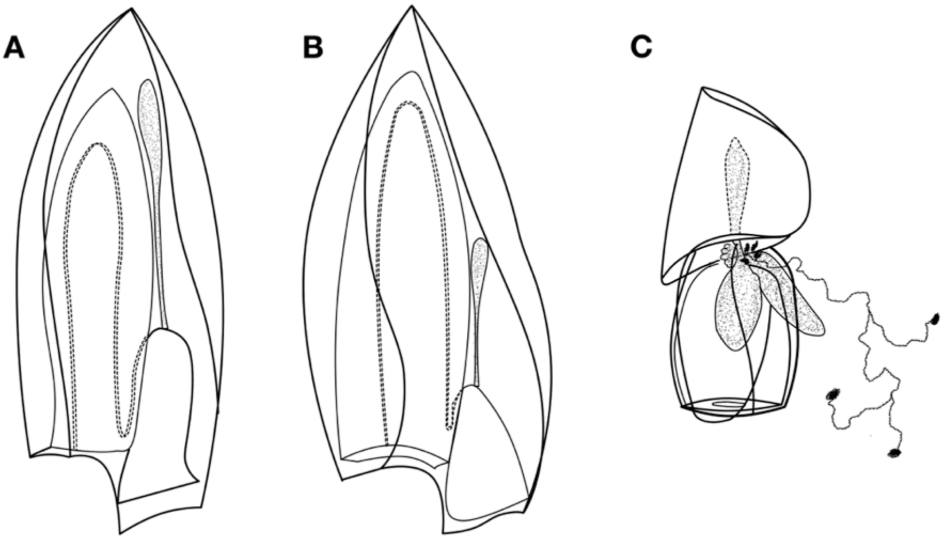

Fig. 1.6. Nectophores of (A) *Muggiaea atlantica* and (B) *Muggiaea kochi* (Redrawn from Kirkpatrick and Pugh, [1984]). (C) Eudoxid stage of *Muggiaea* spp. (Redrawn from Russell [1938]). Not to scale.

1.4.3 Functional biology

1.4.3.1 Locomotion

As an ambush predator (Colin & Costello 2002), *M. atlantica* spends a large proportion of the time motionless in the water column (Mackie & Boag 1963). Locomotion occurs either spontaneously as a part of feeding behaviour (See section 1.4.3.2) or in response to external stimuli (Mackie et al. 1987). Propulsive thrust generated by the nectophore enables the polygastric colony to swim. Contraction of the dense musculature lining the nectosac propagates towards the ostium, forcefully expelling the interstitial water and propelling the colony forward. Regulation of the strength of the contraction together with modification of the ostial aperture through articulation of the velum controls swimming velocity and attitude; *M. atlantica* is not capable of reverse swimming (Mackie et al. 1987).

Bone and Trueman (1982) reported that the diphyid species *Chelophyes appendiculata*, which has two nectophores, performed two modes of swimming not associated with feeding behaviour. One mode, which may act to counter sinking, was spontaneous slow swimming (<1 cm s^{-1}) involving low frequency contraction of only the posterior nectophore. The other mode, which occurred in response to external stimuli, was fast swimming (up to 30 cm s^{-1}) employing high frequency contraction of both nectophores (Bone & Trueman 1982). In my laboratory observations, *M. atlantica* was not observed to employ slow swimming; only rapid swimming was observed, either as a part of the feeding process or as a series of rapid contractions in response to an external stimulus. My observations confirmed that the eudoxid colony employs comparable swimming behaviour, utilising the gonophore as the locomotory unit.

1.4.3.2 Feeding

Siphonophores are generally passive, ambush-predators that deploy a network of tentacles and then remain motionless, capturing prey that come into contact with their nematocyst batteries (Mackie et al. 1987). The polygastric stage of *M. atlantica* employs a specialised swimming behaviour that spreads the siphosome and tentacles into a complex three-dimensional helical structure – the ‘fishing posture’ (Mackie & Boag 1963). As the colony sinks, this causes dissolution of the ‘tentacle net’, stimulating a repetition of the redeployment process. Mackie and Boag (1963) first described this behaviour as the ‘veronica’, after the classic toreador movement that it resembles. The veronica (Fig. 1.7) consists of: (A) retraction of the siphosome, streamlining the colony and protecting delicate siphosomal appendages; (B) a subsequent series of rapid nectophoral contractions propels the colony; (C) the siphosome is progressively relaxed; (D) extension of the siphosome incurs increasing drag that causes the colony to veer in an arc; (E) centrifugal and drag forces cause the tentacles to spread out laterally and the colony stops, having constructed its net; (F) after this, sinking causes dissolution of the net, and the cycle is repeated (Mackie & Boag 1963). Purcell & LaBarbera (unpublished results cited in Purcell 1984) found that drag acting on the siphosome and tentacles was the main force causing the spreading of the tentacle array, facilitated by the increased drag incurred by the bulbous nematocyst batteries at the terminus of the tentacles. During my laboratory observations I observed the eudoxids employing a similar behaviour to spread their single tentacle, utilizing the propulsive thrust of the gonophore. The eudoxids were consistently observed to swim in an arc, and although this curved trajectory was not aided by the same level of helpful drag forces as incurred by the larger polygastric stage, the eudoxid was still able to successfully employ this feeding strategy. It is possible that the mouthplate—situated at the ostium of the gonophore—may have a fin-like function that enhances the eudoxid veronica movement. This veronica feeding strategy is reported to be utilised by a variety of Calycophorae (Biggs 1977a).

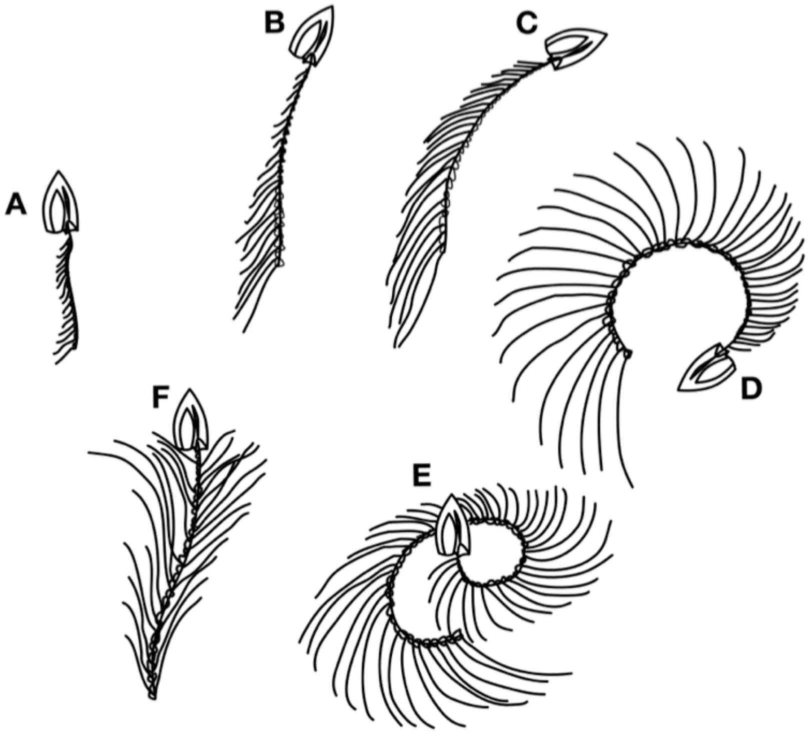

Fig. 1.7. The 'veronica' movement; a feeding strategy used by *Muggiaea atlantica* to spread the tentacles into the feeding posture. See text for explanation. Adapted from Mackie & Boag (1963).

Prey that come into contact with the stretch sensitive terminal filament cause the nematocyst battery to discharge, immobilising and capturing them (Mackie & Boag 1963; Purcell 1984). Transmission Electron Microscopy (TEM) imaging of captured crustacean prey has indicated that capture is facilitated by entanglement through the action of spinate and adherent nematocysts, rather than direct penetration and envenomation (Purcell 1984). This led Purcell (1984) to suggest that calycophoran nematocysts may be unable to penetrate the tough exoskeleton of copepod prey, but could potentially penetrate the softer cuticle at the joints of the exoskeleton of copepods. The nematocyst threads could successfully penetrate a variety of soft bodied prey (Purcell 1984). Mackie and Boag (1963) reported that *Artemia* nauplii prey captured by the physonect *Stephanomia sp.* often continued to struggle as they were ingested, indicating a lack of penetration by the nematocyst threads. However, I observed that *Artemia* nauplii captured by *M. atlantica* were almost instantaneously immobilised, perhaps indicating successful envenomation.

Captured prey is brought toward the gastrozooid via stepwise contraction of the tentacle (Mackie & Boag 1963). This action stimulates the receiving gastrozooid, which elongates and begins writhing movements, indicating excitation (Mackie & Boag 1963; personal observation). Prey are consumed whole (Mackie & Boag 1963). In the laboratory I observed that when consuming relatively large prey, such as *Artemia* nauplii, the gastrozooid 'searches' the long axis of the prey to find its narrowest point and then everts to engulf the prey. Once fully ingested, *Artemia* prey was always rotated so that the larger anterior was located within the bulbous basigaster of the gastrozooid. During laboratory feeding experiments, polygastric colonies (n = 3) took <3 min to fully ingest 1-day old *Artemia* nauplii. Purcell (1981b) reported that gastrozooids of the calycophore *Rosacea cymbiformis* contained, on average 1–4 prey items. My observations indicate that gastrozooids of *M. atlantica* are only capable of accommodating a single prey item at any one time; gastrozooids that were in the process of digestion would frequently capture additional prey, but would not attempt to ingest them and the prey item would remain attached to the tentacle before being released, dead. This difference is probably due to the relatively small size of the gastrozooids of *M. atlantica* compared to those of *R. cymbiformis* (Purcell 1981b; personal observation), or due to the large size of *Artemia* prey.

1.4.3.3 Digestion, assimilation and excretion

Digestion is both intra- and extra-cellular (Carré & Carré 1995). The buccal region of the gastrozooid contains holocrine and merocrine secretory cells that release digestive enzymes while the basigaster performs absorptive functions (Mackie & Boag 1963). Digestion begins with extracellular digestion in the buccal cavity of the gastrozooid (Carré & Carré 1995); this process liberates small fragments that are engulfed by phagocytic cells detached from the endoderm (Carré & Carré 1995). The phagocytised particles are absorbed across the endoderm, dissolve and are subsequently dispersed into the coelomic fluid and distributed throughout the colony (Carré & Carré 1995). Digestion times are both temperature-dependent and prey-size specific (Purcell 1982; Purcell 1983), but typically take between 2–4 h for small copepod prey (Purcell 1982). I recorded similar digestion times (2–3 h, n = 3) for polygastric colonies of *M. atlantica* that were fed *Artemia* nauplii in the laboratory. Postprandial gastrozooids are evident due to their swollen appearance and the presence of digestate in the basigaster (Fig. 1.8A). Preprandial gastrozooids are elongate and semi-transparent (Fig. 1.8B) and often exhibit writhing behaviour, probably in response to the chemical detection of prey (Mackie & Boag 1963; personal observation). The remains of digested prey are egested as coherent faecal pellets, each containing the agglutinated remains of one prey (Purcell 1983); but are not bound by a peritrophic membrane (Biggs 1977a).

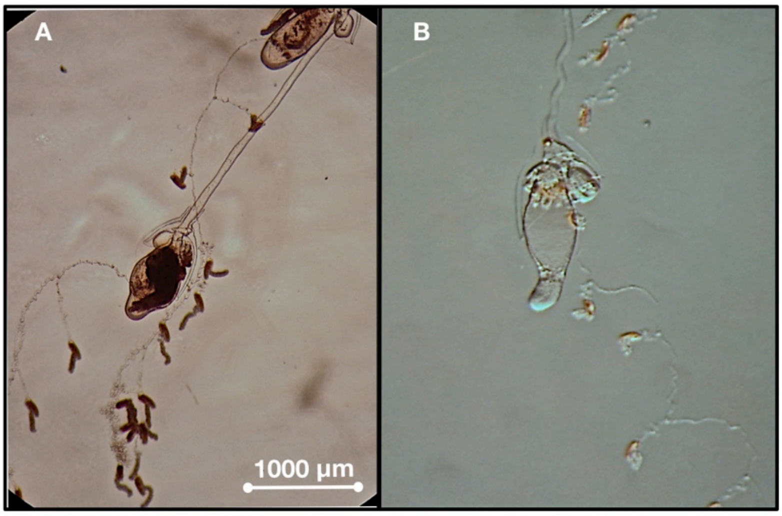

Fig. 1.8. (A) a postprandial gastrozooid of *Muggiaea atlantica* with the prey item (*Artemia* nauplius) visible. (B) The same gastrozooid prior to feeding. Scale bar is approximate.

Assimilation efficiencies of oceanic Calycophorae are typically higher than other planktonic carnivores: 87–90% for carbon and 90–96% for nitrogen (Purcell 1983); no information is available on the assimilation efficiencies of *M. atlantica*.

The siphosome serves as the main gastrovascular canal of the polygastric colony; incessant beating of cilia and periodic peristaltic contractions maintains a nutritive current that distributes metabolites and digestate between the zooids of the colony (Mackie et al. 1987).

1.4.3.4 Metabolism

Siphonophore metabolism is notoriously difficult to measure due to the fragility of their colonies. Metabolic rates of siphonophores collected using nets and pails have been shown to be lower than those collected individually using SCUBA (e.g. Ikeda 1974; vs. Purcell & Kremer 1983), probably indicating elevated respiration associated with physical damage and stress of net capture (Mackie et al. 1987).

Ambient temperature and the nutritional state of siphonophores affect metabolic rates. Biggs (1977b) showed that although warm-water siphonophores could adjust metabolically to gradual changes in temperature, rapid changes had a significant effect: a 5°C drop in ambient temperature elicited a 2–5 fold reduction in respiration. Purcell and Kremer (1983) reported that the metabolism of the calycophoran *Sphaeronectes gracilis* offered high prey densities (20 prey L^{-1}) was 1.7 times faster than that of colonies offered low prey densities (5 prey L^{-1}) as a result of a 2.7 fold increase in ingestion.

Siphonophores allocate the majority of ingested energy to growth (Mackie et al. 1987). Purcell and Kremer (1983) found that respiration and excretion (NH_4) in *S. gracilis* equalled 3% of the siphonophore's carbon and nitrogen content. Given their comparable size and activity Purcell

(1982) adjusted the weight-specific *S. gracilis* metabolic values for differences in temperature (assuming a Q10 of 2), applied them to *M. atlantica,* and estimated that respiration and excretion was equal to 2.3% the carbon and nitrogen content of the siphonophore. More recently *M. atlantica* respiration has been measured directly (Rutherford Jr & Thuesen 2005) where it was shown that *M. atlantica* is an oxyconformer, capable of surviving very low oxygen waters. The critical oxygen partial pressure of *M. atlantica* is lower than many medusae and the ctenophore, *Mnemiopsis leidyi* (Thuesen et al. unpublished data cited in Thuesen et al. 2005), which are well known for their capacity to survive hypoxic waters (e.g. Costello et al. 2012).

1.4.3.5 Growth and reproduction

Siphonophores reproduce both asexually and sexually. Asexual reproduction produces new zooids to increase the size of the colony or to replace lost zooids. Sexual reproduction is restricted to the gonophores, which release gametes that fertilise externally to produce new polygastric colonies.

In *Muggiaea* the polygastric colony reproduces asexually by budding successive cormidia from the siphosomal growth zone; there is no nectosomal growth and the nectophore is probably not capable of being replaced if lost (C. Carré, personal communication cited in Mackie et al. 1987). Siphosomal budding produces a linear chain of cormidia that are progressively more well developed. As the cormidia develop they reach a stage where the gastrozooid becomes 'functional', i.e. equipped with a terminal pore (mouth) and feeding tentacle. The cormidia are then successively detached from the distal terminus of the siphosome as monogastric autonomous eudoxids (Carré & Carré 1991; 1995). In laboratory reared specimens of *M. kochi*, Carré & Carré (1991) recorded cormidial growth rates of c. 2–3 functional gastrozooids day^{-1}. My laboratory observations of asexual reproduction in immature (<10 functional gastrozooids) *M. atlantica* collected from the Western English Channel yielded similar results, with growth rates of 2±0.8 functional gastrozooids day^{-1} (n = 7). However, *in situ* growth rates are likely to be much higher, as Purcell (1982) found that mature (10–45 functional gastrozooids) polygastric colonies of *M. atlantica* produced on average between 7.4–11 eudoxids siphonophore^{-1} day^{-1} without reduction of the number of gastrozooids. The eudoxid production rate is linearly related to the number of functional gastrozooids and also positively related to food availability (Purcell 1982).

The eudoxids of the calycophore, *Chelophyes appendiculata,* are liberated from the polygastric colony by muscular constriction of the siphosome; the eudoxid portion of the siphosome is then sealed off and forms the phyllocyst of the eudoxid bract (Mackie et al. 1987). However, in my laboratory observations of *M. atlantica,* the phyllocyst of the cormidial bract is already fully developed (with evident olleocysts) prior to release of the cormidium as the eudoxid (Fig. 1.9A). After liberation the remainder of the siphosome is resorbed (personal observation).

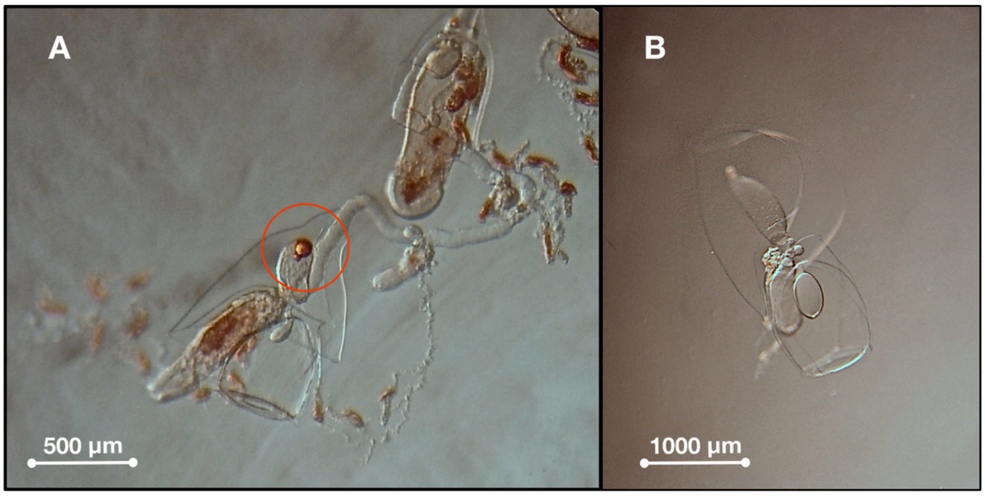

Fig. 1.9. (A) The terminal cormidium of *Muggiaea atlantica* just before it is detached as an autonomous eudoxid. The fully developed phyllocyst is indicated by a red circle. (B) The free-living eudoxid following its release from the polygastric colony. Scale bar is approximate.

The eudoxids are morphologically very similar to their cormidial precursor (Fig. 1.9), except for substantial somatic growth, with a dry weight increase of 5–6 times and an increase in carbon and nitrogen content by up to 16 times (probably a result of gamete development, Purcell 1982). The eudoxids also reproduce asexually, producing a succession of gonophores that serve to produce and disperse the gametes. The gametes develop within the manubrium of the gonophore. Purcell (1982) showed that eudoxid maturation rates are dependent on food availability. It took 6 days (n = c. 18) from liberation of the eudoxid for the gonophores of *M. atlantica* to reach sexual maturity when eudoxids were provided with very high food availability, while this maturation time increased to 9–11 days at lower prey densities (at 8–10°C). My laboratory observations revealed slightly faster maturation rates, with both male and female eudoxid gonophores having developed sexually ripe manubria from rudimentary swellings ~4 d after liberation (n = 6). I provided *Artemia* at similar 'very high prey density' to Purcell (~20 prey L^{-1}). This difference may therefore be due to the elevated temperatures employed during my observations (15 °C). Mature female gonophores were obvious due to the presence of well-developed eggs (Fig. 1.10A) that resemble those expelled spontaneously (Fig. 1.11A); mature male gonophores were evident due to the opacity of the manubrium (Purcell 1982), particularly at its edges (Fig. 1.10B; personal observation).

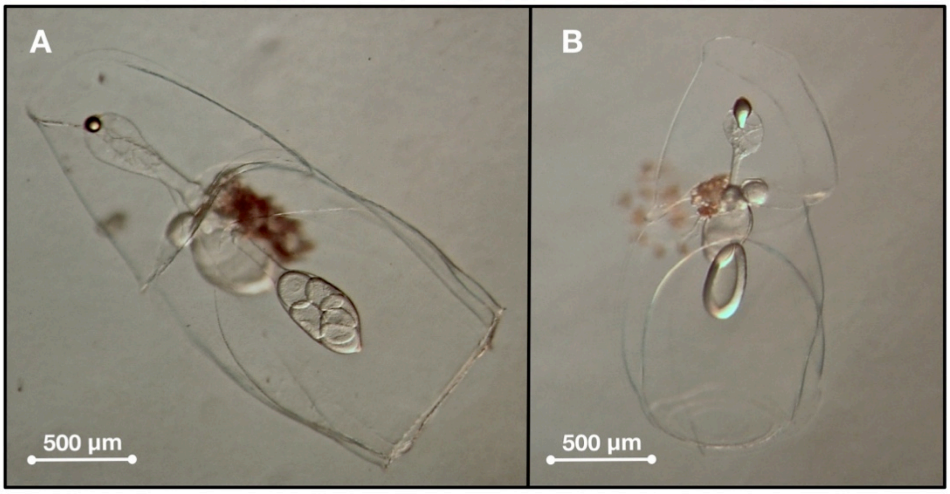

Fig. 1.10. Sexually mature eudoxid gonophores of *Muggiaea atlantica.* (A) Female gonophore with well developed eggs obvious in the manubrium. (B) Male gonophore with characteristic opaque manubrium. The image (B) is composed of two focus-stacked photographs. Scale bar is approximate.

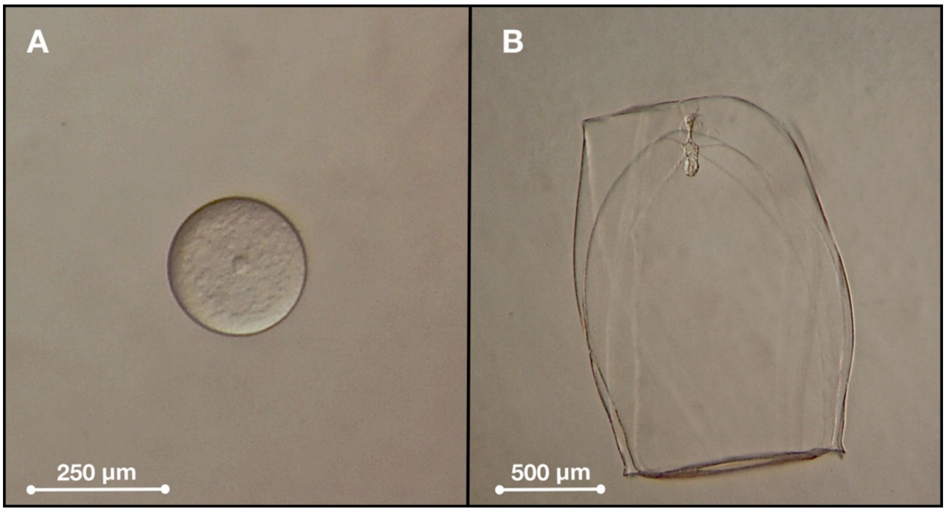

Fig. 1.11. (A) Fertilised egg of *Muggiaea atlantica.* (B) Detached gonophore released from the eudoxid colony following gamete release, note the remnants of the manubrium. Scale bar is approximate.

In field collected Pacific specimens, Purcell (1982) found sexually mature female gonophores contained 30.2±7.0 eggs (n = 10), whereas in Southern California they contained less (18 eggs gonophore^{-1}) (Purcell unpublished data cited in Purcell 1982). Purcell (1982) attributed this to either the effects of reduced food availability, or the increased temperature in Southern California (13 °C compared to 8 °C in the Pacific) facilitating faster maturation at a smaller size and consequent lower fecundity. In my laboratory observations eudoxids maintained at 15 °C with very high prey density (20 prey L^{-1}) contained a maximum of 8 eggs, perhaps supporting the importance of temperature on the rate of eudoxid maturation. The eggs of *M. atlantica* are ~250 μm in diameter, transparent (Fig. 1.11A) and slightly positively buoyant (Russell 1938), probably due to their extensive lipid-rich yolk reserves (Totton 1965). Nothing is known about the fecundity of male gonophores. According to Carré & Carré (1995) the eggs are released en masse from individual pores on the manubrium. Once the gametes are expelled the gonophore is detached from the eudoxid and is rapidly replaced by an already partially developed successor (Carré & Carré 1991) (Fig. 1.12). The detached gonophore typically remains alive for a short period of time, evidenced by their continued swimming contractions, but soon die, presumably due to their inability to feed (personal observation). The manubrium of the gonophores rapidly atrophies after gamete release (Fig. 1.11B). The eudoxids are dioecious at any one time, but the succession of gonophores may be of the same sex or alternate between them (Carré & Carré 1991; personal observation). Carré & Carré (1991) recorded at least four generations of gonophores in *M. kochi*, but the total number of gonophores produced during the life span of the eudoxid is not known (Purcell 1982; Carré & Carré 1991).

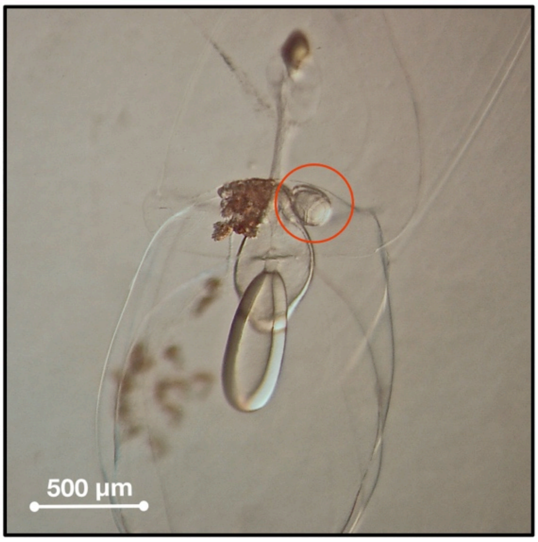

Fig. 1.12. Sexually mature male eudoxid gonophore of *Muggiaea atlantica* with the rudiments of the secondary gonophore indicated with a red circle. Scale bar is approximate.

Fertilisation is always external (Mackie et al. 1987). Spermatozoa are attracted to a structure on the surface of the egg, the cupule, which releases a highly stable, low molecular weight, species-specific chemo-attractant (Mackie et al. 1987; Carré & Carré 1995). The acrosomal reaction is induced at the cupule where fertilisation always takes place (Carré & Carré 1995). Fertilised eggs develop rapidly (~24 h) into planulae larvae ~370μm polar length (Russell 1938). The planula stage is short-lived, lasting ~24h (Carré & Carré 1991; 1995) before rapidly (<48h) developing the larval nectophore (Russell 1938) and primary gastrozooid (Carré & Carré 1991; 1995). Following this, the mid-section of the planula narrows and elongates, representing the future siphosome of the colony (Carré & Carré 1991; 1995). The presence of the larval nectophore and the functional primary gastrozooid represents the development of the second larval stage, the calyconula. Subsequently, a secondary nectophore develops, which represents the definitive nectophore of the future polygastric colony (Carré & Carré 1991). The development of the gastrozooids terminal pore and the population of the tentacle with cnidocytes signifies the transition from the utilisation of energy stored in yolk reserves to a fully-functional feeding larva (Carré & Carré 1991). Once the definitive nectophore has fully developed the larval nectophore is detached (Carré & Carré 1991). There is a short-lived 'post-larval' stage, marked by the presence of both the definitive and larval nectophores, but it lasts only a few hours (Russell 1938; Carré & Carré 1991; 1995). The young monogastric colony continues to grow; developing successive cormidia to form a polygastric colony and the life cycle is repeated (Fig. 1.13).

Carré & Carré (1991) showed that in the northwest Mediterranean the generation time of *M. kochi* was temperature dependent. The species was able to complete its full egg-to-egg life cycle in 2 weeks at 18 °C and 3 weeks at 24 °C. Following the period of eudoxid release, the siphosome degenerated and the polygastric colony rapidly died. However at 13 °C the life cycle was restricted, with the polygastric stage persisting without producing any eudoxids. These observations led Carré & Carré (1991) to propose the existence of two distinct types of life cycles: a 'short cycle' during the spring and summer (18–24°C) and a 'long cycle' during winter (13 °C). It was suggested that this 'long cycle' prevents eudoxid production and the subsequent death of the polygastric colony, thus facilitating overwintering of the population (Carré & Carré 1991).

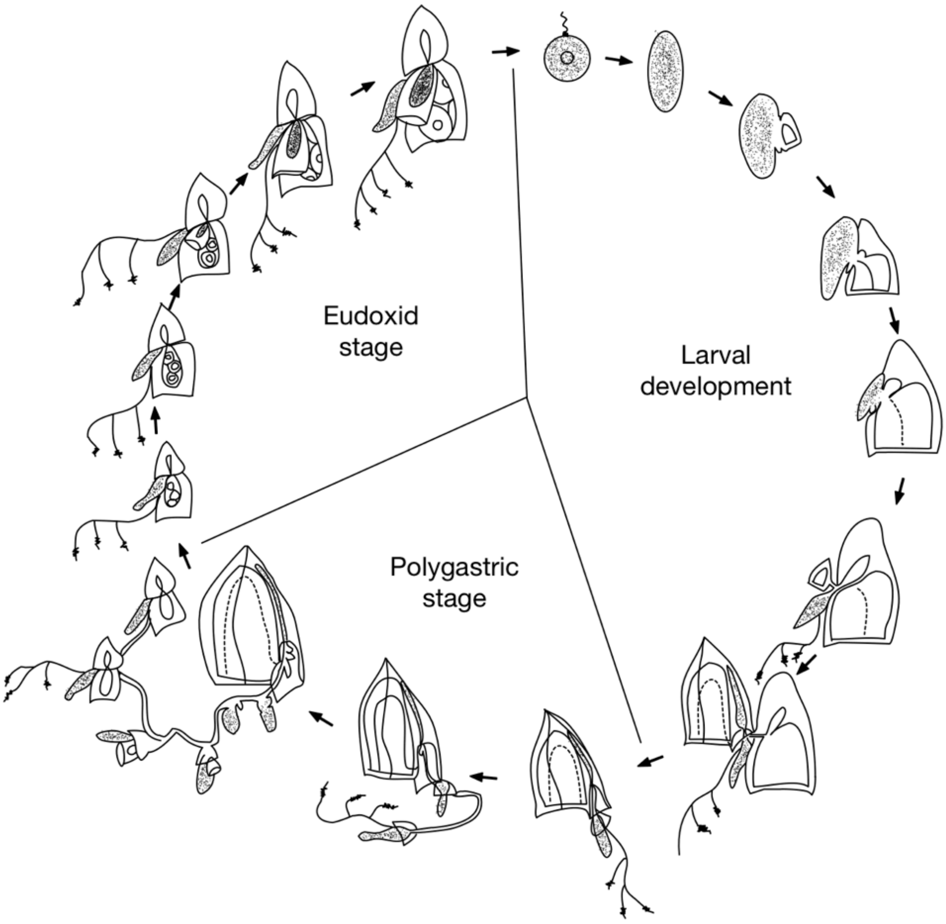

Fig. 1.13. Life cycle of *Muggiaea atlantica.* Redrawn from Carré & Carré (1991).

1.4.4 Ecology

1.4.4.1 Trophic ecology and ecosystem effects

The principal prey of most calycophoran siphonophores is copepods (Purcell 1981a), but a variety of other hard and soft-bodied zooplankton are also consumed (Purcell 1981a; Mapstone 2009). The size range of siphonophore prey is probably related to the size of the gastrozooids; Calycophorae have small gastrozooids and consume mainly small copepods (Purcell 1981a). The gastrozooids of *Muggiaea atlantica* are relatively small (c. 0.5 mm) and the species consumes predominantly small copepods and their developmental stages (0.1–1.0 mm Purcell 1981a). *M. atlantica* exhibits size-based prey selectivity, positively selecting for larger copepods and negatively for copepod nauplii within this size range (Purcell 1982). This selectivity is probably a function of the feeding mechanics of *M. atlantica,* which involves the deployment of a three-dimensional array of fine tentacles (Section 1.4.3.2). Larger prey (that have faster swimming speeds) are more likely to collide with the feeding appendage, thus increasing encounter rates (Purcell 1981a).

Purcell (1982) found that the polygastric colonies of *M. atlantica* consumed an average of 5.5–10.5 prey siphonophore^{-1} day^{-1}; daily feeding rates are dependent upon the size (number of gastrozooids) of the colony. In my laboratory observations, polygastric colonies with a mean (±

standard deviation) of 8.5±2.9 functional cormidia (n = 38) consumed an average of 13.1±4.7 *Artemia* nauplii siphonophore^{-1} day^{-1}. This equates to an average of 1.7±0.9 prey gastrozooid^{-1} day^{-1}. These individual gastrozooid predation rates are remarkably similar those reported Purcell (1982) (0.6 prey gastrozooid^{-1} during the day and 1.5 prey gastrozooid^{-1} at night). There are no published reports of the feeding rates of the eudoxid stage of *M. atlantica*, but as the eudoxid originates as an individual component of the polygastric colony, the feeding rates could be assumed to be similar to one functional gastrozooid. However, it could be misleading to calculate eudoxid feeding rates by simply dividing polygastric feeding rates by the number of functional gastrozooids. My laboratory observations showed that eudoxid feeding rates were higher than those of individual polygastric functional gastrozooids (2–3 prey eudoxid^{-1} day^{-1}, n = 12). This could be due to the eudoxid having a greater size compared to its cormidial precursor, or perhaps due to a reduction in the intraspecific competition associated with the gastrozooids of neighbouring cormidia; however further investigation is required to understand eudoxid-feeding rates.

The laboratory experiments of Purcell (1982) suggested partial saturation of feeding at prey densities of 30 prey L^{-1}. This results indicates that the feeding rates of *M. atlantica* allows them to effectively utilise areas of high prey density, a common feature of jellyfish (e.g. Båmstedt 1990). High feeding rates of *M. atlantica* combined with high population density can result in large impacts on the populations of its prey. During an outbreak of *M. atlantica* in the German Bight, Greve (1994) calculated that the high density of polygastric colonies (500 colonies m^{-3}) could potentially clear the total available abundance of copepods; this was supported by an observed significant reduction in the abundance of copepods. Similarly, high densities of *M. atlantica* in the Adriatic (450 polygastric and 730 eudoxid colonies m^{-3}) were associated with a significant reduction in summer copepod abundance, which the authors attributed to predation by *M. atlantica* (Kršinić & Njire 2001). Employing the measurements of polygastric feeding rates estimated by Purcell (1982), a population of 450 colonies m^{-3} could consume 2475–4725 copepods m^{-3} day^{-1}. Incorporating the eudoxid feeding rates I have measured (considering a population of 730 colonies m^{-3}) results in an estimated total population predation impact of 3935–6915 copepods m^{-3} day^{-1}, a considerable proportion of the summer copepod population (Kršinić & Njire 2001). In addition to the predatory ecological role of *M. atlantica*, the species also functions as a competitor and as a source of prey for a wide range of species, including fish, pelagic molluscs and, in particular, other gelatinous zooplankton (reviewed in Mackie et al. 1987; Mapstone 2009).

The effects of dramatic predation can cascade through pelagic ecosystems (Behrends & Schneider 1995) inducing a range of ecosystem-level effects. As a result of the limited inter-specific predatory pressure experienced by *M. atlantica*, the incorporation of such enormous biomass into its populations inevitably restricts the transfer of energy to competitors, with knock-on effects for productivity across trophic levels. Alvariño (1980 and references within) reported an inverse relationship between the abundance of anchovy larvae and the competitor, *M. atlantica*, while in the German Bight, predation by *M. atlantica* removed grazing pressures, leading to unregulated phytoplankton growth and a significant reduction in nutrient levels (Greve 1994). These examples represent an indication of the type and scale of ecosystem-level effects induced by *M. atlantica*; however our understanding is still in its infancy.

In the absence of sufficient predation, the ultimate fate of the *M. atlantica* biomass is to sink to the benthos. Large pulses of jellyfish biomass may represent an episodic, yet highly significant contribution to the energy flux of benthic communities (Billett et al. 2006). Recent evidence suggests that a wide range of benthic organisms actively seek out and preferentially consume jellyfish depositions (e.g. O'Rorke et al. 2012; Sweetman et al. 2014). Evidence of mass depositions of *M. atlantica* blooms is almost non-existent, probably due to the small size and resultant rapid decomposition of its colonies. However, the invasion of the Adriatic by *M. atlantica* coincided with the mass appearance of gelatinous macro-aggregates and an increase in oncaeaid copepods, which are known to feed on gelatinous material (Kršinić and Njire 2001). Given the massive biomass that populations of *M. atlantica* can attain, these 'jellyfish falls' may have a potentially significant contribution to biogeochemical cycling. Employing estimates of the carbon content of the colonies of *M. atlantica* (Purcell 1982), together with the levels of abundance reported in the Adriatic example previously discussed (500 polygastric and 730 eudoxids m^{-3}; Kršinić and Njire 2001), it is possible to approximate these contributions. Considering an individual carbon content of ~0.13 mg for the polygastric and ~0.04 mg for eudoxid colonies (Purcell 1982) the peak total carbon content of the *M. atlantica* population is estimated to be ($[500 \times 0.13] + [730 \times 0.04]$) ~94.2 mg C m^{-3}. Wassman et al. (1998) estimated the total vertical flux of organic carbon in the Gulf of Trieste (Adriatic) to range from 800 mg C m^{-2} d^{-1} in June to 200 mg C m^{-2} d^{-1} in September. Whilst not directly comparable, these estimates indicate that, when abundant, *M. atlantica* may offer a significant contribution to the vertical flux of carbon in coastal ecosystems. However, other jellyfish, particularly members of the scyphomedusae, prey extensively upon *M. atlantica* (Purcell 1991; Sabatés et al. 2010) introducing additional complexity for the pathways of *M. atlantica* biomass recycling. Further research is required to better understand the ecosystem-level effects of *M. atlantica* and how this translates to the rates and fluxes in biogeochemical cycles.

1.4.4.2 Biogeography in the northeast Atlantic

Alvariño (1974) considered the congeners *M. atlantica* and *M. kochi* as cool- and warm-temperate analogues, respectively, with *M. atlantica* inhabiting the neritic waters of the temperate eastern and western Atlantic, but being substituted by *M. kochi* in the tropical-equatorial waters of the region (Alvariño 1971). However, the distribution of the species often overlaps (Kirkpatrick & Pugh 1984) and alternate periods of dominance of either species have been frequently observed in some areas (Mackie et al. 1987). In this section of the thesis I provide a brief historical overview of the distribution of *M. atlantica* in the northeast Atlantic, highlighting significant biogeographical changes that have occurred since the 1980s. For this overview I have considered published records (1910–2013) from the Greater North Sea, Celtic Seas, Bay of Biscay and Iberian Coast (OSPAR regions II, III and IV) and the Mediterranean Sea. To exclude potentially erroneous conclusions on the presence or absence of these two species, I have only considered records from sampling programmes that covered at least one full year, unless they contributed particularly relevant information (e.g. unusual occurrence, species co-occurrence). I also discuss changes in *M. kochi*, but only in so far as to examine relative changes in the congeners distribution and abundance.

Between 1900 and 1980, the available data shows that the distribution of *M. atlantica* was centred along the Atlantic coast of southwest Europe (Fig. 1.14A). Several studies report *M. atlantica* as the dominant calycophoran siphonophore, common throughout the Bay of Biscay (Patriti 1965; Moreno & Fernandez-Alcazar 1984), Iberian coast (Bigelow & Sears 1937; Patriti 1965; Gili & Fusté 1991), and the entrance to the Mediterranean (Bigelow & Sears 1937; Furnestin 1957). In this area the co-occurrence of *M. atlantica* and *M. kochi* was frequently detected (Beaudouin 1971; Gili & Fusté 1991) and at times *M. kochi* was the dominant species (e.g. Bigelow 1911; Leloup 1933; Beaudouin 1971).

Periods of alternating dominance in the abundance of the two congeners were first observed in the Western English Channel (WEC). Russell (1934) found that between 1913 and 1924 only *M. atlantica* occurred, however in 1925 *M. kochi* first appeared and completely replaced *M. atlantica* until 1931. Alternation in the dominance of the species continued until at least 1965 (Russell 1969). Although Russell (1934) found that the species were mutually exclusive, subsequent records show that the congeners did co-occur, although not at comparable relative densities (Russell 1947; Corbin 1949). In the WEC both species were shown to be transient components of the plankton (Russell 1935) (Fig. 1.14) arriving sporadically via the inflow of southwestern water from the Bay of Biscay (Gough 1905; Corbin 1947; Southward 1962). Further north, Fraser (1967) also detected the exceptionally rare occurrence of the two species in Scottish coastal waters, associated with the inflow of Atlantic waters characteristic of the 'Lusitanian stream', i.e. water originating from the outflow of the Mediterranean mixed with Bay of Biscay water (Fraser 1955).

Records show that the occurrence of *M. atlantica* in the Mediterranean during this period was low relative to that of *M. kochi* (e.g. Gamulin & Kršinic 1993). The sporadic occurrence of *M. atlantica* in the Mediterranean was primarily restricted to the west (Bigelow & Sears 1937; Cervigón 1958; Patriti 1964; Razouls & Thiriot 1968; Gamulin & Kršinic 1993), particularly in the Alboran Sea (Fig. 1.14A); the species was extremely rare in the eastern basin (Bigelow & Sears 1937; Lakkis 1971). The arrival of *M. atlantica* in the Western Mediterranean was associated with the inflow of Atlantic waters through the Gibraltar Strait (Bigelow & Sears 1937; Furnestin 1957). Although the occurrence of *M. atlantica* in the northwestern Mediterranean was primarily sporadic, there were instances when it was very abundant and outcompeted the normally dominant *M. kochi*. Cervigón (1958) found that *M. atlantica* was absent from the coast of Castellón in 1955 and 1956, but suddenly appeared in 1957 when it displaced *M. kochi*. Razouls & Thiroit (1968) reported a similar scenario in the Gulf of Lion, where the dominant *M. kochi* was replaced by *M. atlantica* in 1966, which then disappeared again in 1967.

Since the 1980s, significant changes in the distribution of *M. atlantica* in the Mediterranean have been reported, involving a progressive expansion of *M. atlantica* into the northwestern Mediterranean (Fig. 1.14B). Both Gili et al. (1987) and Riera et al. (1986) found that *M. atlantica* was the dominant siphonophore on the Catalan coast in the early 1980s, replacing the historically dominant species, *M. kochi* and *C. appendiculata*. Licandro et al. (2012) demonstrated that the shift in dominance from *M. kochi* to *M. atlantica* had occurred over an extended period (1985–1999) in the Bay of Villefranche. Then in 1995 *M. atlantica* was recorded for the first time in the Adriatic (Gamulin 2000), where it attained very high population density in 1997 (450 polygastric and 730 eudoxid colonies m^{-3}) (Kršinić & Njire 2001). Subsequent records indicate that the species is now established in the Adriatic (Lucic unpublished data cited in Lucic et al. 2005; Miloš & Malej 2005; Pestorić et al. 2012). These findings suggest that a widespread and persistent change has occurred in the northwest Mediterranean. Licandro et al. (2012) suggested a link between these changes and hydrological changes that occurred in the northwest Mediterranean under the forcing of large-scale climate oscillations.

Evidence exists to suggest that similar changes may have also occurred in the Celtic Seas and North Sea (Fig. 1.14B). Since the late 1960s the abundance of *M. atlantica* has dramatically increased in the WEC, while *M. kochi* has not been as frequently observed (Southward et al. 1995). This decade also saw an increase in the frequency of occurrence of *M. atlantica* in Irish coastal waters (Jeal & West 1970). More recently, in 1989 *M. atlantica* was recorded for the first time in the German Bight (Greve 1994), when very high population density was recorded (500 polygastric colonies m^{-3}). Then in 2002 the species occurred at an unprecedented level of abundance in southern Norwegian coastal waters (Fosså et al. 2003), in an area where it had only previously been detected at very low abundance (Båmstedt et al. 1998). These observations suggest that there may have been an expansion of the distribution of *M. atlantica* in these parts of the northeast Atlantic region. However, these changes have not been the focus of the same level of rigorous analysis as has been applied in the Mediterranean (e.g. Licandro et al. 2012).

Whilst the arrival of *M. atlantica* and *M. kochi* in the WEC has been used as an indicator if southwestern water inflows (Russell 1935; Southward et al. 1995) it has long been recognised that the species' facility for rapid reproduction limits their utility as a water mass indicator (e.g. Gough 1905; Corbin 1947; Southward 1962). The various interactive factors that influence the distribution of these species are complex and present challenges to our understanding. Spatial and temporal changes in the abundance of jellyfish are driven by both biological and physical factors (Graham et al. 2001) and distributional changes could therefore reflect either the establishment of new resident populations or the translocation of individuals from other areas. Investigating the relative importance of these biological and physical factors would increase our understanding of the observed changes in the distribution of *M. atlantica* in the northeast Atlantic.

In this thesis I address long-term changes in the distribution of *M. atlantica* in the Celtic Seas and North Sea. Chapter 2 addresses changes in the WEC and Chapter 4 addresses changes in the east and west coasts of Scotland.

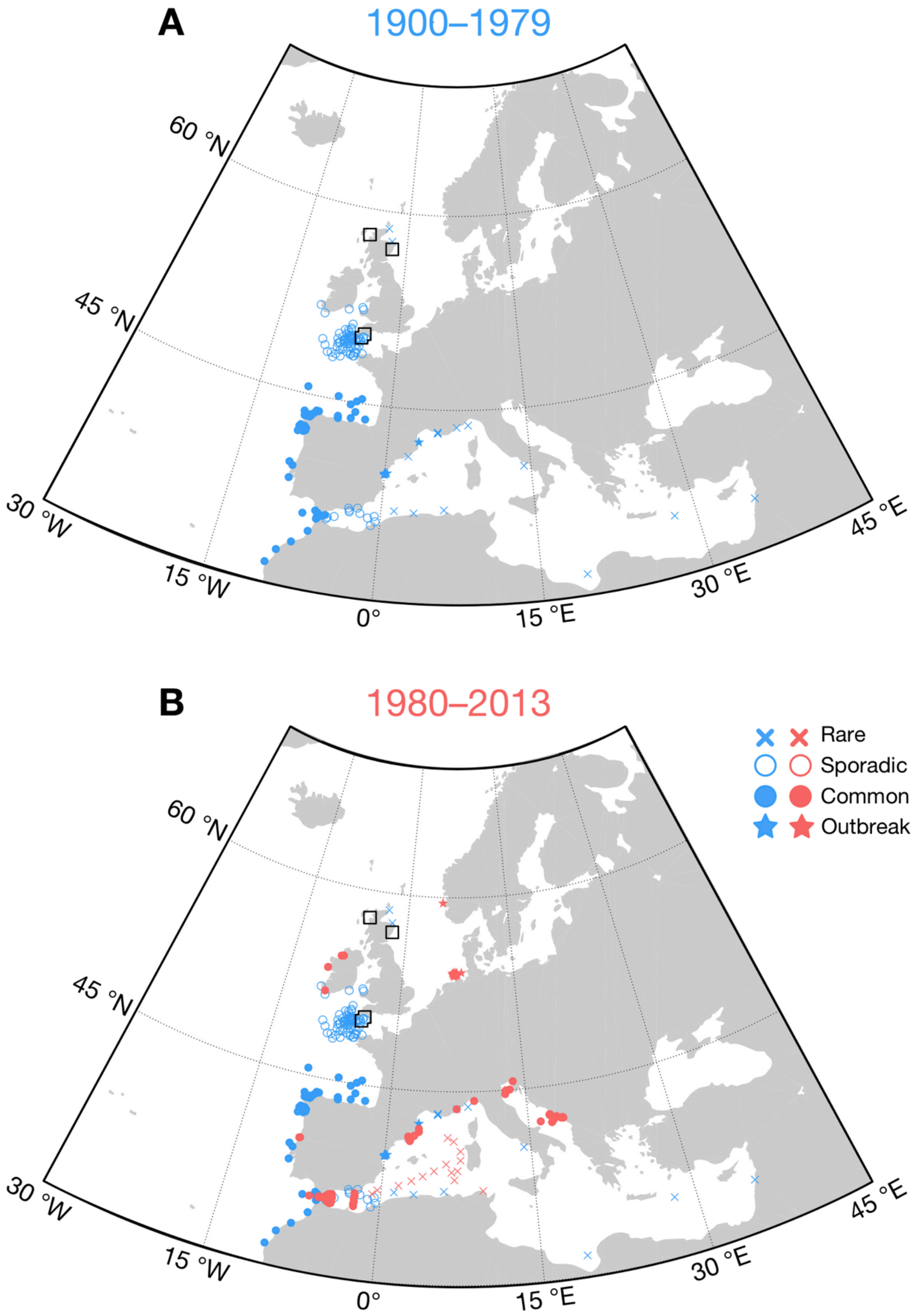

Fig. 1.14. Historic and contemporary distribution of *Muggiaea atlantica* in the northeast Atlantic. (A) Distribution of *M. atlantica* from 1900–1979. (B) Distribution of *M. atlantica* from 1980–2013. Rare records indicate very low abundance and highly sporadic occurrences; Sporadic records indicate low abundance with little temporal continuity; Common records indicate high abundance with temporal continuity; and Outbreak records indicate very high abundance with no temporal continuity. The black squares indicate the sampling locations that were utilised in this thesis.

1.4.4.3 Phenology and population dynamics

As is the case for most species of jellyfish, the abundance of *M. atlantica* is highly seasonal. In the northeast Atlantic the species typically achieves two annual peaks of abundance, consisting of a primary maxima in spring–summer followed by a secondary maxima in autumn–winter (Cervigón 1958; Moreno & Fernandez-Alcazar 1984). However in some years a single high amplitude peak is more consistently observed (e.g. Licandro et al. 2012). Little is known about the mechanisms that regulate these population dynamics. However, high abundance of the species has been consistently associated with a specific temperature range of ~14.0–16.0°C (Moreno & Fernandez-Alcazar 1984; Licandro et al. 2012; Batistić et al. 2013), indicating the importance of suitable thermal conditions for reproduction (e.g. Carré & Carré 1991). However, food availability inevitably also plays a fundamental role in determining the phenology of the species blooms (e.g. Purcell 1982), as has been suggested for other Calycophorae (e.g. Silguero & Robison 2000; Hosia & Båmstedt 2008).

Our understanding of the population dynamics of *M. atlantica* is particularly limited, mainly attributable to the paucity of information that is available on the different life stages. As is to be expected from the life cycle of the Calycophorae, the eudoxid stage is typically more abundant than the polygastric stage (Purcell 1982; Pugh & Boxshall 1984). The relative abundance of the polygastric and eudoxid stages of other species of Calycophorae have been used to infer information on their reproductive cycles (Moore 1949; 1952) and reproductive output (e.g. Dallot et al. 1988). Information on the larval stage(s) and the size distributions of the colonies enable aspects of the population dynamics, such as overwintering strategies and generation shifts (e.g. Hosia & Båmstedt 2008), to be considered. However these data are typically rare. As far as I am aware, Batistić et al. (2013) provide the only published account of the seasonal abundance and succession of the polygastric, eudoxid and calyconula stages of *M. atlantica.* They found that in a marine lake on the island of Mijlet, in the Adriatic, there was a peak in the abundance of eudoxid gonophores in May, which was followed by a peak in the abundance of the polygastric colonies and the calyconulae larvae one month later in June. In the northwestern Mediterranean, Gili et al. (1987) found that there was a peak in the abundance of gonophores two months prior to the peak abundance of the polygastric stage. No information exists on the total number of eudoxids produced by *M. atlantica* polygastric colonies, the lifespan of eudoxids, their gonophore production rates or the total number of gonophores produced by eudoxids. Without developing our knowledge of such fundamental aspects of reproduction our ability to understand population dynamics and estimate productivity is severely limited.

In this thesis I investigate the population dynamics of *M. atlantica* in the WEC. Chapter 3 addresses the functional relationship between the polygastric and eudoxid stages of *M. atlantica*, revealing aspects of the species population dynamics and the influence of environmental conditions.

1.4.5 Human interactions

Human interactions with *M. atlantica* are primarily related to fisheries and aquaculture operations, sectors that represent multibillion-dollar industries and important food sources for humans. These interactions arise primarily as a result of the competitive and predatory relationships between *M. atlantica* and various commercially valuable species of fish, and the capacity for *M. atlantica* to sting and injure farmed fish. In addition, the sting of *M. atlantica* can produce discomfort in humans, potentially affecting tourism activities.

1.4.5.1 Fisheries

Jellyfish interfere with fisheries operations directly by clogging nets, spoiling catches and stinging fishers and indirectly by competing with fish and larvae and by predation on fish eggs and larvae (Section 1.3). The clogging of fishing nets by *M. atlantica* is unlikely, due to its small size (Section 1.4.1) relative to the mesh aperture of most commercial fishing gear. When sufficiently abundant, it is conceivable that the sting from this species could spoil catches and injure fishers; however, there are no known reported incidences. The effects of *M. atlantica* on fisheries operations are primarily indirect, arising as a result of competition with target species and predation of their eggs and larvae. The principal source of prey for *M. atlantica* is small copepods and their developmental stages (Section 1.4.4.1), a dietary characteristic shared by many commercially important species of fish and their larvae. The interactions of *M. atlantica* with fisheries have not been fully explored. However, Alvariño (1980 and references within) reported an inverse relationship between the abundance of anchovy and *M. atlantica* in the Pacific, a factor the authors attributed to the effects of competitive pressures. Alvariño (1980 and references within) also reported observing *M. atlantica* consuming clupeid larvae, however, considering the prey size accepted by *M. atlantica* (0.1–1.0 mm; section 1.4.4.1) the majority of larval clupeids (and other commercially valuable species of fish) probably rapidly outgrow the prey size range for *M. atlantica*.

1.4.5.2 Aquaculture

Whilst problems involving jellyfish and capture fisheries typically involve large jellyfish species that are retained by commercial fishing gear, problems with aquaculture often involve small species that are not excluded by aquaculture nets. When abundant, these small jellyfish species (or fragments of larger species) infiltrate coastal aquaculture pens where they come into contact with fish. Stings can result in skin lesions and gill damage when they are drawn through the mouths and across the gills of fish as they respire (Fig. 1.15A–C). These injuries can result in the spoiling of harvests, reduction of productivity, and in extreme cases, mass mortality (Baxter et al. 2011; Allan & Burnell 2013). In the European Union (EU), the aquaculture industry is valued at €3.2 billion and accounts for one-quarter of all EU production of fish, molluscs and crustaceans. Since the 1980s, aquaculture problems attributed to jellyfish have been increasing (Allan & Burnell 2013). In the EU, problematic species mainly include members of the Hydrozoa: hydromedusae and siphonophores (Baxter et al. 2011; Allan & Burnell 2013), although some larger scyphomedusae also cause significant problems (e.g. *Aurelia aurita* and *Pelagia noctiluca*, Allan & Burnell 2013). *M. atlantica* has been implicated in mass mortalities of farmed salmon in Norwegian (>100,000 mortalities; Fosså 2003) and Irish (>1,000,000 mortalities; Cronin et al. 2004) coastal waters, resulting in significant economic losses. In the Mediterranean, *M. atlantica* has also been identified as the likely cause of farmed sea bass (*Dicentrarchus labrax*) mortalities (Bosch-Belmar et al. 2014). Recently, Baxter (2011) identified *M. atlantica* and a species of hydromedusae (*Solmaris corona*) as the causative agents of clinically significant gill damage (Fig. 1.15D–E) in marine farmed salmon (*Salmo salar*) on the Irish coast. Jellyfish species can also act as vectors for fish diseases and parasites (Ferguson et al. 2010); *M. atlantica* has recently been identified as a vector for the bacterium *Tenacibaculum maritimum* (Fringuelli et al. 2012), a common fish pathogen, that causes bacterial infections in gill tissues. In the UK the majority of aquaculture production is in Scotland, associated with the farming of salmon (*Salmo salar*) and sea trout (*Salmo trutta*)(Ellis et al. 2012). *M. atlantica* is currently considered as an extremely rare species in Scottish coastal waters (Heath et al. 1999) and is thus not considered as a threat to aquaculture operations. However, any potential extension of the range of this species in UK waters could have significant impacts on the aquaculture industry.

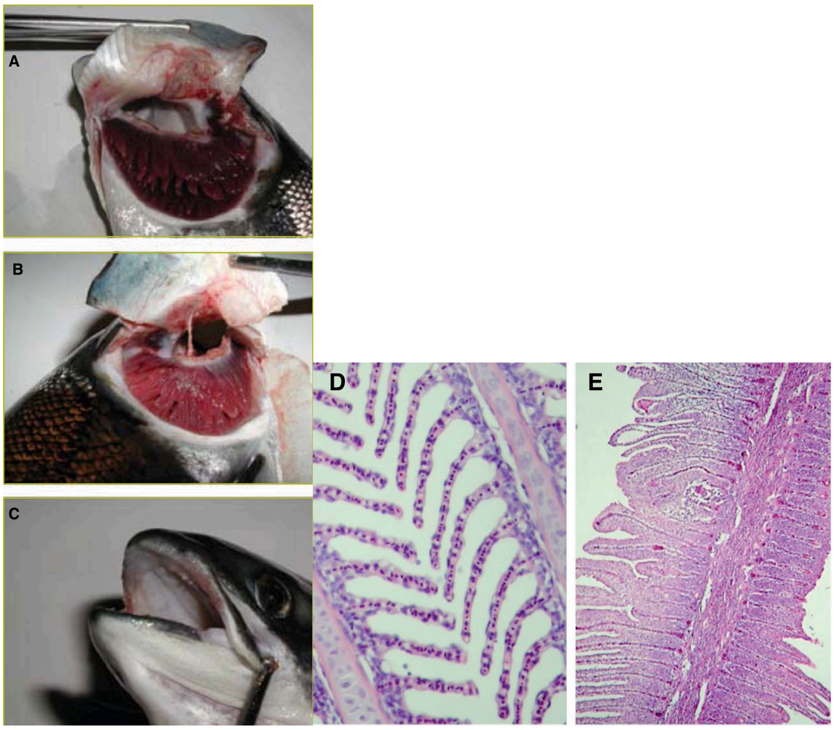

Fig. 1.15. Injuries to farmed salmon *(Salmo salar)* caused by stinging by *M. atlantica.* (A–B) Tissue damage evident on the gills of farmed salmon; (C) skin lesions around the mouth; (D) histological example of healthy salmon gills and (E) histological sample of damaged gills (x200 magnification). A–C adapted from Fosså et al. (2003); D–E adapted from Baxter et al. (2011).

1.4.5.3 Tourism and recreation

Despite the small size of *M. atlantica* it has a potent sting and when abundant it can cause considerable discomfort to humans. The mass occurrence of *M. atlantica* in Norwegian coastal waters in 2002 coincided with localised reports of the stinging of bathers (Fosså 2003). To the best of my knowledge this is the only reported instance of human injuries associated with *M. atlantica* stings. However, in the Mediterranean jellyfish stings represent a serious problem for the tourism industry, with large economic ramifications (Cegolon et al. 2013). Whilst these problems in the Mediterranean are typically associated with larger, more conspicuous jellyfish (i.e. *Pelagia noctiluca*), it is unclear to what extent *M. atlantica* contributes.

1.5 Thesis aims and objectives

Using long-term data collected from a network of coastal monitoring stations, together with data on a range of local and regional environmental factors, thesis aims (1) to assess recent changes in the abundance and distribution of *M. atlantica* in the coastal waters of the United Kingdom; and (2) to investigate the influence of environmental variability on both the biological (i.e. demography) and physical (i.e. dispersal) processes that drive these changes.

The specific objectives of the thesis are to address the following research questions:

1) Have the abundance and distribution of *Muggiaea atlantica* in UK waters changed?
2) Are these distributional changes associated with the establishment of resident populations or alternatively are these transient populations that are dependent on immigration from other areas?
3) What are they key environmental parameters that affect this species' population dynamics and abundance; and how does this affect its distribution?

Chapter 2

Long-term variability of *Muggiaea atlantica* and *M. kochi* in the Western English Channel

2. Long-term population variability of *Muggiaea atlantica* and *M. kochi* in the Western English Channel

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2.1 Abstract

We investigated long-term variability of the calycophoran siphonophores *Muggiaea atlantica* and *Muggiaea kochi* in the Western English Channel (WEC) between 1930 and 2011. Our aims were to describe long-term changes in abundance and temporal distribution in relation to local environmental dynamics. In order to better understand mechanisms that regulate the species' populations, we identified periods that were characteristic of *in situ* population growth and the environmental optima associated with these events. Our results show that between 1930 and the 1960s both *M. atlantica* and *M. kochi* were transient components of the WEC ecosystem. In the late 1960s, *M. atlantica* successfully established a resident population in the WEC, while the occurrence of *M. kochi* became increasingly sporadic. Once established as a resident species, the seasonal abundance and distribution of *M. atlantica* increased. Analysis of environmental conditions associated with *in situ* population growth revealed that temperature and prey were key determinants of the seasonal distribution and abundance of *M. atlantica*. Salinity was shown to have an indirect effect, likely representing a proxy for water circulation in the WEC. Anomalies in the seasonal cycle of salinity, indicating deviation from the usual circulation pattern in the WEC, were negatively associated with *in situ* growth, suggesting dispersal of the locally developing *M. atlantica* population. However, our findings identified complexity in the relationship between characteristics of the environment and *M. atlantica* variability. The transition from a period of transiency (1930–1968) to residency (1969–2011) was tentatively attributed to structural changes in the WEC ecosystem that occurred under the forcing of wider-scale hydroclimatic changes

2.2 Introduction

Blooms of jellyfish (pelagic Cnidaria and Ctenophora) are a characteristic feature of planktonic ecosystems (Boero et al. 2008; Condon et al. 2012) and have been for millennia (e.g. Hagadorn et al. 2002). However, dramatic shifts in the spatio-temporal distribution and abundance of blooms have been identified in numerous marine habitats over recent decades (Mills 2001; Purcell et al. 2007). Jellyfish are important predators (Mills 1995), with complex ecosystem-level effects (Pitt et al. 2009) and a range of socio-economic impacts (Purcell et al. 2007; Lucas et al. 2014a). Therefore developing our understanding of factors affecting their populations is of high importance (Condon et al. 2012).

Both biological and physical factors influence jellyfish populations. Changes in abundance may occur through reproduction and mortality, or through physical processes of aggregation and redistribution (Graham et al. 2001). Environmental factors, including temperature, food availability and salinity, have been shown to directly affect jellyfish populations (Purcell 2005); thus localised environmental variability may regulate populations. However, fluctuations may also occur indirectly, as a result of changes to circulation patterns, i.e. through advection (e.g. Decker et al. 2013 and references therein). Differentiating these 'real' and 'apparent' events (Graham et al. 2001) is important for developing a mechanistic understanding of how jellyfish populations respond to variable environmental conditions (Lucas & Dawson 2014).

The calycophoran siphonophores *Muggiaea atlantica* (Cunningham 1892) and *Muggiaea kochi* (Will 1844) are holoplanktonic colonial jellyfish. They have a metagenic life cycle, comprising an alteration of generations between an asexual polygastric colony and a sexual monogastric eudoxid. Under favourable conditions, short generation times and simultaneous sexual and asexual reproduction can facilitate rapid population growth (Mackie et al. 1987). Typically inhabiting superficial waters (<200m; Pugh 1999), *Muggiaea* are also particularly susceptible to transport in ocean surface currents (Mackie et al. 1987), which may facilitate the formation of 'apparent' blooms or aggregations.

In the Atlantic Ocean and adjacent seas, *M. atlantica* and *M. kochi* inhabit predominantly neritic waters between 55°N–37°S and 48°N–36°S, respectively (Alvariño 1971; Pugh 1999). The congeners rarely co-occur at comparable densities (Mackie et al. 1987 and references therein) and are considered cool-temperate and warm-temperate analogues, respectively (Alvariño 1971). However, recent findings suggest that *M. atlantica* has expanded its distributional range. Since the mid-1980s *M. atlantica* has progressively colonised the Western Mediterranean (Riera et al. 1986; Licandro & Ibañez 2000; Licandro et al. 2012) and Adriatic (Kršinić & Njire 2001; Batistić et al. 2007), probably in response to hydrological variability that occurred under the forcing of large-scale climate oscillations (Licandro & Ibañez 2000; Licandro et al. 2012). Around the same time, unprecedented blooms of *M. atlantica* were also reported in coastal regions of the North Sea (Greve 1994; Fosså et al. 2003).

Large blooms of *M. atlantica* can cause significant ecological and economic impacts. Predation by *M. atlantica* caused a restructuring of the copepod community during its invasion of the Adriatic (Kršinić & Njire 2001) and produced cascading ecosystem effects in the German Bight (Greve 1994). *M. atlantica* has also been identified as the causative agent of mass mortalities in farmed fish (Baxter et al., 2011), causing significant economic loss for aquaculture operations in Norway (Fosså et al. 2003) and Ireland (Cronin et al. 2004). The geographical expansion of *M. atlantica* may have significant impacts on the ecological and economic productivity of newly colonised regions.

The present study is based on long-term observations from the early 20th Century in the Western English Channel (WEC). As a biogeographical transition zone and a boundary region between neritic and oceanic waters (Southward et al. 2005) the WEC ecosystem is highly sensitive to hydroclimatic change (Southward et al. 1995). Previous studies have suggested multi-decadal oscillations of the WEC ecosystem between two quasi-stable states, characterised by northern cold- and southern warm-water planktonic assemblages (see Southward 1980; Southward et al. 1995; Southward et al. 2005 for reviews). *M. atlantica* and *M. kochi* have been considered transient southwest species (Gough 1905; Southward 1962) indicative of the influx of water from the south (Russell 1935; Corbin 1947; Southward 1962). More recent studies (Southward et al. 1995; Coombs & Halliday 2009) indicate that *M. atlantica* abundance has increased dramatically since the late 1960s. However, the congeners have not been the focus of a rigorous analysis and more recent records have not been investigated.

Here we use the updated *Muggiaea* time-series to describe its long-term variability in the WEC and to verify its relationship with local environmental dynamics. In order to better understand mechanisms that regulate the species' populations, we identify annual blooms characteristic of *in situ* population development, and the environmental optima associated with these events.

2.3 Materials and methods

2.3.1 Data sources and descriptions

2.3.1.1 Study site

The Marine Biological Association of the United Kingdom (MBA) has routinely collected data on the abundance of *Muggiaea* in the Western English Channel (WEC) since the early 20th Century. Physical environmental data were collected at an open-shelf station (E1: 50.03°N, 4.37°W) located approximately 30 km off Plymouth (UK), in proximity to the 75 m isobath (Fig. 2.1). At station E1 the water column is well stratified in summer (Pingree & Griffiths 1978), with the pycnocline typically occurring at 20 m depth (Smyth et al. 2010). Biological data were collected primarily at the adjacent station L5 (50.18°N, 4.30°W), which has a depth of 65 m (Fig. 2.1). This station is usually less strongly stratified in summer than E1 (Southward et al. 2005 and references therein). Samples were also collected from E1 and, occasionally, some other local sampling sites (see Southward et al., 2005). Both stations E1 and L5 are free from direct estuarine influence (Southward et al. 2005) and are considered to be representative of the wider WEC area (Southward 1962).

2.3.1.2 *Muggiaea* data

Data on the abundance of *M. atlantica* and *M. kochi* were collected at the sampling stations on a quasi-monthly basis between 1930 and 2011 (with major interruptions during 1941–1945 and 1988–1995). These data were collected using double oblique hauls from ~65 m depth to the surface. A range of sampling gears has been employed; mostly 1 m and 2 m diameter ring nets during the early years then variants of a 0.9 m square inlet net (700–800 um mesh size; see Southward et al. 2005 and references therein). After estimating the total volume of water filtered (assuming 100% filtration efficiency), all counts were adjusted to represent a nominal 4000 m^{-3} sample volume (see Southward & Boalch 1986 for further methodological details). For the present study data were expressed as ind. 100 m^{-3}. Records of *Muggiaea* only concern polygastric colonies; eudoxids were not recorded.

Plankton exhibit heterogeneous spatial distributions (Graham et al. 2001) and sampling effort can influence estimates of jellyfish abundance (e.g. Lynam et al. 2011). Despite this, Southward et al. (2005) have shown that the samples collected in the present study accurately represent seasonal changes in abundance in the wider northern Channel region. The use of different sampling equipment may have also influenced estimates of abundance (Southward 1970), however, it has been shown that nets with a mouth diameter of ~1 m and a mesh size of ~700 μm produce quantitative estimates of colonial gelatinous zooplankton abundance (Braconnot 1971). Standardising counts to unit volume of water sampled mitigates these factors, but some bias undoubtedly still exists (Coombs & Halliday 2009). Nevertheless, seasonal patterns of variability remain representative (Southward 1970; Coombs et al. 2005).

2.3.1.3 Environmental data

Sea surface temperature (SST, °C), depth-integrated salinity (0–50 m) and copepod abundance (ind. 100 m^{-3}) were considered as descriptors of *Muggiaea*'s ambient environment. Temperature and salinity data at 10 m depth intervals (0–50 m) were collected by the MBA at station E1 using a thermometer and salinity bottles between 1930 and 1987 and conductivity, temperature, depth (CTD) probes thereafter (see Smyth et al. 2010 for additional methodological details). Temperature at surface was highly correlated with temperature at 50 m depth (Pearson's correlation, >0.85). Therefore, considering the lower number of missing values in the SST dataset, we used SST, rather than depth-integrated sea temperature, to investigate the long-term variability of seawater temperature in the WEC. This also facilitated comparison with long-term SST records from the wider area (50°N to 50.5°N, 4°W to 4.5°W) obtained from the British Atmospheric Data Centre (BADC) HADISST 1.1 dataset (http://badc.nerc.ac.uk).

Data on the abundance of copepods from a 1° by 2° grid in the study region (49°N to 50°N, −3°W to −5°W) were extracted from the Continuous Plankton Recorder (CPR) database for the period 1958–2011 (see Batten et al. 2003 for details of the sampling methodology). Considering the size range of *M. atlantica* prey (0.1–1.0 mm; Purcell 1981a) and the predominance of copepod stages in its diet (Purcell 1982) we considered data on total copepods <2 mm (ind. 100 m^{-3}). Although the CPR only provides an estimate of the copepod standing stock in surface waters, these data provide a good representation of seasonal patterns of copepod variability in the WEC (John et al. 2001).

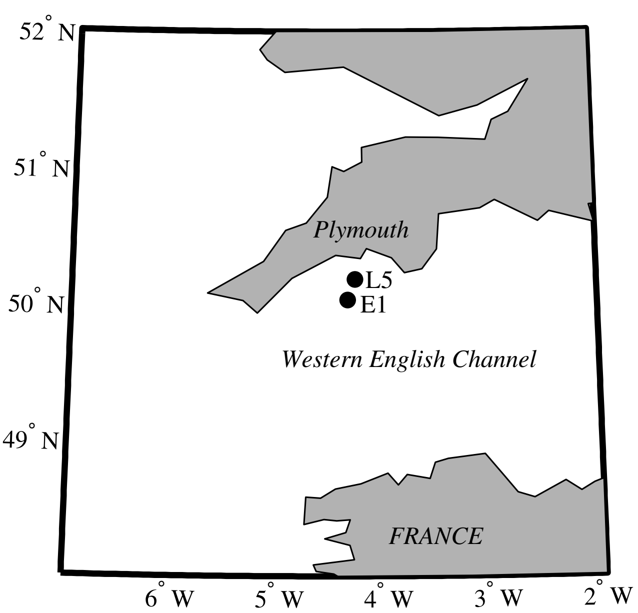

Fig. 2.1. Map of the Western English Channel with the locations of the sampling sites L5 and E1 indicated.

2.3.2 Numerical analysis

2.3.2.1 Treatment of missing data

Extensive gaps due to sampling interruptions and numerous random missing data (due to weather constraints, equipment failure, etc.), prevented the use of traditional time-series analysis tools and necessitated pre-treatment of the data. Sampling frequency was adjusted to monthly values by taking the arithmetic mean when the number of data for a given month was greater than 1. In order to homogenise annual sampling effort, descriptors (excluding SST) were processed in two steps: (1) years comprising less than 7 months of data, or containing more than 4 months consecutive missing data were removed; (2) random missing data (MD) remaining in the truncated data series' were predicted using the eigenvector filtering (EVF) method (Colebrook 1978; Ibañez & Conversi 2002). The EVF method involves a Principal Component Analysis (PCA) performed on an autocovariance matrix composed of the original series (with MD) lagged progressively. The MD are then predicted through iterative computation of the autocorrelation function (Ibañez & Conversi 2002). Although our descriptors represent discontinuous time-series, the EVF provided a suitable method as all variables exhibited strong seasonal cycles and the windows of prediction were small (<4 consecutive missing data). In the case of SST, missing data were replaced by their corresponding HadISST values after verifying the high correlation of the two series (Pearson's correlation, $r = 0.97$, $p = <0.001$).

2.3.2.2 Temporal variability

Monthly values of biological data collected between 1930 and 2011 were transformed (log 10 [x + 1]) to reduce data variance. These data were then represented together with environmental data as contour plots to show the main patterns of seasonal and interannual variability. Interannual variability was also represented by standardised anomalies (z-scores), computed as deviations from the mean of the time series divided by the standard deviation of the time series.

2.3.2.3 *In situ* population growth of *Muggiaea*

Following the methodology described in Licandro et al. (2006), we distinguished gradual population increases characteristic of biological production *in situ* from random events. First, peaks and troughs of abundance (turning points) were identified following Kendall's information theory (Kendall 1976). Second, the quantity of information (QI) associated with the probability to observe a turning point was calculated using the algorithm of Ibañez (1982). Turning points with high QI represent gradual changes over time, whereas those with low QI reflect abrupt (random) events. Ibañez (1982) demonstrated that turning points characterised by QI > 4.3 bits can be considered non-random at the 95% significance level.

We considered consecutive months between a significant trough and peak as an informative period (IP), i.e. a period in which the population was developing *in situ* under the influence of local environmental conditions. Conversely, turning points characterised by low QI were considered random events, indicative of lateral advection from surrounding areas. To ensure that only chronological months contributed to IPs, turning points identified close to the boundaries of missing data were disregarded.

2.3.2.4 Environmental preferences of *Muggiaea*

Considering the informative periods (IP), environmental conditions associated with high abundance were identified using the method proposed by Perry & Smith (1994). This method compares the cumulative distribution function (CDF) of the environmental conditions during the IP, against the CDF of the environmental data that have been weighted by species abundance. Similar CDFs imply a random association between abundance and environmental conditions, whereas dissimilar CDFs indicate a consistent association between species abundance and particular environmental conditions. The maximum difference between the two CDFs represents the environmental condition associated with maximal species abundance; this was considered to represent the optimal environmental condition. The significance of the association was tested using a randomisation test with 10,000 permutations.

2.3.2.5 Environmental influence on seasonal distribution of *Muggiaea*

We explored the influence of local environmental variability (SST, salinity and copepod abundance) on the seasonal distribution of *Muggiaea* using the multi-table STATIS method (Lavit et al. 1994). STATIS is an extension of Principal Component Analysis designed to analyse multiple data tables describing sets of variables measured on the same observations. STATIS has been used previously in the field of ecology, mainly to assess spatial (e.g. Gaertner et al. 1998) or temporal (e.g. Licandro & Ibañez 2000) variability in species assemblages. In the present study we utilised STATIS to investigate interannual variability in the seasonal structure of the local environment. Relationships between environmental characteristics and the seasonal distribution of *Muggiaea* were explored by incorporation of *Muggiaea* as supplementary variables.

Records of SST, salinity and copepod abundance were arranged into yearly data tables with columns describing environmental variables and rows describing monthly observations. The columns of each table were centred and normalised (sum of squared elements = 1) and each table was then normalised (total variance = 1) to ensure all tables participated equally in the analysis. The STATIS analysis proceeded in three steps, which are described below, following the methodology of Abdi et al. (2012):

2.3.2.5.1 Interstructure analysis

The interstructure analysis involves the eigendecomposition of the tables' similarity structure. This provides an ordination of the years, identifying similarities based on their environmental characteristics. The first eigenvector of this eigenanalysis also provides table weights used to compute the compromise.

2.3.2.5.2 Compromise analysis

For the compromise analysis the individual tables are gathered to form the compromise table. The generalised singular value decomposition of this table, under the constraints of the table weights, provides an ordination of the tables' global structure. This represents the information common to all the tables, in our case the average seasonal environmental cycle. At this step we also projected the average seasonal cycle of *Muggiaea* as supplementary variables by computing correlation coefficients with the axes of the compromise.

2.3.2.5.3 Trajectories analysis

The trajectories analysis involves the projection of the individual tables onto the axes of the compromise. This step allows visualisation of the similarities and differences amongst the years' structures, i.e. environmental cycles. At this step *Muggiaea* were incorporated as supplementary variables by computing correlation coefficients with the axis of the compromise. Both the compromise and trajectories analyses were presented in two-dimensional maps inside a circle of correlation (radius = 1).

At the interstructure step we also included a cluster analysis; average linkage hierarchical agglomerative clustering based on the Euclidean distance was used to identify groups of similar years. Also, in addition to projecting *Muggiaea* species as supplementary variables, months characterised by *in situ* growth (IPs) were superimposed on plots of the trajectories.

In summary, the STATIS analysis produced three main results: (1) the interstructure, which identifies the similarity between years' environmental characteristics; (2) the compromise, which represents the typical annual environmental cycle; and (3) the trajectories, which reveal the similarities and differences amongst the years.

All analyses were programmed using MATLAB® (R2013b 8.2.0.701), with the exception of the informative periods which utilised the PASTECS library (Ibañez et al. 2009) for R (R Core Team 2012).

2.4 Results

2.4.1 Temporal variability of environmental conditions

The mean annual sea surface temperature (SST) was generally below or around the long-term mean (12.63 ± 0.42 °C) from 1930 to 1994 (with the exception of 1949, 1959–1960, and 1989–1990), while values consistently higher were recorded afterwards (Fig. 2.2A). The highest positive anomalies were recorded in 1959, 1989 and 2007, while the lowest were in 1963 and 1986.

The seasonal cycle of SST was characterised by a sinusoidal pattern, with minimum values in February and maxima in August (Fig. 2.3A). Temperature at surface ranged from 8.80 °C to 10.55 °C in winter (January–March), 10.52–12.90 °C in spring (April–June), 14.80–17.55 °C in summer (July–September) and 11.97–14.10 °C in autumn (October–December). Maximum SST values were recorded in August 1976 (19.10 °C) and July 1983 (19.26 °C), while minima were recorded in February 1947 (7.42 °C) and March 1986 (7.50 °C).

Mean annual depth-integrated salinity (0–50 m) was generally below the long-term average (35.21 ± 0.10) during the 1930s (with the exception of 1934, 1935 and 1938) and from 1977 to 1985 (except 1979, Fig. 2.2B). On the other hand, salinity was mostly close to, or above the long-term average from 1948 to 1976, and constantly above average after 2005. Minimal yearly averages of salinity were recorded in 1936 and 1982, while maxima occurred in 1956 and 1965.

Maximum values of depth-integrated salinity were typically observed during the winter months. Minima generally occurred in summer, although pulses of reduced salinity were common throughout the years, particularly in 1936, 1977, 1982 and 1983 (Fig. 2.3B). Salinity varied on average from 35.10 to 35.46 during winter, 34.94–35.40 in spring, 34.91–35.38 in summer and 35.08–35.47 in autumn.

From 1958–1990 copepod abundance was generally above or around the long-term average (20268 ± 9010 ind. 100 m^{-3}), except during 1963–1968 and 1972–1974 (Fig. 2.2C). After 1990 copepod abundance was variable until stabilising around the long-term mean after 2001.

A common seasonal feature of copepod abundance was a recurrent spring peak (Fig. 2.3C). Secondary peaks were also common in summer, particularly from 1980 to 2000. Since 2001 copepods typically peaked in May and their abundance remained high throughout the summer. Lowest densities were normally observed in January–February. Particularly high copepod abundance was observed during spring of 1959 and 1987, summer of 1964 and autumn 1978 and 1987.

2.4.2 Temporal variability of *Muggiaea*

During the study period *M. atlantica* was the dominant species of *Muggiaea* in the Western English Channel (WEC), being recorded in 74% of the 636 months sampled (Fig. 2.3D). The appearance of the congeneric *M. kochi* was infrequent, occurring in only 19% of sampled months (Fig. 2.3E).

From 1930 until 1968 *M. atlantica* abundance was low; its mean annual abundance being consistently below the long-term average (Fig. 2.2D). During the 1970s *M. atlantica* abundance was close to the long-term mean. Then, after 1980, its abundance increased considerably, with yearly averages consistently above the long-term mean. Maxima were observed in 1996, 2005, 2006 and 2009 (Fig. 2.2D).

M. atlantica seasonal distribution was highly variable (Fig. 2.3D). Prior to the late 1960s its appearance was episodic. High seasonal abundance was recorded during August–December, with maxima typically recorded in September–October (max 300 ind. 100 m^{-3}). A noticeable change took place after the late 1960s, when *M. atlantica* started to be regularly recorded in the WEC. In the 1970s *M. atlantica* distribution became predominantly bimodal, with seasonal maxima occurring in August and secondary peaks developing in the autumn. Particularly high densities of *M. atlantica* were observed in August 1970 (1000 ind. 100 m^{-3}) and 1978 (1100 ind. 100 m^{-3}), whilst 1979 exhibited unusually low annual abundance. Years following 1980 were characterised by an extended seasonal occurrence, with *M. atlantica* being consistently recorded from April to December. Throughout the 1980s maximum abundance was observed in June–July with secondary peaks in autumn. From the late 1990s abundance typically remained high through summer and autumn after seasonal maxima in June–July. High amplitude seasonal maxima were recorded in 1996, 2005 and 2010 (max 1100–2200 ind. 100 m^{-3}).

From 1930 to 2011 *M. kochi* was occasionally recorded in high abundance in the WEC (i.e. in 1931, 1933, 1957–59, 1964, 1997–1998, 2007 and 2010) (Fig. 2.3E). Maximal annual anomalies were recorded in 1931, 1933, 1957 and 2010 (Fig. 2.2E). High seasonal abundance of *M. kochi* typically developed during August–November (max 2.5–88 ind. 100 m^{-3}; Fig. 2.3E). Whilst not mutually exclusive, *M. kochi* displayed a strong tendency to occur when *M. atlantica* was absent or scarce.

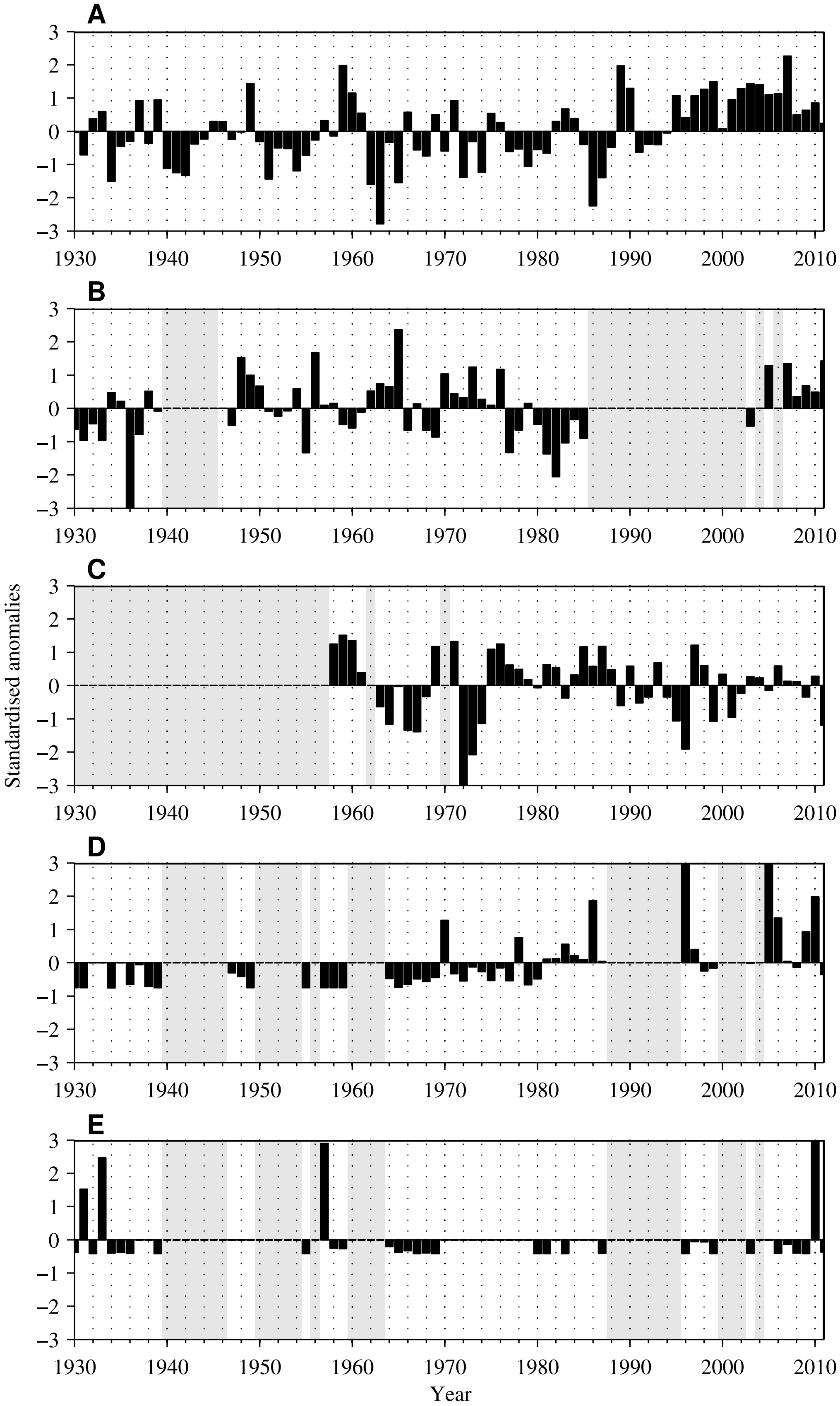

Fig. 2.2. Standardised anomalies of mean annual (A) sea surface temperature, (B) depth-integrated salinity (0–50 m), (C) copepods, (D) *Muggiaea atlantica*, and (E) *M. kochi*. Grey areas represent missing data.

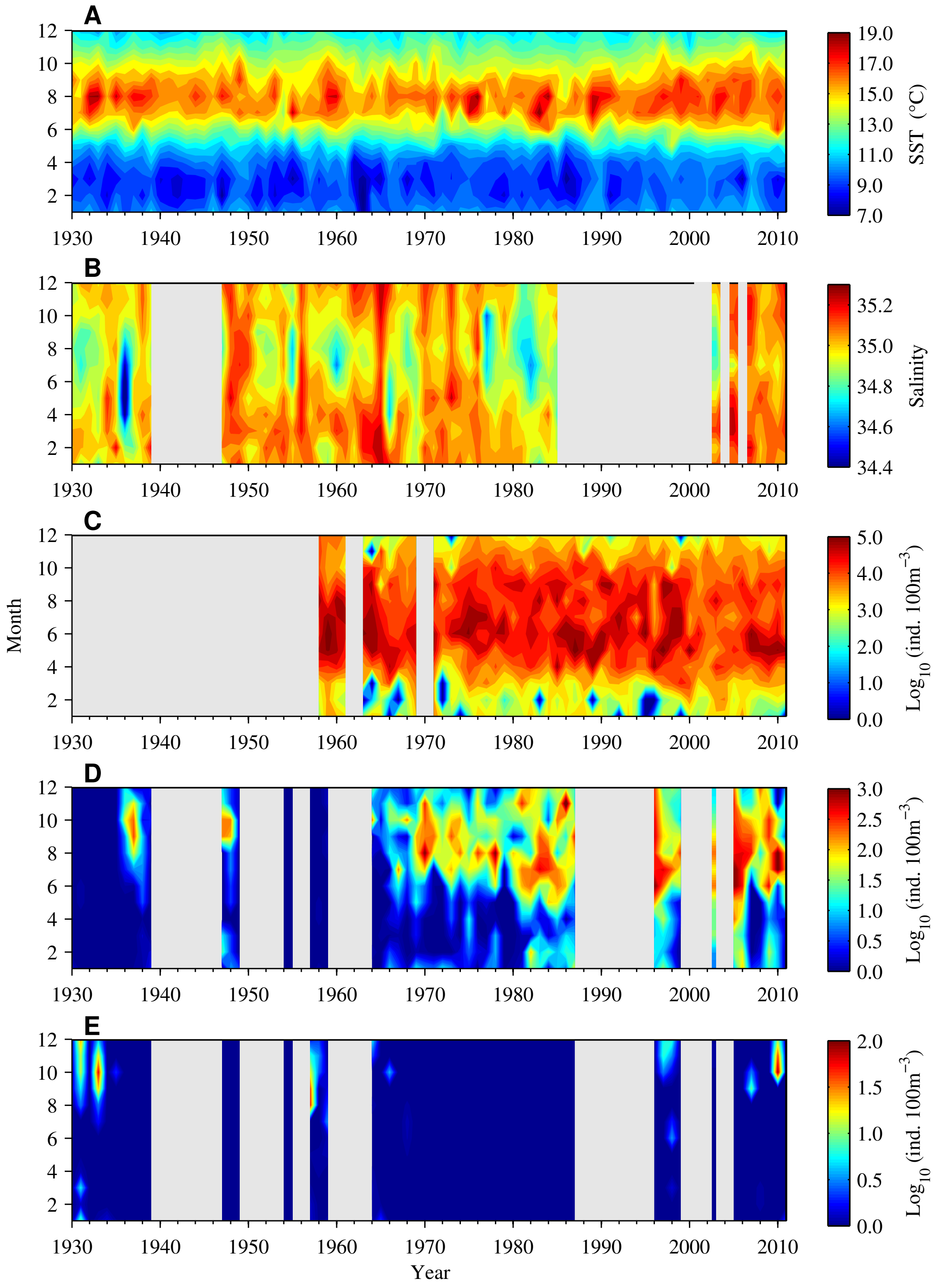

Fig. 2.3. Interannual and seasonal variability of (A) sea surface temperature, (B) depth-integrated salinity (0–50 m), (C) copepods, (D) *Muggiaea atlantica* and (E) *M. kochi*. Grey areas represent missing data.

2.4.3 *In situ* population growth

From 1930–2011 a total of 137 peaks and troughs were identified in the seasonal abundance of *M. atlantica* (Fig. 2.4). Before the late 1960s the majority of peaks and troughs were not statistically significant (75% and 81%, respectively), which we attribute to advection events and not *in situ* population growth. However, the population was developing *in situ* during May and October in 1936, 1937, 1938, 1948 and 1967 and during July–October in 1966 and 1969. During the 1970s seasonal patterns were predominantly related to *in situ* growth (73% of peaks and 50% of troughs were significant), with IPs observed in all but two years (1971 and 1972). Excepting 1979, IPs encompassed two peaks, indicating that the population diminished slightly between successive peaks. The onset of IPs varied from February (1975) to June (1974 and 1978) and extended to September–November. Primary peaks generally occurred in August with secondary peaks developing in autumn. From the 1980s onwards *M. atlantica* exhibited consistent *in situ* population growth every year (58% and 49% significant peaks and troughs, respectively). During the 1980s (not including 1987) the *M. atlantica* annual cycle was characterised by two distinct IPs, which were separated by a significant decrease in abundance. Primary peaks occurred in June–July while the onset of IPs was generally in April–May. The timing of IPs was variable. From the late 1990s onward the onset of IPs was variable but generally occurred in March–April, with peaks developing in June–August. Some years exhibited IPs with connected (1996 and 1997), or disconnected peaks (2009 and 2011), while single IPs were observed in 1999, 2003, 2005 and 2006. *In situ* growth was highly ephemeral in 2007 and 2010, lasting only two months (July–August). No IPs were identified in 2008.

The *M. kochi* population developed *in situ* in 1931, 1933, 1957, 1958 and 1959 (Fig. 2.4). Respectively, only 13% and 14% of the 54 peaks and 55 troughs identified over the whole study period were associated with significant QI. This suggests that the *M. kochi* population was developing in the area of study only rarely. The timing of *M. kochi* IPs was highly variable, with peaks occurring from June to December. No IPs were found in 1997, 1998 or 2010, despite relatively high abundance. *In situ* population growth of *M. kochi* and *M. atlantica* was mutually exclusive.

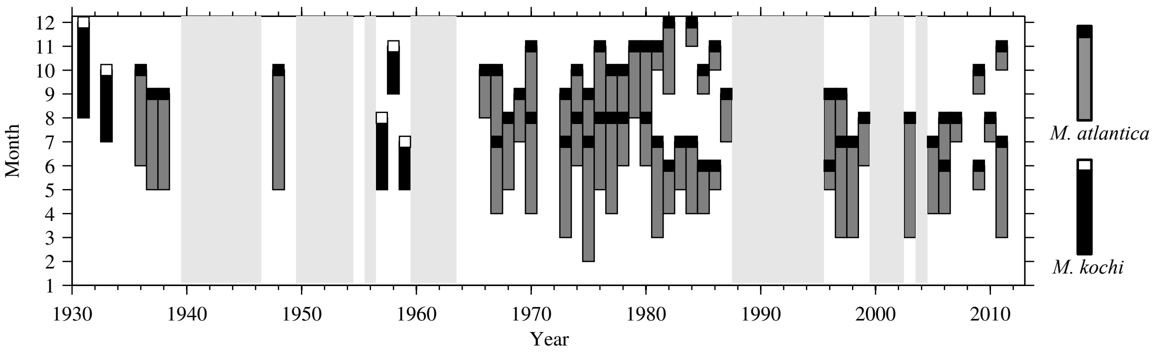

Fig. 2.4. *In situ* population growth of *Muggiaea* in the Western English Channel. Bars represent informative periods, i.e. months during which the population was developing *in situ*, while squares represent significant peaks of abundance. *Muggiaea atlantica*: grey bars and black squares; *Muggiaea kochi*: black bars and white squares. Light grey areas represent missing data.

2.4.4 Association of environmental descriptors with informative periods

The IPs of *M. atlantica* and *M. kochi* were characterised by similar environmental conditions. The *M. atlantica* population was developing *in situ* within a SST range of 8.9–19.3 °C, a depth-integrated salinity range of 34.52 and 35.46, and prey (copepod) abundance between 666 and 180,330 ind. 100 m^{-3}. The environmental conditions recorded during *in situ* development of the *M. kochi* population were SST between 11.2 and 18.8°C, salinities of 35.02–35.27, and prey densities between 12,061 and 198,100 ind. 100 m^{-3}, respectively.

Both temperature and prey abundance significantly influenced the distribution of *M. atlantica* informative periods (Fig. 2.5A and B). Peaks of abundance were significantly associated with temperatures of 14.6–15.5 °C ($p = <0.005$) and copepod abundance of 20,400–22,100 ind. 100 m^{-3} ($p = <0.1$; Table 2.1). No association with salinity was apparent (Table 2.1, Fig. 2.5C). High abundance of *M. kochi* was related to slightly higher temperatures than *M. atlantica*, i.e. SST of 15.0–16.0 °C ($p = <0.1$; Table 2.1, and Fig. 2.5D). Although few prey data were available during the IPs of *M. kochi*, the data that were available did not show any significant association between peaks of *M. kochi* and prey abundance ($n = 9$; Fig. 2.5E). Salinity preferences were not considered, due to the narrow salinity range observed during periods of *M. kochi* population growth *in situ*.

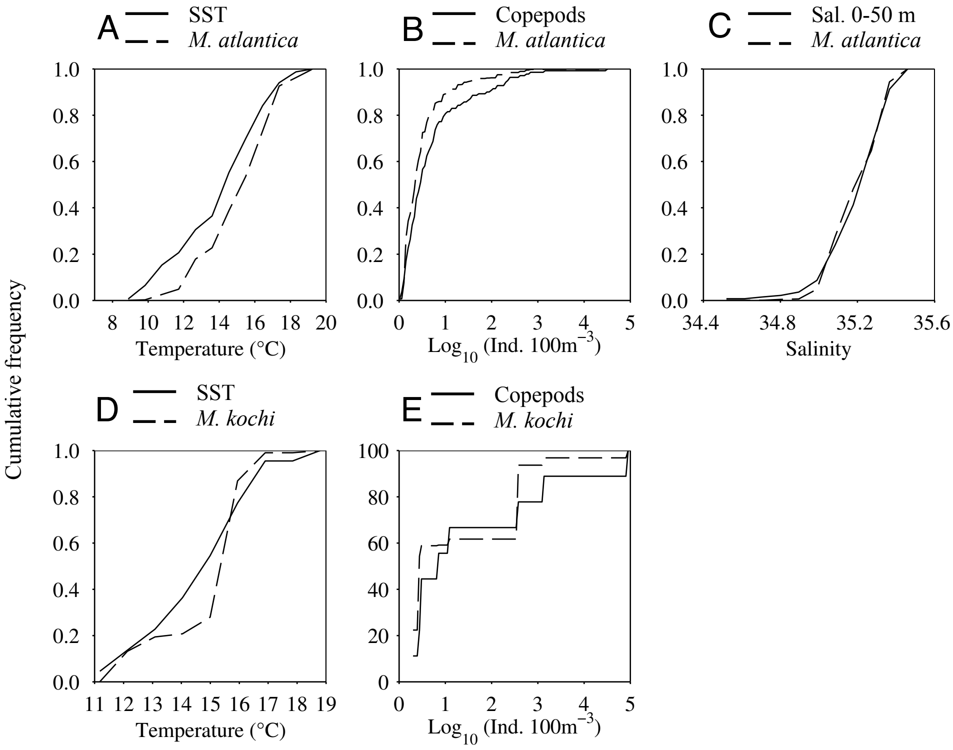

Fig. 2.5. Cumulative distribution functions (CDFs) of siphonophore abundance (dashed lines) in relation to environmental conditions (solid lines) during periods of *in situ* population growth. (A) *Muggiaea atlantica* and sea surface temperature, (B) *Muggiaea atlantica* and copepod abundance, (C) *Muggiaea atlantica* and depth-integrated salinity (0–50 m), (D) *Muggiaea kochi* and SST, and (E) *Muggiaea kochi* and copepod abundance.

Table 2.1. Environmental preferences of *Muggiaea atlantica* and *Muggiaea kochi* identified by analysis of environmental descriptors during periods of *in situ* population growth. Asterisks indicate optimal conditions significantly associated with an increase in the abundance of the species.

Species	SST (°C)	Salinity (0–50 m)	Copepods (ind. 100 m^{-3})
Muggiaea atlantica	14.6–15.5**	35.18–35.27	20,400–22,100*
Muggiaea kochi	15.0–16.0*	N/A	17,600–19,500

$^{*}p < 0.1$

$^{**}p < 0.005$

2.4.5 Environmental influence on seasonal distribution of *Muggiaea*

2.4.5.1 Interstructure analysis.

The interstructure identifies the similarity between years based on their environmental characteristics. The first principal component (PC1) explained 71% of the total variation and the second principal component (PC2) explained 5% (Fig. 2.6). Cluster analysis identified 4 separate groups of years and a single individual year. The groups G2 (1964, 1967, 1984 and 2005) and particularly G1 (1968, 1975, 1977, 1978, 1979, 1980, 1981, 1982 and 2003) exhibited strong association with PC1, indicating similar structures and good representation by the compromise. The years of G3 (1965, 1966, 1969, 1985, 2007 and 2010) represented an intermediate group, associated moderately to PC1 and negatively to PC2. The group G4 (1958, 1959, 1971, 1973, 1974, 1976, 1983, 2008, 2009 and 2011) displayed reduced association with PC1 and contained years with more distinctive environmental structures. The year 1972 was unusual, with a particularly strong link to PC2.

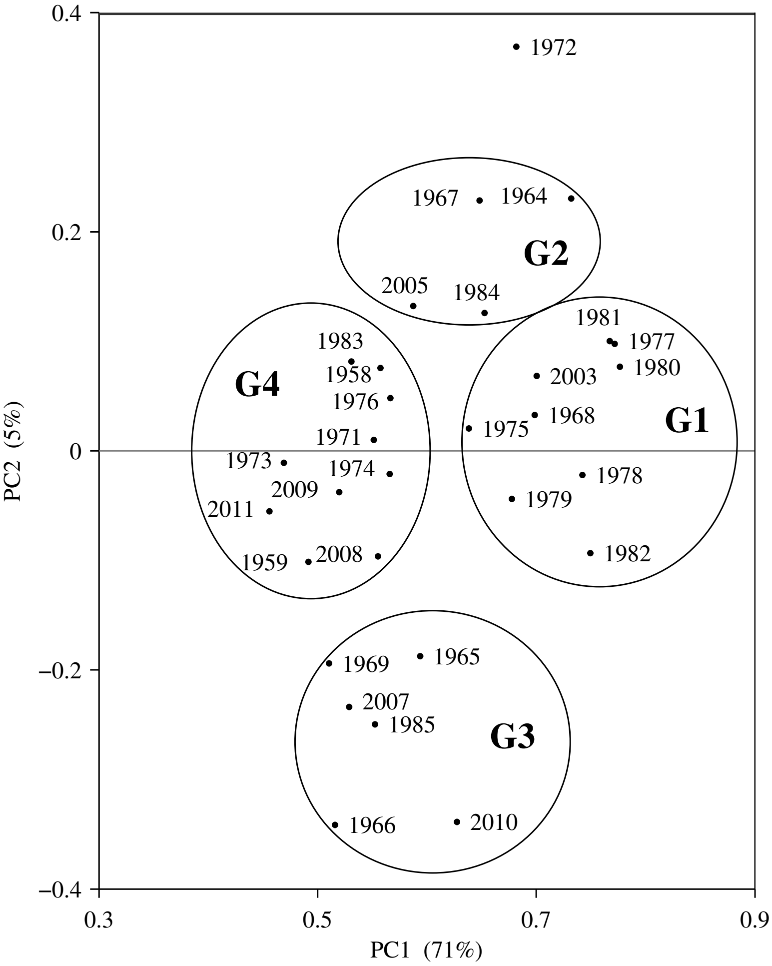

Fig. 2.6. Interstructure of the STATIS analysis. This plot shows the similarity of the 30 years based on their environmental characteristics (sea surface temperature, salinity and copepod abundance). The importance of each year in the compromise is indicted by the strength of association with the first principal component (PC1). Groups of similar years have been identified using hierarchical cluster analysis.

2.4.5.2 Compromise analysis

The compromise analysis (Fig. 2.7) represents the typical annual environmental structure common throughout the years. PC1 accounted for 60% of the total variance and differentiated the winter and summer months, while PC2 (14% of the total variance) separated spring and autumn (Fig. 2.7A). Examination of the relationships between descriptors (SST; salinity, SAL; copepod abundance, PRY) and the principal components (Fig. 2.7B) reveals the underlying structure of the compromise. Overall, SST was positively related to PC1 whilst salinity (SAL) was negatively associated, confirming that winter months were typically characterised by high salinity and low temperature whilst summer months exhibited the inverse relationship. Copepod abundance (PRY) was linked positively to PC1 and negatively to PC2, indicating a general pattern of high prey abundance in spring/summer and minimal abundance in late autumn/winter.

The seasonal distribution of *M. atlantica* (ATL) was positively related to PC1, revealing an overall positive relationship with SST and copepod abundance, and a negative link with salinity (Fig. 2.7B). Overall, *M. atlantica* was most abundant in the summer months when temperature and copepod abundance were high and salinity was low. In contrast, *M. kochi* (KOC) associated weakly with PC2, indicating a tendency to occur in autumn, but with high variability. A weak link was found between *M. kochi* seasonal distribution and SST, while salinity and copepod abundance appear unrelated to the seasonal occurrence of this species.

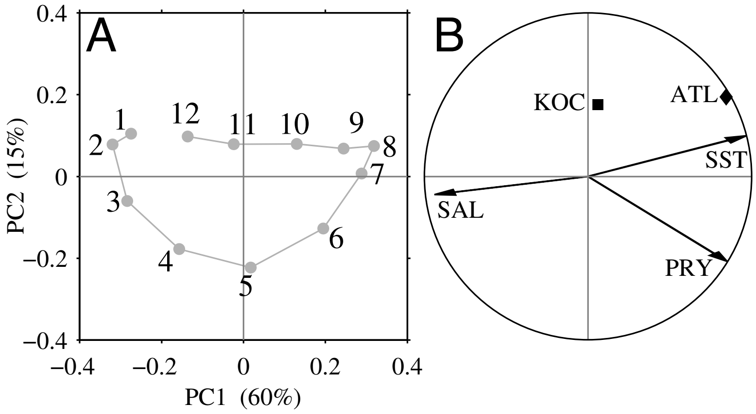

Fig. 2.7. The compromise of the STATIS analysis. This plot represents the typical annual environmental structure in the Western English Channel. (A) The position of the months (January = 1–December = 12) in the compromise space. (B) The association of the environmental descriptors (sea surface temperature, SST; salinity, SAL; copepod abundance, PRY) and species abundance (*Muggiaea atlantica*, ATL; *Muggiaea kochi*, KOC) with the axes of the compromise. The x-axis is the first principal component (PC1) and the y-axis is the second principal component (PC2).

2.4.5.3 Trajectories

The trajectories show the structures of the individual years, revealing similarities and differences between them. The trajectories (Fig. 2.8–Fig. 2.11; and Fig. A2.1) revealed high interannual variability in the seasonal structure of the environment. However, three broad typologies were evident, corresponding to groups of years clustered in the interstructure. Differences in the shape of trajectories between years were predominantly driven by high variability in the annual cycle of salinity, whereas SST and copepod abundance displayed less variability. The analysis revealed interesting associations between environmental typologies and specific patterns of *M. atlantica* seasonal growth and distribution.

Typology 1 (Fig. 2.8) resembled the characteristic structure of the compromise and characterised the years of groups G1 (1968, 1975, 1977, 1978, 1979, 1980, 1981, 1982 and 2003) and G2 (1964, 1967, 1984 and 2005). This typology was consistently associated with *in situ* development of the *M. atlantica* population, which took place in all G1 years and G2 except for 1964. Typically (years 1968, 1975, 1977, 1980, 1981, 2003) the *M. atlantica* population began developing in early spring when conditions were cool and saline (Fig. 2.8), and peaked in summer, when temperatures were maximal and salinity was minimal. However, in 1978, 1979 and 1980 population growth *in situ* started relatively late, despite similar environmental characteristics (Fig. A2.1). During G2 years (except 1964) the *M. atlantica* population was developing in phase with copepods (Fig. 2.8).

Two alternative typologies were characterised by their distinct annual salinity patterns. Typology 2 (Fig. 2.9) comprised the years of G3 (1965, 1966, 1969, 1985, 2007 and 2010) and exhibited salinity minima in spring and maxima in autumn. This typology corresponded to atypical patterns of growth and distribution of the *M. atlantica* population. *In situ* population growth was late and ephemeral (1966, 1969, 2007 and 2010), or did not occur (1965), and was out of phase with the peak of prey abundance, suggesting these conditions were unfavourable for growth (Fig. 2.9). It is noteworthy that 1966, 1969 and 2007 exhibited intense freshening events in spring, with salinities as low as 34.62 (2007).

Typology 3 (Fig. 2.10) was characterised by salinity maxima in early spring and minima in early autumn. This typology characterised the majority of G4 years (1958, 1959, 1971, 1974, 2008, 2009), which were also associated with peaks of *M. atlantica* abundance out of phase with prey abundance. Under these conditions *M. atlantica* was reproducing *in situ* only during 2 of the 6 years (1974 and 2009; Fig. A2.1).

Some years of group G4 (1973, 1976, 1983, 2011) exhibited trajectories dissimilar to the regular typologies. These years were characterised by relatively stable salinity patterns and consistent *in situ* growth periods of *M. atlantica* (Fig. 2.11). The year 1972 displayed a distinctive trajectory due to particularly late seasonal abundance of copepods. The *M. atlantica* population was not recorded developing *in situ* during this year.

In situ population growth of *M. kochi* was only recorded in two of the thirty years analysed by the STATIS technique (1958 and1959). Both years were categorised as typology 3 conditions, displaying highly similar environmental characteristics but dissimilar patterns of growth and distribution (Fig. 2.10).

The annual peak of *M. atlantica* generally occurred in summer or autumn under all environmental typologies (except 1958), while *M. kochi* tended to exhibit peaks in all four seasons under a wide range of environmental conditions.

In summary, the STATIS analysis highlighted (1) a tendency for *M. atlantica* populations to develop *in situ* with stable salinity conditions and abundance of prey; (2) restricted population growth under atypical salinity conditions and low prey concentration; (3) that the seasonal distribution of *M. atlantica* was generally associated with defined hydroclimatic conditions, while this was not the case for *M. kochi*.

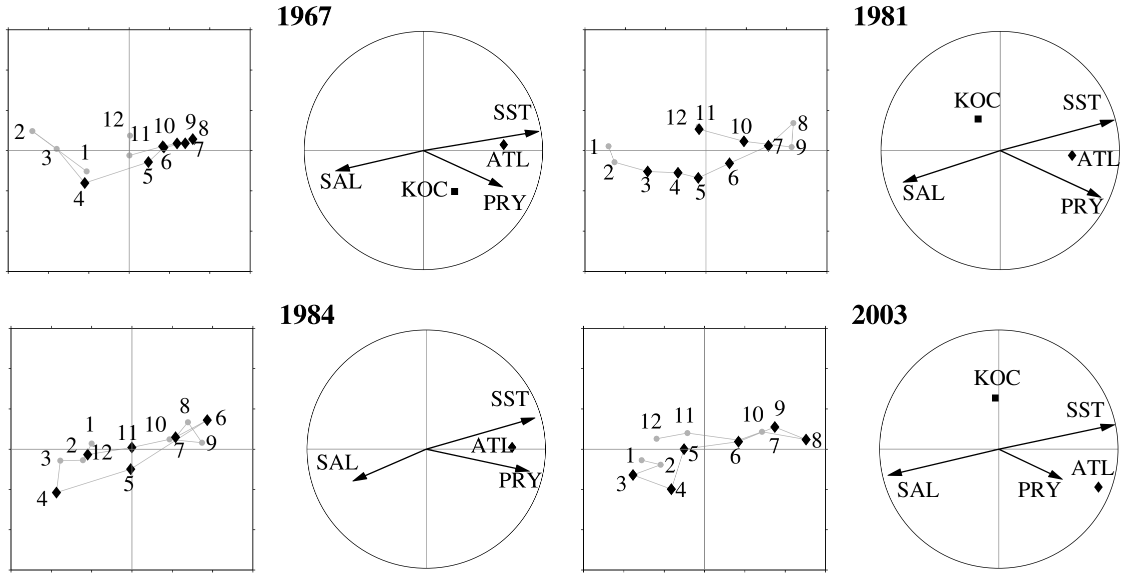

Fig. 2.8. Environmental typology 1 trajectories. Typical annual environmental conditions associated with consistent *in situ* population growth of *M. atlantica*. Months during which the *M. atlantica* population was developing *in situ* are represented by black diamonds.

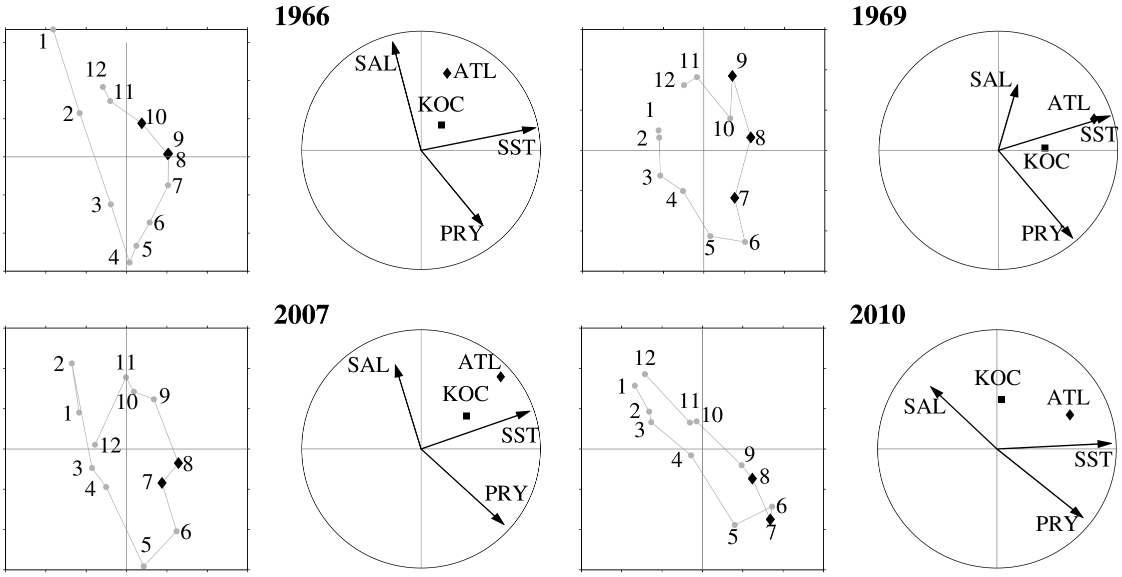

Fig. 2.9. Environmental typology 2 trajectories. Annual environmental conditions characterised by spring salinity minima and restricted *in situ* population growth of *M. atlantica*. Months during which the *M. atlantica* population was developing *in situ* are represented by black diamonds.

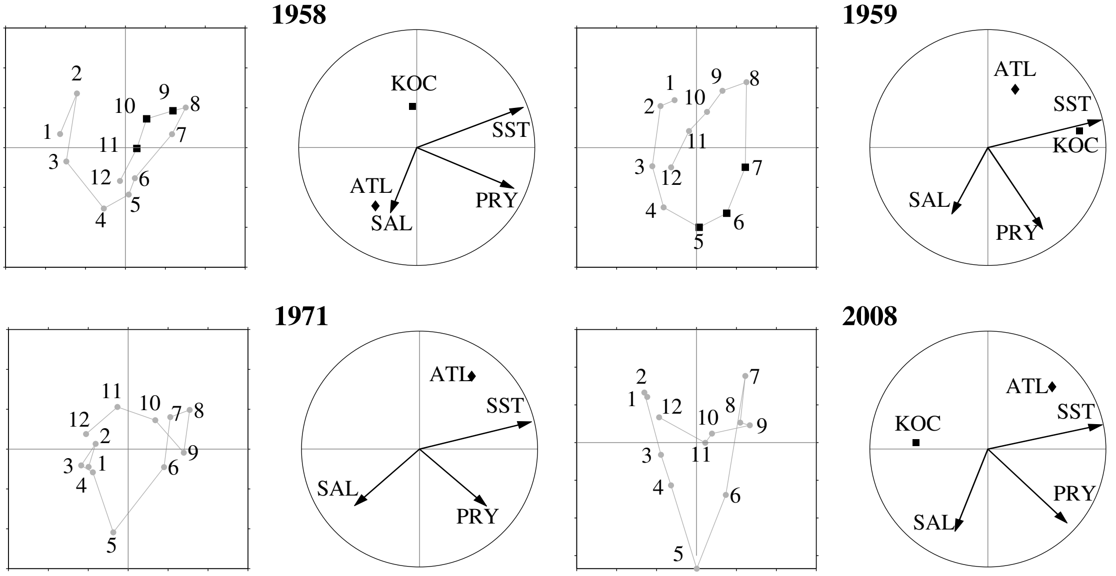

Fig. 2.10. Environmental typology 3 trajectories. Annual environmental conditions characterised by spring salinity maxima and restricted *in situ* population growth of *M. atlantica* and *M. kochi*. Months during which the *M. kochi* population was developing *in situ* are represented by black squares.

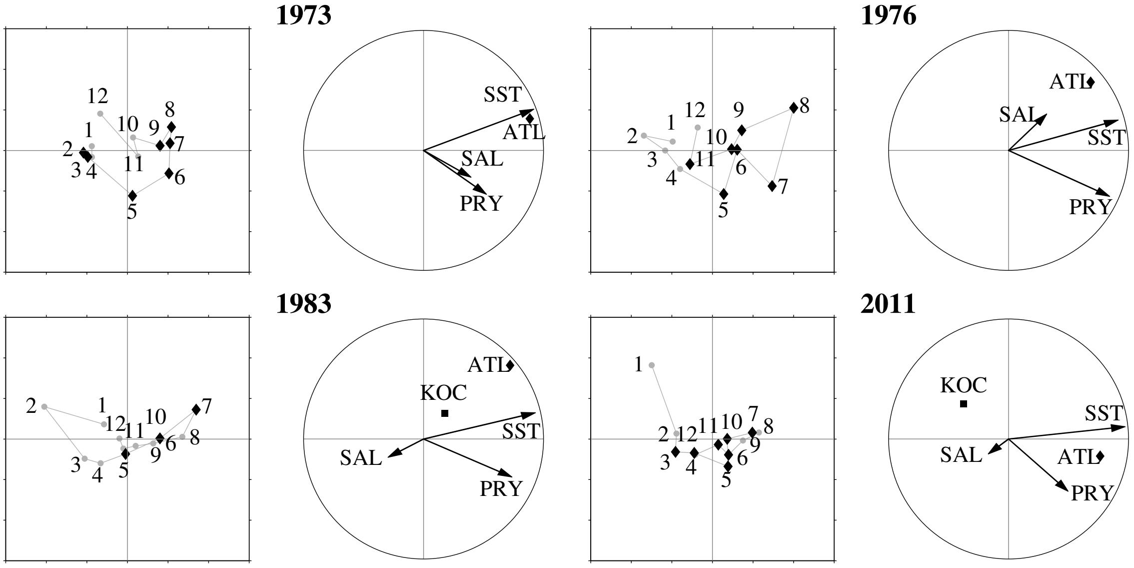

Fig. 2.11. Stable environmental trajectories. Annual environmental conditions characterised by stable salinity patterns and consistent *in situ* population growth of *M. atlantica*. Months during which the *M. atlantica* population was developing *in situ* are represented by black diamonds.

2.5 Discussion

Our study shows that between 1930 and the late 1960s *Muggiaea atlantica* and *Muggiaea kochi* were transient components of the Western English Channel (WEC) ecosystem. Their sporadic occurrence and infrequent *in situ* population development at this time indicated the influence of advection, probably from source populations to the south (Corbin 1947; Southward 1962). Following this period dramatic changes were identified. From the late 1960s the occurrence of *M. kochi* became increasingly sporadic and *in situ* population development of this species was no longer recorded. In contrast, after 1968 the *M. atlantica* population was regularly developing *in situ* and this species was observed throughout the seasons of every year, with a progressive expansion of seasonal abundance. These results provide strong evidence that *M. atlantica* established a self-sustaining population in the WEC and suggest that, as documented in several species of phytoplankton (Hays et al. 2005) and copepods (Beaugrand et al. 2002), *M. atlantica* has undergone a northwards distributional shift in recent decades.

The STATIS compromise analysis suggested that sea surface temperature (SST), salinity, and to a lesser extent, prey (copepod) abundance were key factors determining the seasonal occurrence of *M. atlantica* in the WEC. In contrast, *M. kochi* was only correlated with SST, albeit weakly. Experimental studies have shown that the reproductive capacity of *Muggiaea* is positively related to temperature and food availability (Purcell 1982; Carré & Carré 1991). Analysis of the environmental descriptors associated with informative periods confirmed the significance of temperature as a determinant of *Muggiaea*'s seasonal distribution. Both *M. atlantica* and *M. kochi* populations were successfully developing *in situ* when SST was within species-specific temperature ranges, i.e. 9–19 °C for *M. atlantica* and 11–19 °C for *M. kochi*. Within these tolerable reproductive ranges we identified optimal temperatures (SST), i.e., 14.6–15.5 °C for *M. atlantica* and 15.0–16.0 °C for *M. kochi*, that were consistently associated with rapid population growth.

Increased temperatures promote faster lifecycles and higher reproductive rates in *M. kochi* (Carré & Carré 1991) and many other species of jellyfish (Purcell 2005). The thermal optima (SST) we identified for *M. kochi* are lower than those reported from the Mediterranean (17–21 °C; Licandro et al. 2012), but represented the most commonly available maximal SST range in the WEC (<20% of SST values were >16 °C). The relatively low *M. kochi* abundance observed in the present study, compared to other regions (e.g. Licandro et al. 2012), may therefore be explained by a restricted reproductive capacity due to the temperature regime in the WEC. Carré & Carré (1991) suggested that in response to low temperature (13 °C) in the Mediterranean, *M. kochi* employs a suspended reproductive phase that facilitates overwintering of the polygastric population. In the present study the lower limit of *M. kochi*'s tolerable reproductive range (11 °C) suggests the threshold at which it enters this phase in the WEC. These results indicate that the species is able to acclimate to some extent, an adaptation that is well known for certain species of jellyfish (e.g. Lucas 2001). However, winter temperatures in the WEC (average SST 1930–2011, 9.6 °C) are likely below a critical thermal limit for *M. kochi* survival. Consequently the polygastric stage of this species cannot successfully overwinter in the WEC and the population must rely on annual re-colonisation via advective transport.

In contrast, the thermal optima (SST) identified for *M. atlantica* in the present study are in close agreement with results from warmer regions, (e.g. Licandro et al. 2012). At more southerly latitudes *M. atlantica* typically exhibits annual peak abundance 1–2 months earlier than observed in the WEC in recent years (Patriti 1964; Moreno & Fernandez-Alcazar 1984). The WEC has experienced a pronounced increase in sea surface temperature since the 1980s (Smyth et al. 2010; Fig. 2.2) and earlier seasonal maxima of *M. atlantica* observed in the region during this period are concomitant with temperature changes. This suggests that *M. atlantica* has a well-defined thermal niche that dictates its reproductive phenology. In the present study we found that the *M. atlantica* population did not develop *in situ* when SST was below 9 °C. This is in accordance with preliminary experimental results from the Mediterranean that identified the threshold for suspended reproduction as around 10 °C (Pagès et al., unpublished data from the north-western Mediterranean). Evidently, minimal sea temperature in the WEC does not go below critical thermal limits for *M. atlantica* survival, as polygastric stage *M. atlantica* can successfully overwinter in the region.

Copepods form the dominant component of the diet of calycophorans (Purcell 1981a; 1982). However, our results show that high abundance of *Muggiaea* is often, but not necessarily associated with high abundance of copepods. This suggests that copepods form an important dietary component at specific times, but that other prey sources must also be important, particularly during autumn, when copepods are scarce but the *M. atlantica* population is often developing *in situ*. The importance of other prey sources is also highlighted when considering that *M. kochi* exhibited no significant association with copepod abundance when developing *in situ*. Furthermore, years in which the *M. atlantica* population was developing in phase with copepods, did not exhibit increased abundance, which could be expected given access to a rich prey resource. Other prey resources, such as meroplankton (Mapstone 2009), that were not considered in the present study, may have been important factors influencing the congeners temporal distribution and abundance.

We found that high seasonal abundance of *M. atlantica* in the WEC occurred under lower salinity conditions in the summer. Siphonophores are generally considered strictly oceanic (Pugh 1999) and intolerant of low salinity waters (Mackie et al. 1987). However, the neritic *M. atlantica* can exploit both low salinity (Kitamura et al. 2003; Marques et al. 2008; Primo et al. 2012) and high salinity waters (Licandro et al. 2012). Salinity may however have an indirect effect, representing a proxy for physical processes. Annual trajectories of the STATIS analysis showed that summer periods characterised by lower salinity corresponded to extensive periods of *in situ* population development. These conditions correspond to highly stratified waters (Smyth et al. 2010) and represent the typical annual cycle in the WEC (Pingree 1980; present study). Previous studies have already suggested that calm conditions and intense stratification may favour the accumulation and reproduction of *M. atlantica* (Graham et al. 2001; Licandro et al. 2012; Batistić et al. 2013).

Annual trajectories of the STATIS analysis revealed that deviation from the characteristic annual salinity cycle negatively influenced the *in situ* population development of *M. atlantica*. In particular, low salinity events occurring in the spring were associated with late and restricted development of the *M. atlantica* population *in situ*. Salinity represents a proxy for water circulation in the WEC (Southward et al. 2005). For instance, in the southern region of the Channel low salinity events in spring represent the intrusion of low salinity surface waters (LSSW; <35) originating from freshwater plumes of the Loire and Gironde rivers in the Bay of Biscay (Kelly-Gerreyn et al. 2006). Gough (1905) and Corbin (1947) identified LSSW as a vector for the transport of *M. atlantica* into the WEC. However, our results indicate that during the period of study, high abundances of *M. atlantica* were not associated with the occurrence of LSSW. Considering that this species is tolerant of very low salinities (i.e. down to nearly 20; Primo et al. 2012) a negative relationship between low salinity and *M. atlantica* abundance in spring suggests that anomalies in the usual circulation patterns may have dispersed the locally developing population. The arrival of *M. atlantica* in the WEC has also been attributed to the intrusion of high salinity Atlantic waters from the southwest (Southward 1962). However, we only found one instance when the sudden appearance of high *M. atlantica* abundance coincided with these high salinity events (2008; data not shown). In general *M. atlantica* was sparse or absent throughout the duration of high salinity events in spring, suggesting a similar dispersal effect as speculated during the occurrence of low salinity events.

We identified three main environmental typologies that were associated with the *in situ* development of the *M. atlantica* population. Those conditions occurred at different times without temporal continuity, indicating that the establishment of *M. atlantica* as a resident species of the WEC was not due to a persistent shift in local temperature, salinity or prey availability. Rather, community composition changes that occurred during the study period in response to different hydroclimatic regimes (Edwards et al. 2013a; Alheit et al. 2014) may have determined the establishment of a resident *M. atlantica* population in the WEC. During the period of *M. atlantica* transiency (1930–1968) the WEC ecosystem was characterised by a low abundance of warm-water southwestern plankton species and low intermediate trophic level diversity (Southward et al. 2005). Intense predation by an abundant pilchard (*Sardina pilchardus*) population during this period has been suggested as a driver of low zooplankton abundance and diversity (Southward 1980). Limited prey resource and strong competitive, and perhaps predatory pressure (e.g. Mapstone 2009 and references therein) from pilchards may have therefore limited the success of the *M. atlantica* population. During this period the WEC represented a 'sink' habitat (Pulliam 1988) where *in situ* reproduction was insufficient to balance local mortality, and the population relied on immigration from nearby 'source' areas.

The establishment of the *M. atlantica* population in the late 1960s occurred after a transition to a cool-water community characterised by an abundant and diverse northwestern plankton assemblage and a rapid decline in pilchard abundance (see Southward et al. 1995; Southward et al. 2005 for detailed reviews). A reduction in competitive pressure from pilchards, and increased prey resources may have contributed to the establishment of the *M. atlantica* population. Similar structural changes in the Irish Sea ecosystem following a decline in the herring (*Clupea harengus*) population have been linked to the increased frequency of cnidarian material present in CPR samples after 1970 (Lynam et al. 2011). After 1968 the WEC likely transformed from a 'sink' to a 'source' habitat for *M. atlantica* (Pulliam 1988), with local reproduction outweighing mortality and immigration.

However, changes to prevailing wind patterns in the WEC may have also contributed to the establishment of *M. atlantica*. During the 1970s there was a reduction in westerly wind strength and a strengthening of southerly winds (Smyth et al. 2010). Southerly winds drive waters of a southern origin into the WEC (Pingree & Griffiths 1980). Increased southerly winds during the 1970s could have transported increased numbers of *M. atlantica* from the Armorican Shelf region, where source populations exist (Mackie et al. 1987 and references therein). Changing wind conditions has been shown to be an important factor influencing planktonic community composition through bio-physical interactions (e.g. Hinder et al. 2012). Therefore, increased immigration combined with improved habitat suitability may have facilitated the establishment of the *M. atlantica* population in the WEC.

Around 1985 the WEC ecosystem switched back to its current warm-water state, but without the low in zooplankton abundance and diversity associated with the first warm-water period (see Southward et al. 1995; Southward et al. 2005 for detailed reviews). During this period *M. atlantica* exhibited a pronounced increase in abundance and seasonal distribution concomitant with an increase in sea surface temperature. Historically, both *M. atlantica* and *M. kochi* have been considered as southwestern indicator species, indicative of the influx of warm southern waters (Russell 1935; Southward et al. 2005). However, we found no temporal association between *M.*

atlantica variability and the predominance of southwestern warm- or northwestern cool-water plankton community composition. *M. atlantica* was transient during the first warm-water community period, then established a resident population during the cool-water community period and subsequently proliferated after transition back to the current warm-water community period. Therefore *M. atlantica* should no longer be considered as an indicator of southern water inflow in the WEC. However, *M. kochi* was mostly absent during the cold-water state, in accordance with its warm-water affinity and transient nature, and may still provide utility as an indicator species in the WEC.

During the period 1930 to the late 1960s *M. atlantica* and *M. kochi* underwent alternating periods of dominance, a phenomenon that has also been observed in other regions (Mackie et al. 1987 and references therein). During this early period both *M. atlantica* and *M. kochi* were transient components of the plankton, probably dependent upon advection into the area, which suggests that patterns of dominance in the sink habitat of the WEC should mirror patterns of dominance in lower latitudinal regions supporting source populations. Evidence promoting this hypothesis is found by comparing records from our study area and other Atlantic coastal regions. For instance, *M. kochi* was dominant in the region of Gibraltar in the early 1930s (Leloup 1933), as it was in the WEC (Russell 1934; present study) while in the 1910s *M. atlantica* predominated in both regions (Russell 1934; Bigelow & Sears 1937). Since establishment of a resident *M. atlantica* population in the WEC, *M. kochi* has failed to predominate. This could be possibly due to competitive exclusion by *M. atlantica*, given the latter's greater reproductive fitness in the WEC temperature regime.

Our study provides useful information about the environmental parameters that are associated with the maintenance of resident populations of *M. atlantica* and *M. kochi.* Although the interactive effects of environmental conditions are complex, our study confirms that temperature plays a fundamental role in determining species' geographical distributions (e.g. Beaugrand et al. 2002; Hays et al. 2005). Predicted future increases in sea surface temperature (IPCC 2007) could result in other more northerly latitudes providing suitable environments for the establishment of *M. atlantica* populations. For example, Greve et al. (1996) hypothesised that low winter temperatures in the German Bight prevented *M. atlantica* residency after its invasion in 1989 (Greve 1994). Our results suggest that if temperatures continue to increase *M. atlantica* could successfully overwinter and establish a resident population, a situation also applicable to the wider North Sea.

Changes in the abundance of other species of jellyfish have already been reported in neighbouring ecosystems of the Irish Sea and North Sea (e.g. Lynam et al. 2004; Lynam et al. 2011). Whilst sea temperature consistently emerges as a key driver of changes in these regions (Licandro et al. 2010; Lynam et al. 2011) the influence of variable hydroclimatic conditions is complex and often region- and species-specific (e.g. Lynam et al. 2004). The WEC is a highly dynamic biophysical environment prone to shifts of community equilibria that show complex, non-linear responses to climatic oscillations (Southward 1980; Alheit et al. 2014). Further research and continuing observations are required to decipher whether changes in the WEC and neighbouring areas represent actual shifts in baseline conditions or oscillations associated with long-term hydroclimatic variability (Condon et al. 2013)

Chapter 3

Population ecology of *Muggiaea atlantica* in the Western English Channel

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3.1 Abstract

Recent observations suggest that the siphonophore *Muggiaea atlantica* is expanding its geographical distribution. The mechanisms behind this expansion remain unclear due to our limited knowledge of the species' ecology. We modelled the functional relationship between the 2 main life-cycle stages of *M. atlantica* over a 5-year period (2009–2013) in the Western English Channel. Our aims were to determine the key features of the species' population dynamics and the influence of local environmental conditions on its population development. Our results highlighted a strong coupling between the timing of specific environmental conditions and the development of the *M. atlantica* population, thereby explaining interannual differences in the phenology of its blooms. Population development commenced with the initiation of eudoxid production by the overwintering polygastric stages. This reproductive event was linked to the onset of a spring temperature threshold, suggesting a critical basal limit of 10 °C for eudoxid production. Interannual variability in the timing of this threshold modulated the degree of mismatch between the developing *M. atlantica* population and the availability of copepod prey. Unusually cold conditions in the spring of 2010 and 2013 limited the capacity for *M. atlantica* to initiate eudoxid production leading to poor trophic phasing and the production of single autumn cohorts. In contrast, warmer conditions during spring 2009, 2011, and 2012 facilitated earlier population development, optimal trophic phasing and the production of both summer and autumn cohorts. These findings represent an important addition to our understanding of the ecology of *M. atlantica* in the Northeast Atlantic.

3.2 Introduction

Cnidarian jellyfish (medusae and siphonophores) are a ubiquitous component of the pelagic ecosystem. These animals play a key ecological role as predators and competitors that can modulate the structure and dynamics of marine communities (Mills 1995; Pitt et al. 2009). Most cnidarian jellyfish have opportunistic life history traits (high reproductive potential and high feeding rates) that enable rapid population increase in response to favourable environmental conditions (Lucas & Dawson 2014). The seasonal abundance of these species fluctuates dramatically, with dense accumulation separated by periods of absence or rarity (Lucas & Dawson 2014). Consequently, their structuring effect on the pelagic community is complex and dynamic (e.g. Matsakis & Conover 1991). Knowledge of the mechanisms that regulate gelatinous predator populations is fundamental to our understanding of the functioning of marine ecosystems (Condon et al. 2013).

The population dynamics of cnidarian jellyfish are the result of life cycle and life history adjustments (sensu Boero et al. 2008), modulated by myriad environmental factors. Most cnidarian jellyfish have complex, metagenic life cycles alternating between sexual and asexual generations. Meroplanktonic species typically employ life cycle adjustments (qualitative changes at the individual level) and may persist locally as sexual pelagic or asexual benthic life stages at different times (Boero et al. 2008). In contrast, holoplanktonic species tend to adopt life history adjustments (quantitative changes at the population level) and may undergo alternating periods of high and low absolute abundance (Boero et al. 2008). Improving our knowledge of the inter-relationships between different cnidarian jellyfish life-cycle stages and the influence of environmental factors would enable a better understanding of their population dynamics (Lucas 2001; Lucas & Dawson 2014).

Calycophoran siphonophores are holoplanktonic colonial cnidarian jellyfish (Mackie et al. 1987). These typically small and active species are ambush predators that release a network of tentacles to entrap zooplankton prey (Mackie & Boag 1963). The life cycle of the Calycophora is characterised by an alternation between an asexual polygastric stage and a sexual eudoxid stage. Polygastric colonies asexually produce a chain of cormidia (each cormidium comprising single nutritive, reproductive and buoyant zooids) along a central stem. As the chain grows successive cormidia are released as autonomous sexual eudoxid colonies. The eudoxid stage buds successive reproductive gonophores that, via external fertilisation, recruit new polygastric colonies through 2 short-lived larval stages, the planula and calyconula (Carré & Carré 1991). Simultaneous asexual and sexual reproduction, high fecundity, rapid growth rates and short generation times enable the rapid development of large multivoltine blooms (Mackie et al. 1987).

In temperate biomes of the 3 great oceans the calycophoran siphonophore *Muggiaea atlantica* represents a major component of neritic gelatinous zooplankton (Mapstone 2009; 2014). Recent observations suggest that *M. atlantica* has expanded its geographical distribution, establishing new populations in the Western English Channel (Blackett et al. 2014; Chapter 2) and the Mediterranean and Adriatic (Licandro et al. 2012; Batistić et al. 2013), probably in response to hydroclimatic changes. Large blooms of *M. atlantica* have caused dramatic ecological (Greve 1994; Kršinić & Njire 2001) and economic (Fosså et al. 2003; Baxter et al. 2011) ramifications, particularly in novel habitats. Knowledge of the population dynamics and environmental requirements of this species is needed to fully appreciate its role in coastal marine ecosystems. However, our understanding is hampered by a paucity of data on its different life stages.

The present study is based on observations of the polygastric and eudoxid life stages of *M. atlantica* and the congeneric *Muggiaea kochi* in the Western English Channel between 2009 and 2013. We investigated seasonal changes in the abundance of these key life-cycle stages to better understand the dynamics that characterise their population development. Identifying the main biological and physical factors that influenced population development allowed us to explore environmental cues that influence their phenology in the Western English Channel.

3.3 Materials and methods

3.3.1 Sampling station

Data analysed in the present study were collected as a part of ongoing zooplankton research conducted by the Western Channel Observatory (www.westernchannelobservatory.org.uk). Data were collected weekly at a coastal station, L4 (50.25° N, 4.22° W) located 7.5 nautical miles (~13.9 km) southwest of Plymouth, UK, in proximity to the 50 m isobath. Station L4 is characterised by high seasonal variability. Intense primary productivity occurs during the spring and autumn (Widdicombe et al. 2010), with the summer period characterised by stratified and nutrient-depleted waters (Smyth et al. 2010). Patterns of water circulation are typically characterised by an eastward coastal trajectory, delivering waters of a more northerly or southerly origin, dependent upon the prevailing wind patterns (Pingree & Griffiths 1980). Strong tidal influence (Pingree 1980) and periodic fluvial input from the Tamar estuary (Smyth et al. 2010) are also dominant hydrographic features.

3.3.2 Physical data

A SeaBird SBE 19plus Profiler was used to obtain depth profiles of temperature, salinity, density and dissolved oxygen (see Smyth et al. 2010 for further methodological details). Temperature (°C) and salinity data were integrated between the surface and 50 m depth. Water column stratification was assessed in terms of mixed-layer depth (MLD), estimated as the depth at which water density (kg m^{-3}) exceeded a near-surface (10 m) reference value by a set threshold (0.003 kg m^{-3}) (de Boyer Montégut et al. 2004). Dissolved oxygen data were not included in the analysis because they were highly correlated with temperature ($r = -0.86$).

3.3.3 *Muggiaea* and other zooplankton data

Zooplankton samples were collected in duplicate by vertical hauls from the sea floor to surface using a WP2 net (mesh size = 200 μm, mouth area = 0.25 m^2) (UNESCO 1968). To reduce inter-sample variability, duplicate samples were averaged and data represented as the number of individuals and/or colonies per cubic metre (see Eloire et al. 2010 for a detailed description of the sampling methodology).

Siphonophore colonies are fragile and are rarely collected intact by nets. However, the number of *Muggiaea atlantica* and *Muggiaea kochi* nectophores provided a direct estimate of their polygastric abundance as species of the genus *Muggiaea* develop only a single nectophore (Mackie et al. 1987). Enumeration of the *Muggiaea* spp. eudoxid stage was based upon the number of detached bracts and intact colonies. The eudoxid stages of the genus *Muggiaea* are morphologically indistinguishable (Kirkpatrick & Pugh 1984) and were represented by their total abundance.

Specific zooplankton taxa were selected as potential sources of prey using size-range (100–1000 μm) (Purcell 1981) and prey-suitability (Purcell 1982; Mapstone 2009) criteria (Table 3.1).

3.3.4 Numerical analyses

3.3.4.1 Data preparation

To stabilise variance, biological data were log10(x + 1) transformed. For both physical and biological variables, randomly spaced missing data (~12% of the total 260 weekly observations) were interpolated using the eigenvector filtering with missing data method (Ibañez & Conversi 2002). All analyses were programmed using MATLAB (R2014b 8.4.0.150421).

3.3.4.2 Eudoxid stage identity

Since the eudoxid stage is produced directly (asexually) by the polygastric stage (Carré & Carré 1991), and eudoxid production rates are linearly related to the size of the polygastric colony (Purcell 1982), a tight coupling of their abundance could be expected. Indeed, previous observations have shown that the sexual and asexual stages of both *M. atlantica* and *M. kochi* typically covary in phase (Dowidar 1992). Consequently, the relative contribution of *M. atlantica* and *M. kochi* to the total abundance of *Muggiaea* spp. eudoxid stages was estimated using simple linear regression. *Muggiaea* spp. eudoxid stage abundance (response variable) was regressed on *M. atlantica* and then *M. kochi* polygastric abundance (explanatory variables) to quantify the strength of each species association with the total abundance of *Muggiaea* spp. eudoxid stages. The regression model assumptions of linearity, homogeneity of variance, normality and independence of residuals were carefully monitored. Standard Newey-West heteroscedasticity and autocorrelation consistent covariance estimators (HAC) were used to provide robust estimates of regression parameter variance and facilitate sound statistical inference (Andrews & Monahan 1992).

3.3.4.3 Seasonal variability

The dominant modes of temporal variability were extracted for the biological and physical variables using the eigenvector filtering (EVF) method (Colebrook 1978; Ibañez & Etienne 1992). The EVF method involves a principal component analysis performed on an autocovariance matrix composed of the original series lagged progressively; the number of lags (8–11 weeks) was defined as the time lag at which the autocorrelation function of the original series first passed zero (Ibañez & Etienne 1992). The EVF technique decomposes a time series into successive signals of decreasing variance. A cumulative variance threshold of 80% was used to determine the number of principal components (PC) retained (Ibañez & Conversi 2002). The main periodicities that characterised the PCs were then estimated using the autocorrelation function (Legendre & Legendre 2012).

3.3.4.4 Population dynamics

The functional relationship between the abundance of eudoxid and polygastric stages was investigated using simple linear regression. Following the procedure described for eudoxid stage identity, regression analyses were computed between the PCs of the polygastric (explanatory variable) and eudoxid (response variable) life-cycle stages and the studentised residuals were retained for analyses. The residuals represent deviations from the typical linear relationship between the abundance of eudoxid and polygastric stages. Positive residuals indicate that increased abundance of the eudoxid stage was observed relative to that which would be expected from the linear eudoxid–polygastric relationship, while negative residuals indicate the inverse. We considered residuals greater than ±1 SD as significant deviations from the expected abundance of the eudoxid stage.

3.3.4.5 Correlations with environmental variables

Hypothetical links between variability of *M. atlantica* and physical environmental factors (as the PCs) were evaluated using Pearson product moment correlation analyses. Links with biological variables (as the PCs) were explored using partial correlation analyses, allowing the effects of controlling physical variables to be removed. For all correlation analyses, the effective degrees of freedom (df_a) were corrected for autocorrelation following the modified Chelton method proposed by Pyper & Peterman (1998). All data were standardised at zero mean and unit deviation (z-scored) for correlation analyses.

3.3.4.6 Critical environmental ranges

For environmental factors that were significantly correlated with the PC2 of *M. atlantica* and residuals of the expected abundance of eudoxids, we identified critical environmental ranges using quotient plot analysis (Van der Lingen et al. 2001). Quotient plot analysis quantifies the association of species abundance with categories of environmental parameters, providing an estimate of positive and negative associations.

Quotient values (Q_i) were computed as:

$$Q_i = \frac{M_i}{E_i}$$

where M_i is the percentage of the total abundance of *M. atlantica* in environmental category *i* and E_i is the percentage frequency of occurrence of environmental category i. Q_i = 1 indicate a random association of species abundance and related environmental categories, whereas Q_i >1 indicate a positive association and Q_i <1 indicate a negative association. The statistical significance of associations was evaluated using a randomisation test with 10,000 permutations to compute confidence intervals with $\alpha = 0.05$. For this analysis the negative and positive residuals were analysed separately. This procedure involved first inverting the negative residuals, then re-scaling both the positive and negative residual between 0 and 1. This procedure enabled the association of both positive and negative residuals with environmental categories to be assessed. The intervals of environmental categories were chosen by a compromise between the resolution of the profiles and the number of data points within each category. To ensure representation of data within each category, copepod abundance scores in excess of the 95th percentile were omitted from this stage of the analysis (< 7% of the 260 observations).

3.4 Results

3.4.1 Eudoxid stage identity

Inspection of the raw data showed that the abundance of the polygastric stage of *M. atlantica* and the eudoxid stage of *Muggiaea* spp. fluctuated in phase (Fig. 3.1). Polygastric *M. kochi* were less abundant and did not vary in the same way (Fig. 3.1, Table 3.2). Linear regression analysis confirmed a significant relationship between the raw abundance (decimal logarithm) of the polygastric stage of *M. atlantica* and the *Muggiaea* spp. eudoxid stage (b = 1.15, $r^2 = 0.80$, F = 989, df = 258, $p < 0.001$). The number of *M. kochi* polygastric colonies was not associated with eudoxid stage variability (b = 0.27, $r^2 = 0.003$, F = 1.4, df = 258, $p > 0.05$) nor the residuals from the *M. atlantica*–eudoxid model (b = 0.33, $r^2 = 0.03$, F = 10.4, df = 258, $p > 0.05$). These results provided a clear indication that the eudoxid population was composed primarily of *M. atlantica*. Whilst the possibility of a small contribution from *M. kochi* cannot be completely eliminated, it was considered negligible. Total eudoxid abundance was considered to represent *M. atlantica* eudoxid abundance and *M. kochi* was not included in further analyses.

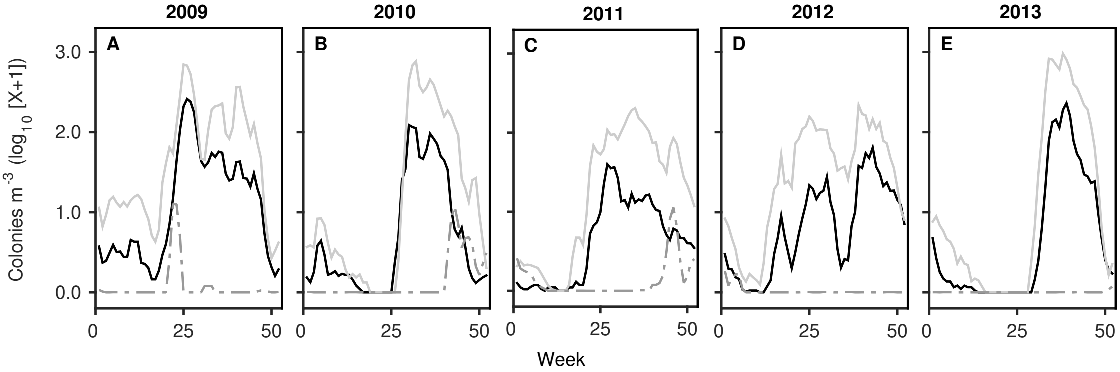

Fig. 3.1. Temporal fluctuation in the abundances of *Muggiaea atlantica* polygastric stage (solid black line), *Muggiaea kochi* polygastric stage (dash-dotted grey line), and *Muggiaea* spp. eudoxid stage (solid grey line) at station L4 in the Western English Channel between 2009 and 2013. Data are weekly abundance values that have been smoothed with a 3-week moving average to improve legibility.

Table 3.1. Percentage relative contribution of different taxa to the total potential prey availability for *M. atlantica* at the sampling location. Taxa were selected following size range and prey suitability criteria derived from the literature (Purcell 1981, 1982; Mapstone 2009).

Season	Prey taxa							
	Calanoida (CVI)	Calanoida (CI–CV)	Cyclo-poida	Harpacta-coida	Poecilo-stomatoida	Copepoda (napulii)	Bivalvia	Cirri-pedia
Winter	22.0	17.1	13.4	0.6	17.4	1.7	0.9	2.6
Spring	20.1	20.0	10.3	0.8	2.8	0.7	0.1	16.1
Summer	22.4	24.5	9.8	0.5	2.8	3.1	0.6	0.7
Autumn	25.9	20.4	3.8	1.6	14.9	1.3	1.2	0.5

Table 3.2. Mean ± standard deviation and 95th percentile abundance (colonies m^{-3}) of *Muggiaea* spp. at station L4 in the Western English Channel between 2009 and 2013.

	2009	2010	2011	2012	2013
Muggiaea atlantica					
Mean	39 ± 69	25 ± 60	8 ± 12	14 ± 20	32 ± 76
95th percentile	229	123	35	69	222
Muggiaea kochi					
Mean	3 ± 16	1 ± 5	1 ± 3	0 ± 0	0 ± 0
95th percentile	0	6	7	0	0
Muggiaea spp. eudoxid					
Mean	136 ± 212	128 ± 305	55 ± 66	66 ± 74	165 ± 344
95th percentile	505	567	186	241	1145

3.4.2 Seasonal variability

Eigenvector filtering (EVF) decomposed the polygastric and eudoxid stage *M. atlantica* time series into 2 principal components: PC1 and PC2 (Fig. 3.2). PC1 accounted for 58% and 62% of the respective total polygastric and eudoxid stage variability, while PC2 explained a further 25% and 24%. These components represented harmonics of the seasonal cycle, with periodicities of 54 weeks (PC1) (Fig. 3.3A) and 22 weeks (PC2) (Fig. 3.3B). PC1 represented broad-scale changes in the absolute magnitude and distribution of seasonal abundance (Fig. 3.2A–E), while PC2 represented the underlying fine-scale dynamics that drove this variability (Fig. 3.2F–J).

Inspection of the broad-scale seasonal variability (PC1) revealed that in 2010 and 2013 polygastric and eudoxid stage *M. atlantica* exhibited restricted periods of abundance that occurred relatively late in the year, during the autumn weeks (Fig. 3.2B,E). This pattern was in contrast to the other 3 years analysed (2009, 2011 and 2012), during which periods of high abundance occurred earlier (summer) and were more extensive. Compared to the other years analysed, the magnitude of peak abundance of the eudoxid, and particularly the polygastric stage, was comparatively low in 2011 and 2012. The winter minima separating these 2 years was also less extreme (Fig. 3.2C,D).

Fluctuation at the fine-scale (PC2) revealed the underlying dynamics behind patterns of seasonal variability (Fig. 3.2F–J). During the years 2010 and 2013, which were characterised by restricted periods of seasonal *M. atlantica* abundance, single high-amplitude peaks of abundance were observed in September (weeks 34 and 38, respectively). This pattern was in contrast to the other 3 years analysed. In 2009 and 2012, 2 discrete low-amplitude peaks of abundance were evident, the first occurring in week 27 (June) and the second during weeks 42–44 (October). In 2011, a low-amplitude peak of abundance occurred in week 27 (June), after which abundance remained relatively high. Very low amplitude peaks of abundance in the winter were also a common feature, although this peak was less apparent in 2012.

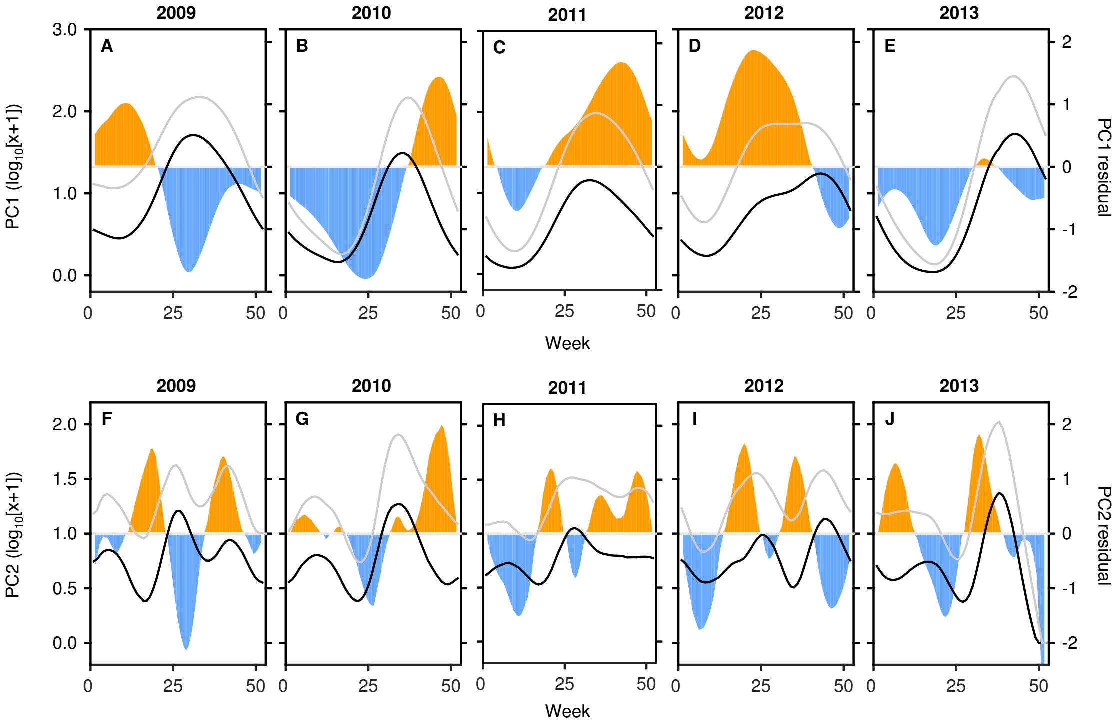

Fig. 3.2. (A–E) Broad scale (PC1), and (F–J) fine temporal scale (PC2) population dynamics of *Muggiaea atlantica* between 2009–2013, showing polygastric stage (black lines) and eudoxid stage (grey line) abundances. Orange and blue shaded areas represent, respectively, positive and negative residuals of the expected eudoxid stage abundance

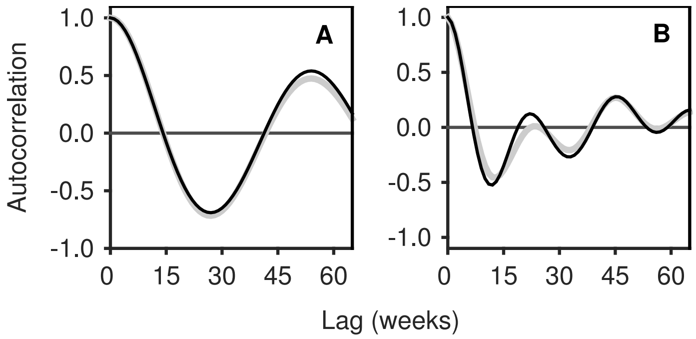

Fig. 3.3. Periodicity of (A) broad-scale and (B) fine-scale fluctuation in the abundance of *Muggiaea atlantica* polygastric (black line), and eudoxid (grey line) stages derived from the autocorrelation function

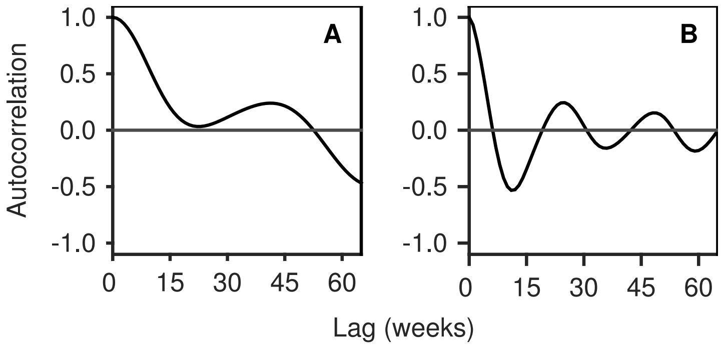

Fig. 3.4. Periodicity of (A) broad-scale and (B) fine-scale residuals of the expected abundance of the eudoxid stage of *Muggiaea atlantica*, computed using the autocorrelation function. The residual eudoxid abundance is the studentised residuals derived from the linear regression of the eudoxid and polygastric stages and indicates deviations from the expected abundance of eudoxids based on their typical relationship

3.4.3 Population dynamics

Linear regression analyses revealed strong relationships between the PC1 of polygastric and eudoxid stage abundance ($b = 1.23$, $r^2 = 0.92$, $F = 2783$, $df = 258$, $p < 0.001$). The residuals derived from this regression model oscillated with a periodicity of 44 weeks (Fig. 3.4A) and represented broad-scale changes in the absolute magnitude of eudoxid stage abundance relative to that of the polygastric stage (Fig. 3.2A–E). In 2011 and 2012, PC1 residuals were consistently positive, indicating that these years were characterised by high relative abundance of eudoxid stage compared to the other years studied (Fig. 3.2C,D).

The residuals derived from the linear regression of PC2 eudoxid and polygastric stage abundance ($b = 1.19$, $r^2 = 0.87$, $F = 1127$, $df = 258$, $p = < 0.001$) fluctuated regularly (Fig. 3.2F–J) with a periodicity of 26 weeks (Fig. 3.4B). The PC2 residuals represented deviations from the expected abundance of the eudoxid stage associated with cycles of production and decline.

High positive residuals were typically observed in the initial phases of population increase (Fig. 3.2F–J). These spikes of higher than expected eudoxid abundance suggested periods of accelerated eudoxid production. However, in 2010 the period of population increase was characterised by negative residuals, suggesting that during this year the rate of eudoxid production was comparatively low. Otherwise, negative residuals were typically observed following peaks of abundance (Fig. 3.2F–J), which indicated that the abundance of the eudoxid stage typically declined more rapidly than the polygastric. However, in 2010 the period of population decline was characterised by positive residuals (Fig. 3.2G), suggesting that during this period the eudoxid stage was more persistent than in the other years.

3.4.4 Correlations with environmental variables

The results of correlation analysis between the principal components of environmental factors and *M. atlantica* variability are presented in Tables (Table 3.3 & Table 3.4). Both the PC1 and PC2 of *M. atlantica* polygastric and eudoxid stage abundance were positively correlated with depth-integrated temperature (Fig. 3.5A–E, Table 3.3). The less extreme minima observed in the PC1 signals of temperature and *M. atlantica* abundance in 2011 and 2012 indicated increased survivorship during the warmest winter of the 5 years. In contrast, the PC1 abundance of the eudoxid stage decreased considerably during the 2 coldest winters (2010 and 2013). The PC2 residuals were also positively correlated with temperature (Table 3.3), confirming the importance of temperature to the phenology of *M. atlantica*. Depth-integrated salinity also emerged as a potentially important variable, being correlated positively with PC1 of both eudoxid abundance and the residuals (Fig. 3.6A–E, Table 3.3). The analysis showed that certain prey items were potentially important covariates after the effects of temperature were controlled for using partial correlation analysis (Table 3.4). Positive correlations were found between the PC1 and PC2 residuals and the abundance of calanoid (particularly copepodid stages CI–CV) and cyclopoid copepods (Stage CVI) (Fig. 3.6F–J, Table 3.4). The abundance of polygastric and eudoxid stages was positively correlated with the abundance of bivalve larvae at the fine-scale (PC2) (Fig. 3.5F–J, Table 3.4).

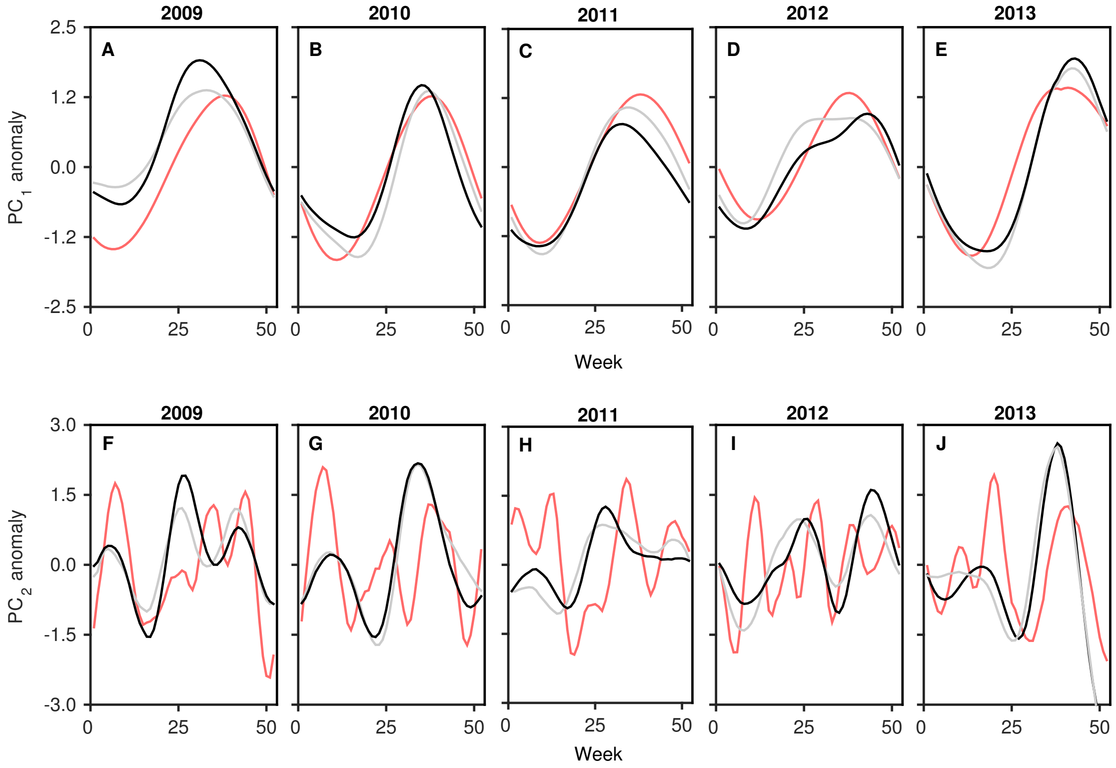

Fig. 3.5. Synchronous fluctuation of the abundance of *Muggiaea atlantica* polygastric (black lines) and eudoxid (grey lines) stages and environmental variables (red lines) at different temporal scales. (A–E) Broad-scale variability (PC1) of polygastric and eudoxid abundance with depth-integrated temperature (r = 0.87, p = 0.01, and r = 0.88, p = 0.01, respectively). (F–J) fine-scale fluctuation (PC2) of polygastric and eudoxid abundance with the PC2 abundance of bivalve larvae (r = 0.38, p = 0.01, and r = 0.31, p = 0.05, respectively)

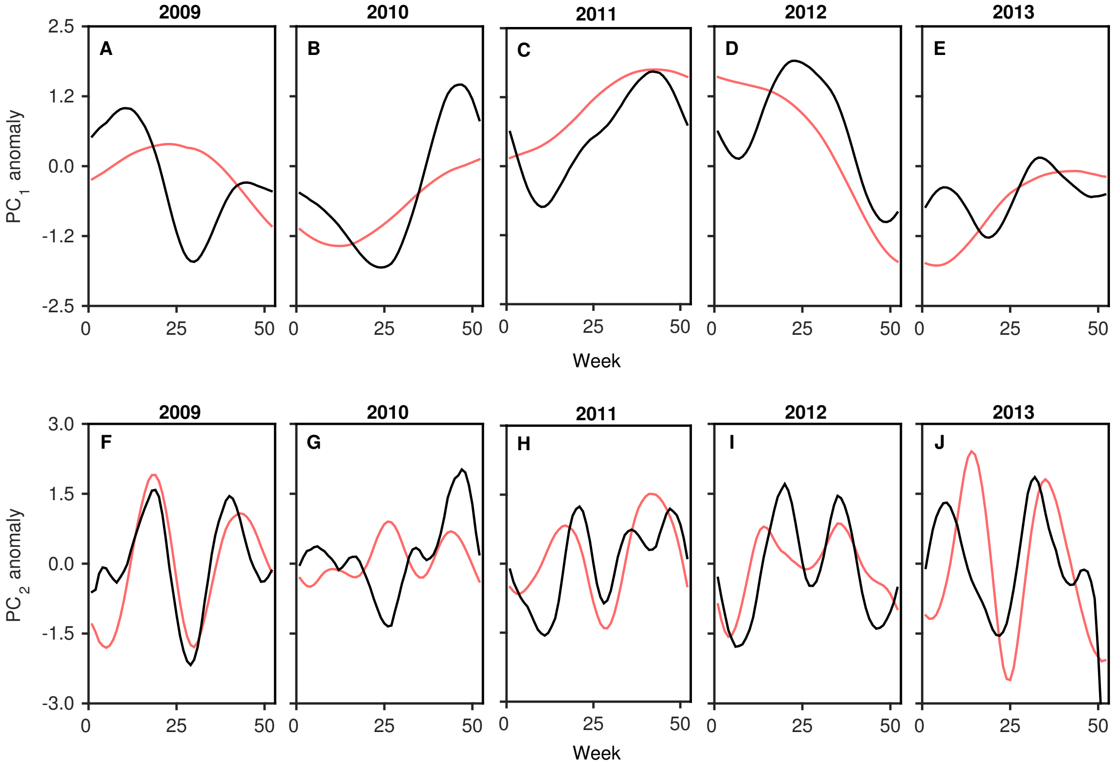

Fig. 3.6. Synchronous fluctuation of *Muggiaea atlantica* residual eudoxid abundance (black lines) and environmental variables (red lines) at different temporal scales. (A–E) broad-scale variability (PC1) of residual eudoxid abundance with depth-integrated salinity (r = 0.67, p = 0.01). (F–J) fine-scale fluctuation (PC2) of residual eudoxid abundance with the PC2 abundance of calanoid copepodids (r = 0.51, p = 0.02)

Table 3.3. Pearson product moment correlations for *Muggiaea atlantica* polygastric, eudoxid, and residuals of eudoxid abundance as a function of physical environmental variables at broad (PC1) and fine (PC2) temporal scales. *T*: temperature; MLD: mixed layer depth. df_a: degrees of freedom after correction for autocorrelation. Bold values indicate statistical significance ($p < 0.05$)

	Polygastric			Eudoxid			Residual		
	r	p	df_a	r	p	df_a	r	p	df_a
PC1									
T	**0.87**	**0.01**	**7**	**0.88**	**0.01**	**7**	0.19	ns	19
Salinity	0.12	ns	53	**0.31**	**0.03**	**51**	**0.67**	**0.01**	**13**
MLD	−0.35	ns	11	−0.28	ns	11	0.21	ns	17
PC2									
T	**0.57**	**0.00**	**23**	**0.68**	**0.00**	**20**	**0.41**	**0.02**	**32**
Salinity	0.15	ns	27	0.21	ns	24	0.19	ns	39
MLD	0.01	ns	258	0.00	ns	258	0.00	ns	258

Table 3.4. Partial correlation analyses of *Muggiaea atlantica* polygastric, eudoxid, and residual eudoxid abundance as a function of biological environmental variables at broad (PC1) and fine (PC2) temporal scales. Partial correlation analysis allowed the effect of temperature to be controlled for. dfa: degrees of freedom after correction for autocorrelation. Bold values indicate statistical significance

	Polygastric			Eudoxid			Residual		
	r	p	df_a	r	p	df_a	r	p	df_a
PC1									
Copepoda									
Calanoida (CVI)	0.09	ns	33	0.17	ns	34	0.17	ns	17
Calanoida (CI–VI)	0.16	ns	22	0.20	ns	22	**0.27**	**0.03**	**17**
Cyclopoida	0.22	ns	26	0.32	ns	27	**0.41**	**0.03**	**28**
Poecilostomatoida	−0.05	ns	10	0.02	ns	10	0.26	ns	17
Harpacticoida	−0.28	ns	13	−0.26	ns	14	0.03	ns	23
Nauplii	0.35	ns	13	0.32	ns	13	−0.03	ns	32
Bivalvia	0.27	ns	11	0.28	ns	11	0.07	ns	26
Cirripedia	−0.17	ns	17	−0.17	ns	17	−0.04	ns	41
PC2									
Copepoda									
Calanoida (CVI)	0.12	ns	21	0.30	ns	23	**0.44**	**0.05**	**21**
Calanoida (CI–VI)	0.12	ns	22	0.27	ns	24	**0.51**	**0.02**	**20**
Cyclopoida	0.22	ns	36	0.24	ns	41	**0.25**	**0.10**	**46**
Poecilostomatoida	0.00	ns	23	0.04	ns	22	0.11	ns	23
Harpacticoida	−0.11	ns	50	−0.01	ns	58	0.12	ns	35
Nauplii	0.13	ns	122	0.12	ns	136	0.02	ns	113
Bivalvia	**0.36**	**0.02**	**42**	**0.29**	**0.05**	**47**	−0.13	ns	39
Cirripedia	−0.01	ns	63	0.02	ns	77	0.10	ns	49

3.4.5 Critical environmental ranges

Quotient plot analyses revealed critical thermal ranges associated with the development and phenology of the *M. atlantica* population (as PC2). The analysis did not reveal any associations with specific conditions of salinity or water column stratification. For both the polygastric and eudoxid stages, high PC2 abundance was significantly associated with temperatures above 12.9 °C, while a negative association was found with temperatures below 12.8 °C ($p < 0.001$) (Fig. 3.7A,B). High positive PC2 residuals, indicating accelerated eudoxid production, were significantly associated initially with a spring increase in temperature to a critical range of 10.1–11.0°C ($p < 0.001$) (Fig. 3.7C). Subsequent periods of accelerated eudoxid production in autumn were significantly associated with temperatures of 13.8–15.6°C ($p < 0.001$) (Fig. 3.7C). Periods of negative PC2 residuals, indicating accelerated eudoxid decline, were significantly associated with a winter decrease in temperature to a critical thermal range of 8.3–9.5°C ($p = 0.001$) (Fig. 3.7D).

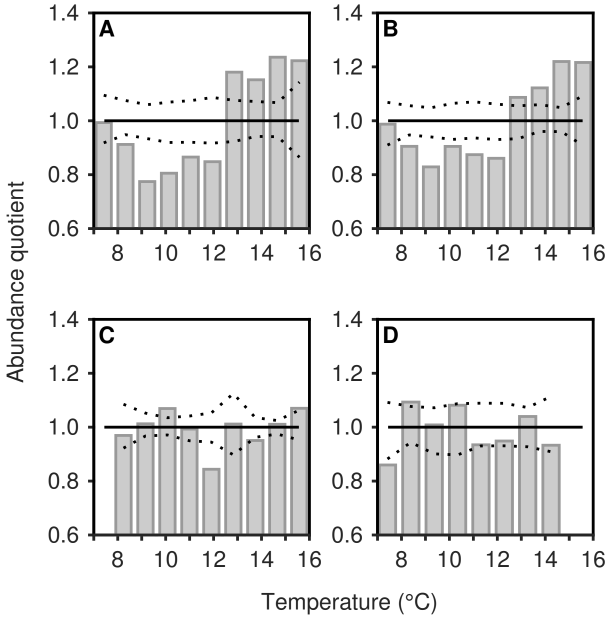

Fig. 3.7 Thermal preferences of *Muggiaea atlantica* identified by quotient plot analysis. (A) Polygastric stage abundance, (B) eudoxid stage abundance, (C) positive residuals, indicating accelerated eudoxid production, and (D) negative residuals (inverted), indicating accelerated eudoxid decline. Bars represent abundance quotients within each category of temperature. Solid line denotes quotient value = 1 (indicating random selection), quotients > 1 indicate positive association, and quotients < 1 indicate negative association. Dotted lines denote 95% confidence intervals

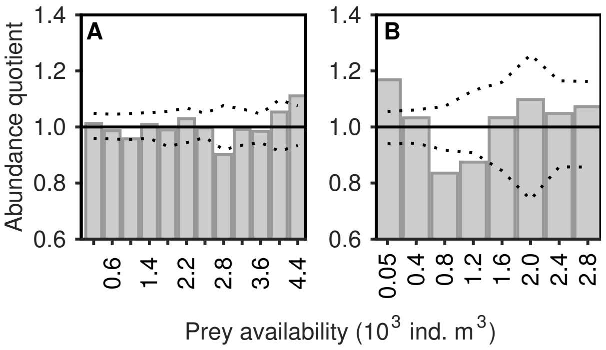

Fig. 3.8. Critical ranges of copepod and copepodid (Calanoida and Cyclopoida) prey availability associated with the residual *Muggiaea atlantica* eudoxid abundance identified by quotient plot analysis. (A) Positive residuals, indicating eudoxid production, and (B) negative residuals, indicating eudoxid decline. Bars represent abundance quotients within each category of temperature. Solid line denotes quotient value = 1 (indicating random selection), quotients > 1 indicate positive association, and quotients < 1 indicate negative association. Dotted lines denote 95% confidence intervals

The analysis also showed a significant association between the residuals of eudoxid abundance (as PC2) and specific ranges of abundance of copepods and copepodids (Calanoida and Cyclopoida) (Fig. 3.8). Positive residuals (eudoxid production) were significantly associated with the maximum (as the 95th percentile) abundance of copepods (4392–4768 ind. m^{-3}), while negative residuals (eudoxid decline) were significantly associated with the minimum abundance of copepods (53–449 ind. m^{-3}).

Our analysis identified a significant influence of temperature and the abundance of copepod prey (particularly calanoid copepodid stages CI–CV) on the residuals of *M. atlantica* eudoxid abundance. Interannual differences in the seasonal dynamics of temperature and prey and how this variability modulated changes in the production and decline of the eudoxid stage is summarised in Fig. 3.9. During the years 2009, 2011, and 2012 the *M. atlantica* polygastric and eudoxid population exhibited seasonal peaks of abundance in summer and autumn that were preceded by periods of accelerated eudoxid production (Fig. 3.9A,C,D). These years were characterised by the co-occurrence of maximal copepodid abundance and the onset of a critical thermal threshold for eudoxid production in spring (10°C). In contrast, the years 2010 and 2013 were characterised by single, comparatively late, seasonal peaks of abundance that occurred in autumn (Fig. 3.9B,E). During both these years the critical thermal threshold for accelerated eudoxid production was reached in week 22, considerably later than during the other years analysed (weeks 15–18). In 2010 (Fig. 3.9B), the onset of the critical thermal threshold in late spring was concurrent with moderate copepodid abundance and decelerated eudoxid production. In 2013 (Fig. 3.9E), the abundance of copepodid prey was at the seasonal minimum when the critical thermal threshold was reached in late spring; under these conditions accelerated eudoxid decline was observed, with accelerated eudoxid production occurring subsequently, concurrent with increased copepodid prey abundance.

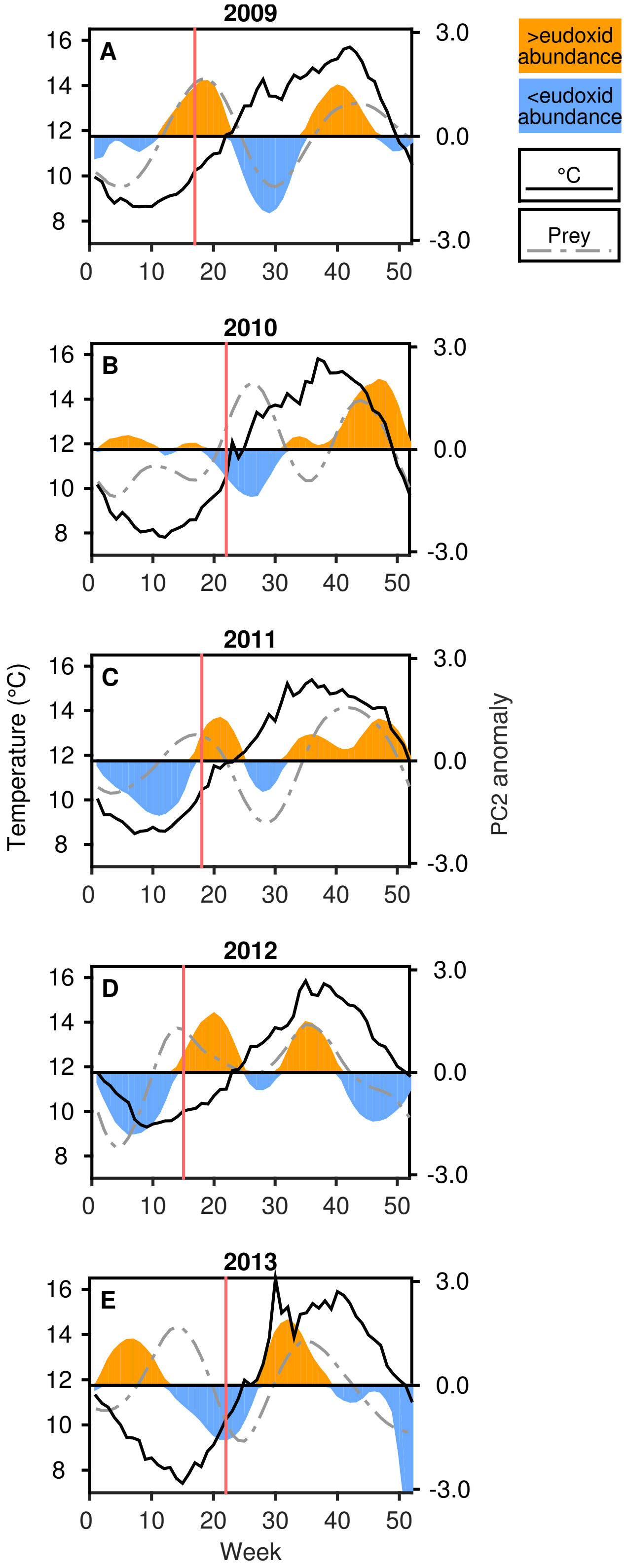

Fig. 3.9. Representation of the population dynamics of *M. atlantica* in response to interannual variability in temperature (solid black line) and food availability (abundance of calanoid copepodid prey [as the PC2 anomaly]; dash-dotted grey line) in the Western English Channel between 2009 and 2013. Vertical red lines denote the timing of the onset of the critical thermal threshold for eudoxid production. Shaded areas represent positive (orange) and negative (blue) residuals of the expected abundance of the eudoxid stage

3.5 Discussion

Here we modelled the functional relationship between the 2 main life-cycle stages of *Muggiaea atlantica*, revealing key features of its population dynamics. Our results highlighted a tight coupling between the timing of specific environmental conditions and the development of the *M. atlantica* population, thereby explaining interannual differences in the phenology of its blooms in the Western English Channel.

Both *M. atlantica* and the congeneric *Muggiaea kochi* occur in the Western English Channel (Blackett et al. 2014; Chapter 2). However, our results only demonstrated a link between the abundance of the polygastric stage of *M. atlantica* and the unidentified *Muggiaea* spp. eudoxid stage. The congeners *M. atlantica* and *M. kochi*, have slightly different thermal tolerances and are considered cool-temperate and warm-temperate analogues, respectively (Alvariño 1971). Blackett et al. (2014; Chapter 2) have shown that *M. atlantica* is resident in the Western English Channel, whereas *M. kochi* is a transient non-resident, probably restricted by low winter temperatures in the Channel. These factors provide strong support for our decision to identify the eudoxids recorded in the present study as *M. atlantica*.

We extracted the dominant modes of temporal variability that characterised the *M. atlantica* population. This procedure allowed us to focus our analysis on seasonal changes in abundance (PC1), and also, the underlying fine-scale dynamics (PC2) that drove this variability. Our results revealed 2 distinct phenological patterns: (1) early spring population development leading to an extended period of abundance with population maxima in both summer and autumn, and (2) late spring population development resulting in a restricted period of abundance with a population maximum in autumn. Phenological variability in calycophoran populations is common at coastal locations in temperate regions (Mackie et al. 1987). In some areas this variability appears to be related to localised changes in seasonal hydrographic conditions (Mackie et al. 1987), the effects of which are often difficult to quantify. Indeed, many cnidarian jellyfish populations seemingly appear and disappear irregularly (Graham et al. 2001; Boero et al. 2008). Whilst a multitude of environmental factors undoubtedly contribute, at different levels, to the dynamic of a population (e.g. Hutchinson 1957), our analysis revealed regularity in the phenological response of the *M. atlantica* population to localised variability in temperature and food availability.

Knowledge of the population dynamics of calycophoran siphonophores is sparse. Cyclical changes in the relative abundance of the polygastric and eudoxid stage have been used as an indicator of the life span of generations (Moore 1949; 1952) and as signals of reproductive cycles (Patriti 1964; Mills 1982). In the present study we used the residuals from linear regression analysis to detect when the eudoxid stage was more or less abundant than expected. Considering the fine-scale (PC2) population fluctuation, periods of higher than expected eudoxid abundance were recorded at the onset of *M. atlantica* population growth in spring. Large polygastric colonies typically persist through the winter (Hosia & Båmstedt 2008) and eudoxid production rates are positively linked to the size of the polygastric colony (Purcell 1982). These factors suggest that periods of higher than expected eudoxid abundance recorded in spring represent the initiation of eudoxid production by the overwintering polygastric population. The spring pulse of *M. atlantica* eudoxid production recorded in the present study was associated with the occurrence of a specific temperature range (10.0−11.1°C). Laboratory experiments on the congeneric *M. kochi* in the Mediterranean have shown that polygastric colonies exist in a suspended reproductive state at typical winter temperature, but successfully reproduce at characteristic spring temperature (Carré & Carré 1991). Since polygastric colonies typically die after asexual reproduction, Carré & Carré (1991) proposed that reproductive dormancy facilitates overwintering of the polygastric population. Our results support this hypothesis and suggest a critical basal limit of 10 °C for asexual reproductive activity of *M. atlantica* in the Western English Channel. This thermal limit is in agreement with the results of Blackett et al. (2014; Chapter 2) who showed that local development of the *M. atlantica* polygastric population at an open-shelf station in the Western English Channel only occurred when the sea surface temperature was above 9 °C.

In addition to the thermal requirements, siphonophore reproduction is also dependent on food availability (Purcell 1982). Our analysis identified a positive link between deviations from the expected abundance of eudoxids and the abundance of calanoid and cyclopoid copepods. Field studies have shown that copepods and their developmental stages represent the dominant dietary component of *M. atlantica* (Purcell 1982). Therefore, the availability of copepod prey concurrent with the onset of suitable temperature conditions seems to be an important factor influencing the initiation of asexual reproductive activity in spring. Indeed, high rates of eudoxid production were associated with the maximum abundance of copepod prey, while peak eudoxid decline was associated with the minimum abundance, echoing the experimental results of Purcell (1982). However, copepod availability rapidly declined following the inception of population development, which suggests that other prey taxa must be important during subsequent population growth. We identified a positive relationship between the population density of *M. atlantica* and the abundance of bivalve larvae. Bivalve larvae represent a common prey resource for many other small cnidarian jellyfish (Hansson et al. 2005), and Batistić et al. (2013) reported a similar link with *M. atlantica* in the Adriatic.

The spring pulse of eudoxid production provides the kernel for population development. Sexual reproduction by the eudoxid stage supplies new recruits to the polygastric population that in turn increases the source of eudoxids. During the years 2009, 2011, and 2012, the critical thermal limit for eudoxid production (10 °C) was reached in early spring, coincident with the primary maxima of copepod abundance. These conditions provided high food availability leading up to the onset of eudoxid production by the overwintering polygastric stage, likely increasing their reproductive capacity (Purcell 1982). Then as temperature and the abundance of bivalve larvae continued to increase, the high feeding rates and reproductive capacity of *M. atlantica* (Purcell 1982; Carré & Carré 1991) allowed rapid population growth that culminated in summer population maxima.

Field studies have indicated an upper thermal limit of 24°C for the survival of *M. atlantica* (Marques et al. 2008; Batistić et al. 2013). Therefore high temperature was unlikely to be a limiting factor in the present study as the maximum average temperature in the Western English Channel is ~16.5 °C (Smyth et al. 2010). Decline of the *M. atlantica* population following summer maxima was instead correlated with the reduced availability of larval bivalve prey, suggesting that food limitation was the trigger for population decline. Food limitation is considered a major cause of population decline for many species of cnidarian jellyfish (Pitt et al. 2014 and references therein). Indeed, the effect of food limitation on the abundance of *M. atlantica* eudoxids was pronounced, with the period following the summer maxima being characterised by lower than expected abundance. This decline is probably explained by the combined effect of the cessation of eudoxid production in response to food limitation (Purcell 1982) and the rapid mortality of existing eudoxids that usually have a shorter life span than the polygastric stage (Carré & Carré 1991). A similar mechanism was responsible for the decline of the *M. atlantica* population in winter, although the decline was compounded by low winter temperatures. Temperatures < 9.5°C represented a limit below which the abundance of eudoxids rapidly declined, potentially signalling the temperature at which the polygastric stage enters reproductive dormancy.

The significance of food availability is further demonstrated by the initiation of secondary population growth during the years characterised by early spring development (2009, 2011, and 2012). Secondary population growth (in autumn) developed in the same way as documented in spring, starting with a pulse of higher than expected eudoxid abundance. This sequence probably represents the initiation of eudoxid production by polygastric colonies remaining from the summer cohort. Given the thermal tolerances of *M. atlantica* previously documented, a temperature cue for this secondary population development seems unlikely. The pulse of eudoxid production was coincident with the autumn copepod population maxima, suggesting that relaxation of food limitation could have been the trigger for secondary population development. Subsequent population growth was again correlated with the abundance of bivalve larvae. The similarity between population development in spring and autumn lends weight to our hypothesis that *M. atlantica* population development is in phase with regular cycles of prey and temperature conditions.

The United Kingdom experienced exceptionally cold conditions during the winter of 2009–2010 and the spring of 2013 (www.metoffice.gov.uk/climate/uk/summaries). These cold conditions extended throughout central and northern Europe (Cattiaux et al. 2010; Andrews 2013) with effects on populations of various aquatic (Edwards et al. 2013b) and terrestrial (Glądalski et al. 2014) animals. In the Western English Channel the critical thermal limit for eudoxid production (10 °C) occurred 4–7 weeks later than during the other years. These cold conditions caused a delay to the initiation of *M. atlantica* population development, which had the effect of disrupting the phasing of eudoxid production with food availability. This trophic mismatch resulted in the development of single autumn population maxima, rather than the summer and autumn peaks recorded during the warmer years.

During 2010 the late onset of *M. atlantica* population development was characterised by a lower rate of eudoxid production than was identified during the other years analysed. During this year the copepod population displayed an atypical phenology, characterised by a summer, rather than spring, primary maximum. This pattern resulted in an extended period of low copepod prey availability during the winter and spring. Food limitation and low temperatures during this period may have reduced survivorship and limited the growth potential of the overwintering polygastric stages. The reduced eudoxid production at the onset of the critical thermal limit likely reflects the impact of these negative factors on the reproductive capacity of the overwintering polygastric population.

The disruption of phasing between food availability and eudoxid production was more severe in 2013. During this year the critical thermal limit for eudoxid production occurred after the primary (spring) copepod population maxima; instead coinciding with their mid-season minimum. Under these conditions, despite the onset of suitable temperature, eudoxid production was restricted by insufficient food availability. As a result, population development was delayed and only commenced once food availability increased with the autumn copepod peak. The subsequent population maximum occurred in late autumn, 5 weeks later than the time of the 2010 population maximum.

Dramatic seasonal variation of upper-ocean environmental conditions is characteristic of temperate regions (Longhurst 1998). Zooplankton must be able to adapt to variability in the timing and extent of these changes to optimise the phasing of their life cycles with favourable environmental conditions (Mackas et al. 2012). The degree of mismatch between the environmental conditions and the species' environmental requirements influences fitness (Cushing 1990; Durant et al. 2007), with potentially profound effects on the size and phenology of zooplankton populations (Ji et al. 2010; Mackas et al. 2012). Our results highlight the fundamental importance of temperature in shaping cnidarian jellyfish populations. Changes to the seasonal temperature cycle in the Western English Channel produced dramatic shifts in the phenology of the *M. atlantica* population by modulating the degree of trophic mismatch experienced during the initial phases of population development. Temperature variability has been shown to modify the timing of important developmental events of numerous other species of zooplankton (Beaugrand et al. 2002; Edwards & Richardson 2004). With direct and indirect effects on virtually all aspects of marine ecosystems (e.g. biological, physical and chemical components), temperature consistently emerges as the most common phenological correlate (Mackas et al. 2012).

Marine organisms with long life spans, such as fish, often employ mechanisms that lead to fixed seasonal timing for reproduction (Cushing 1990). This strategy ensures that, over the long term, reproduction will be in phase with favourable conditions at least during some years, despite interannual variability in the timing of environmental conditions (Cushing 1990; Durant et al. 2007). Because most zooplankton have short (<1 year) life spans, a fixed seasonal timing window increases the risk that in the event of a 'mismatch', the population will not survive to reproduce in a subsequent year (Mackas et al. 2012). Therefore, zooplankton species tend to reproduce episodically, in response to environmental cues (Mackas et al. 2012). *Muggiaea* sp. typically have a life cycle in the order of weeks to months (Carré & Carré 1991). Although we have implied that *M. atlantica* initiates reproduction in response to a fixed thermal threshold (10°C), we do not consider this temperature as a thermal cue, but rather a physiological limitation. The Western English Channel represents the most northerly recorded habitat supporting a self-sustaining population of *M. atlantica* in the Northeast Atlantic (Blackett et al. 2014; Chapter 2). At this latitude, *M. atlantica* is likely at the extreme of its thermal tolerance limits. However, the thermal requirements of cnidarian jellyfish are usually location-specific and different populations can adapt to different temperature regimes (Lucas & Dawson 2014). For instance, the *M. atlantica* population on the Pacific northwest coast of the United States successfully reproduces at temperatures of 8–10 °C (Purcell 1982).

The original match-mismatch hypothesis (Cushing 1990) states that a trophic mismatch between predator and prey leads to poor growth, survival and subsequent recruitment. In our study a trophic mismatch with the copepod prey population in the Western English Channel resulted in dramatic phenological shifts of *M. atlantica*; however the effect on population size was less extreme. Cold spring conditions restricted *M. atlantica* population development, leading to trophic mismatch and the development of single autumn population maxima with low mean annual abundance. However, the amplitude of these single autumn maxima was higher than peaks during those years where both summer and autumn maxima were recorded. This disparity highlights the resilience and adaptability of *M. atlantica*, and cnidarian jellyfish in general. Their opportunistic life history traits and physiology enable high feeding rates, rapid growth rates, high fecundity and short generation times (Purcell et al. 2007; Acuña et al. 2011). These traits afford cnidarian jellyfish populations great flexibility, enabling rapid conversion of available food energy into large population biomass. The negative impact of a trophic mismatch can be quickly overcome in response to subsequent favourable conditions.

Despite optimal phasing between the onset of eudoxid production and copepod prey availability, during 2011 and 2012 the *M. atlantica* population density was lower than during the other years analysed. This low abundance was particularly pronounced in the polygastric stage, indicating that the high residual abundance of the eudoxid stage was probably a consequence of reduced polygastric stage production during these 2 years. This result was not linked to a reduction in copepod or bivalve larvae prey availability (data not shown). However, the years 2011 and 2012 were characterised by warmer and more saline conditions than the other years analysed. Although many Calycophora thrive under warm and high salinity conditions (e.g. Buecher 1999), *M. atlantica* displays euryhaline characteristics and is known to tolerate salinities outside the extremes recorded in the present study (Blackett et al. 2014; Chapter 2). As changes in the salinity conditions could reflect modification to water circulation patterns in the Western English Channel (Pingree 1980), it is possible that advection and migration of *M. atlantica* could explain the low densities recorded in 2011 and 2012.

The seasonal dynamic of the *M. atlantica* population revealed a recurrent low amplitude peak of abundance in winter (weeks 5–10). It is conceivable that this peak could reflect local reproduction during the relatively warm winter conditions of 2013. However, recurrent reproductive activity in winter would appear unlikely given that the winter temperatures typically experienced are below the thermal tolerances of *M. atlantica* discussed above. The *M. atlantica* population in the Western English Channel likely represents the northern component of a spatially extensive Northeast Atlantic metapopulation (Blackett et al. 2014; Chapter 2). Pulses of winter abundance observed in the present study could thus indicate immigration from a sub-population located to the south, probably within the Bay of Biscay (reviewed in Mackie et al. 1987). However, the paucity of spatially resolved data within the Channel region limits our understanding of these processes.

In conclusion, this study used *in situ* observations to establish a theoretical model for *M. atlantica* population dynamics and highlight the significance of the temporal dynamics of temperature and food availability. These findings represent an important addition to our understanding of the ecology of this gelatinous predator, providing preliminary indications of the key temperatures and food ranges that are important for the development and maintenance of its populations in the Northeast Atlantic. However, our ability to interpret and understand observed changes *in situ* is hampered by our limited knowledge of the species' reproductive biology. Laboratory experiments are required to quantify the reproductive capacity, life spans, and survival of the different life-cycle stages of *M. atlantica* and of other calycophoran siphonophores. Developing an empirical understanding of the ecology of these planktivorous predators can facilitate their incorporation into studies modelling the ecosystems in which they play a fundamental role (e.g. Pauly et al. 2009). Increasing our understanding of the interaction of climate and phenology at the species level and across trophic levels is fundamental to our understanding of the functioning and resilience of marine ecosystems in a changing climate (Ji et al. 2010).

Chapter 4

Blooms of the siphonophore, *Muggiaea atlantica*, in Scottish Coastal waters: source or sink?

4. Blooms of the siphonophore, *Muggiaea atlantica*, in Scottish Coastal waters: source or sink?

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4.1 Abstract

As a result of their opportunistic ecology, jellyfish populations fluctuate dramatically in space and time. These fluctuations are driven by biological factors that affect their demographic rates and also by physical factors that influence their dispersal. The siphonophore *Muggiaea atlantica* has expanded its distribution in the northeast Atlantic over recent decades. However, these changes are not clearly understood because the processes involve a complex interaction of the biological and physical factors. We investigated a recent (1999–2013) increase in the abundance of *M. atlantica* in Scottish coastal waters, a region where the species was historically extremely rare. The concept of source-sink dynamics was applied to investigate whether these changes represented either the establishment of a resident population (i.e. a source), or a transient population reliant on immigration (i.e. a sink). At both sampling locations we show that local production was often sufficient to account for recruitment, a characteristic of a source. However, during some years recruitment was not explained by local production, suggesting the importance of immigration, a characteristic of a sink. To confirm their categorisation we then modelled the relationships between the annual abundance of *M. atlantica* and potential immigration (as indexed by the European Slope Current, ESC), and the environmental parameters that were shown to significantly influence local production (Sea Surface Temperature and food availability). By using partial linear regression analysis, we were able to discriminate between the exclusive effects of local production and immigration. On the west coast (Loch Ewe), our results showed that interannual variability in the abundance of this species is determined by, in order of increasing importance: (1) the availability of suitable local environmental conditions (16%); (2) the role of the ESC in modulating these environmental conditions (16%); and (3) the immigration of *M. atlantica* via the ESC (40%). These results provide strong support for the categorisation of Loch Ewe as a sink habitat for *M. atlantica*. However, on the east coast our results did not reveal a clear link with the ESC, probably due to its less direct influence. It is suggested that low winter temperatures prevent overwintering in Scottish coastal waters, necessitating the annual re-colonisation via immigration. The analysis did not support our hypothesis that a source population in the Western English Channel (WEC) was the dominant source for migration into Scottish waters, suggesting the importance of a network of other sources, which has been reported in other species of jellyfish.

4.2 Introduction

Jellyfish (Cnidaria and Ctenophora) represent an important functional group of secondary consumers in marine pelagic ecosystems (Condon et al. 2012; Lucas et al. 2014b). Over recent decades, increases in the abundance and distribution of jellyfish have been reported in many regions of the world (Purcell et al. 2007; Brotz et al. 2012). These changes have generated concern as the ecological interactions of jellyfish can modify the structure and function of marine ecosystems (Mills 1995; Pitt et al. 2009), with knock-on effects for a range of ecosystem services (Purcell 2012). Developing our understanding of the factors and mechanism that drive shifts in the abundance and biogeography of jellyfish is an important objective for marine ecologists. A critical aspect of this understanding is our capacity to distinguish the effects of both biological (i.e. changes to demographic rates) and physical (i.e. changes to immigration and emigration rates) processes on jellyfish populations (Graham et al. 2001).

The concept of source-sink dynamics provides a theoretical framework to help understand how dispersal and habitat-specific demography influence species abundance and distribution (Pulliam 2000). In source habitats, local production exceeds local mortality, and emigration exceeds immigration (dispersal), whereas in sink habitats, the opposite is true. Source habitats are, by definition, self-sustaining; they provide the necessary conditions for a species to complete its full life history and to persist indefinitely – independent of the contribution of immigration. Conversely, unsuitable conditions in sink habitats prevent the species from persisting indefinitely and populations must rely upon immigration to balance losses to local mortality (and emigration). The result is that, in spatially complex landscapes, habitat heterogeneity can generate spatially explicit population structures composed of networks of source- and sink-habitats all connected via dispersal (Dunning et al. 1992). Recent studies have demonstrated the importance of source-sink dynamics in the modulation of the spatial and temporal distribution of jellyfish populations (Costello et al. 2012; Chen et al. 2014).

The cnidarian jellyfish *Muggiaea atlantica* (Siphonophorae, Calycophora) is an important gelatinous predator in low- to mid-latitudinal coastal waters of the three major oceans (Mapstone 2014). During the late twentieth century, expansion of the species' distribution has been reported in a number of different regions including the Mediterranean (Licandro et al. 2012) and South Pacific (Palma et al. 2014). Intense predation by *M. atlantica* can deplete prey resources, restricting the available energy for other functional groups and disrupting the balance of the biocenoses (Greve 1994; Kršinić & Njire 2001). As a vector for disease (Fringuelli et al. 2012), and by injuring and killing farmed fish (Baxter et al. 2011), *M. atlantica* is capable of inflicting significant economic losses on aquaculture operations (Fosså et al. 2003; Cronin et al. 2004). To predict and manage these impacts, it is important to better understand the processes that influence the population dynamics and spatio-temporal patterns of *M. atlantica* in different regions.

Throughout the twentieth century, *M. atlantica* was almost entirely absent from the Scottish Continental Shelf (Totton & Fraser 1955; Fraser 1967; Heath et al. 1999). However, more recent observations suggest that the species' frequency of occurrence has dramatically increased (K. Cook unpublished data). We previously demonstrated the transition of the Western English Channel (WEC) from a sink- to a source-habitat for *M. atlantica* in the late 1960s (Blackett et al. 2014; Chapter 2). The formation of this new source may have augmented the species' dispersal range, enabling the formation of new populations in the previously uninhabited Scottish region (e.g. Bolte et al. 2013). In jellyfish, source and sink habitats are connected via current-driven transport (Costello et al. 2012; Chen et al. 2014). The European Slope Current (ESC) flows along the northwest European Continental Shelf from the Bay of Biscay to the Faroe-Shetland Channel (Xu et al. 2015) and the presence of *M. atlantica* in the Scottish Continental Shelf has been associated with the inflow of these waters (Fraser 1967). An investigation into the role of source-sink dynamics would aid our understanding of the apparent northward biogeographical shift of *M. atlantica* in the northeast Atlantic Ocean.

In this study we used data from the source habitat of the WEC and two potential habitats on the east and west coasts of Scotland to investigate how source-sink processes influence temporal patterns of *M. atlantica* abundance in Scottish waters. At the Scottish sampling locations we identified local production and the influence of key local environmental parameters chosen on the basis of published studies. Then, using a form of variation partitioning we examined the respective contribution of local production (as indexed by the key local environmental parameters) and immigration (as indexed by the ESC and source abundance) on the annual abundance of *M. atlantica* in Scottish coastal waters. The aims of this study were: (1) to confirm the species increased frequency of occurrence in Scottish waters; (2) to assess the status of Scottish waters as either sources or sinks; and (3) to determine the role of the WEC as a source of *M. atlantica* propagules for immigration into Scottish waters. Through these efforts we attempt to add to our understanding of the mechanisms that drive changes in the biogeography of *M. atlantica* in the northeast Atlantic Ocean and adjacent seas.

4.3 Materials and methods

4.3.1 *Muggiaea* data

Data on the abundance of *Muggiaea atlantica* in Scottish coastal waters were obtained from two coastal plankton-monitoring stations operated by Marine Science Scotland: (1) Loch Ewe, a sea loch in the Northwest Highlands of Scotland and (2) Stonehaven, a North Sea station ~5 km off the coast of Aberdeen (Fig. 4.1 & Table 4.1). Data from the Western English Channel (WEC) were derived from time series records provided by the Western Channel Observatory (Table 4.1) and previously described by Blackett (Blackett et al. 2014; Blackett et al. 2015; Chapters 2, 3).

Details of the different sampling protocols are summarised in Table 4.1. For all data sets the number of *M. atlantica* nectophores was used as a direct estimate of the abundance of the polygastric stage, as species of the genus *Muggiaea* develop only a single nectophore (Mackie et al. 1987). The eudoxid stage of *M. atlantica* was enumerated using the number of detached bracts and intact colonies. Whilst the eudoxid stages of the genus *Muggiaea* are morphologically indistinguishable (Kirkpatrick & Pugh 1984), eudoxid identity was attributed to *M. atlantica* because: (1) it was the only species of *Muggiaea* recorded at the Scottish sampling locations and (2) it was the monodominant species recorded in the Western English Channel throughout the study period (Blackett et al. 2014; Blackett et al. 2015; Chapters 2, 3).

4.3.2 Local environmental data

Sea Surface Temperature (SST), salinity and food availability were recorded simultaneously with *Muggiaea* data (Table 4.1). Temperature and food availability were essential parameters to consider due to their proven effects on reproduction in *Muggiaea* (Purcell 1982; Carré & Carré 1991). Whilst *M. atlantica* displays euryhaline characteristics (Palma et al. 2014), salinity was still an important variable to consider due to its utility as a water mass indicator (Blackett et al. 2014; Chapter 2). Total calanoid copepod abundance (excluding species with <25% frequency of occurrence) was used as an index of food availability as they represent the main dietary component for *M. atlantica* (Purcell 1981a).

4.3.3 European Slope Current data

Flowing along the northwest European Continental Shelf from the Bay of Biscay to the Faroe-Shetland Channel, the European Slope Current (ESC) is a major section of the poleward flow of Atlantic water into the North Sea and Nordic Seas (Xu et al. 2015). We used the ESC as an index of the potential immigration of *M. atlantica* into the Scottish sampling locations. Interannual variability in the magnitude of the ESC was assessed using the 20-year time series constructed by Xu (Xu et al. 2015). Satellite altimetry derived maps of absolute dynamic topography were used to compute seasonal and interannual variations in the mean geostrophic flow across 8 continental slope sections (each ~100 km in length) from Portugal to Shetland. Validation was performed by comparisons with *in situ* oceanographic measurements (Acoustic Doppler Current Profiler data). For a detailed description of the methodology see Xu (Xu et al. 2015). In the present study a subset of the 8 sections (extending from the Bay of Biscay to the Shetland Channel; Fig. 4.1) were used to calculate the annual ESC time-series.

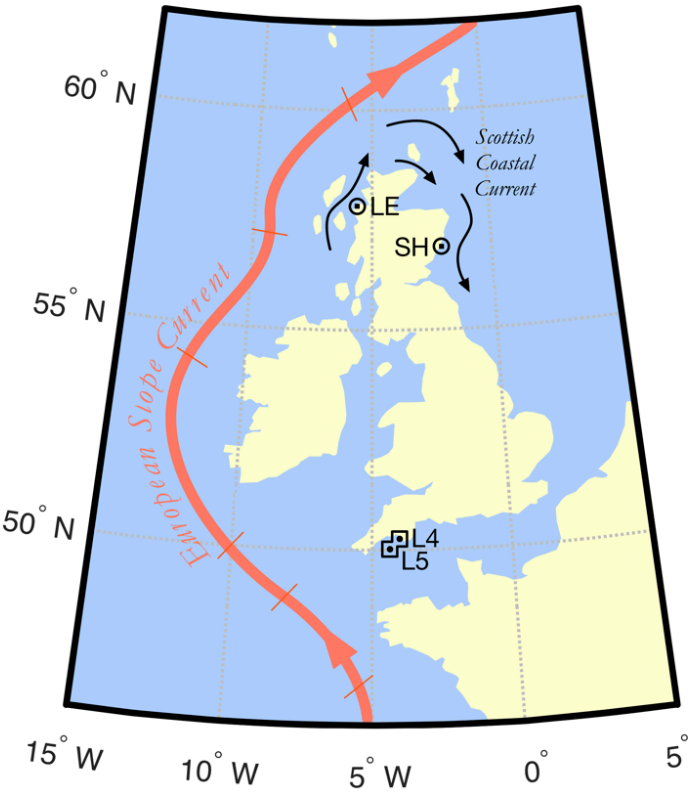


Fig. 4.1 Map of the British Isles with the sampling locations and the general patterns of water circulation indicated. LE: Loch Ewe; SH: Stonehaven; Western English Channel coastal station (L4) and shelf station (L5). The red bars represent the European Slope Current sampling sections

Table 4.1. Sources and characteristics of plankton and environmental data used in this study.

Location	Data	Units	Coverage	Frequency	Methodology	Source
Stonehaven 56.96°N 02.10°W	Food availability	Ind. m^{-3}	1999–2013	Weekly	Vertical hauls ø = 0.4 m mesh = 200 µm	MSS
	Polygastric	Col. m^{-3}	1999–2013			
	Eudoxid		2001–2006			
	Sea surface temperature	°C	1999–2013	Weekly	Reversing thermometer	
	Salinity				Salinometer	
Loch Ewe 57.85°N 5.65°W	Polygastric	Col. m^{-3}	2003–2013	Weekly	Vertical hauls ø = 0.4 m mesh = 200 µm	MSS
	Eudoxid					
	Food availability	Ind. m^{-3}				
	Sea surface temperature	°C	2003–2013	Weekly	Reversing thermometer	
	Salinity				Salinometer	
WEC L5 50.03°N 04.37°W	Polygastric	Col. 100 m^{-3}	2005–2012	Monthly	Double-oblique hauls A = 0.4 m^2 mesh = 700 µm	WCO/1
WEC L4 57.85°N 05.65°W	Polygastric	Col. m^{-3}	2009–2012	Weekly	Vertical hauls A = 0.25 m^2 mesh = 200 µm	WCO/2
	Eudoxid					
NW European shelf	Slope Current	±cm s^{-1} (anomaly)	1999–2012	Annual	Satellite altimetry/*in situ* observations	3

WEC: Western English Channel; MSS: Marine Science Scotland; WCO: Western Channel Observatory; 1: Blackett et al. (2014); 2: Blackett et al. (2015); 3: Xu et al. (2015)

Food availability was represented by calanoid copepod abundance; ø: Diameter; A: Area; Col.: Colonies; Ind.: Individuals.

4.3.4 Numerical analysis

All data manipulation and statistical analysis was conducted in the MATLAB© environment (R2014b 8.4.0.150421).

4.3.4.1 Data preparation

Random missing values (<10% of the total observations) in the weekly plankton abundance and local environmental data were estimated using shape-preserving piecewise cubic interpolation. The sampling frequency was then adjusted to a monthly frequency. To stabilise variance the monthly plankton time series were transformed ($\log_{10}$ [x+1]). The next step was to compute annual time series. For the Scottish sampling locations, we focussed on the seasonal period during which *M. atlantica* was present; the annual scores were calculated as the arithmetic mean (i.e. using the back-transformed plankton data) of the consecutive months displaying a greater than 25% frequency of occurrence of *M. atlantica*. For the Western English Channel locations, the annual time series were calculated using all twelve months, as the species is typically present throughout the year (Blackett et al. 2014; Blackett et al. 2015). Annual scores were then transformed ($\log_{10}$ [x+1]) to stabilise variance before being standardised to zero mean and unit deviation (z-scored). Finally, the presence of any significant interannual trends was tested using up and down runs tests (Legendre & Legendre 2012).

Before 2009, siphonophore species were enumerated collectively at the coastal Western English Channel station (L4); species-level data on the abundance of *M. atlantica* were only recorded after that date. We found that between 2009 and 2013 *M. atlantica* represented the majority (92.63±16.00%) of the total siphonophore density and that their abundance significantly co-varied (Section A3). Consequently, we used linear regression models of the relationship between *M. atlantica* and total siphonophore abundance during 2009–2013 to extrapolate data for the earlier period 1999–2008 (Fig. A3.1 & Fig. A3.2). Because data on the abundance of the polygastric stage were available from the adjacent open-shelf station (L5) for a concurrent period (2005–2012), we were able to validate the accuracy of the extrapolation by comparing the coefficients of correlation computed between the two WEC stations inclusive and exclusive of the extrapolated data period (Table A.3.1).

4.3.4.2 Identification of local *M. atlantica* production

In source habitats, local production must be sufficient to account for recruitment (Pulliam 2000). We identified periods of local biological production using the technique described by Blackett (Blackett et al. 2014; Chapter 2). This procedure involved the identification of the quantity of information associated with peaks and troughs (turning-points) in the monthly time series of *M. atlantica* abundance. Turning-points associated with a high quantity of information represent the culmination of gradual monotonic changes in abundance, whereas those turning points associated with a low quantity of information reflect abrupt (random) fluctuations. We considered the consecutive months between troughs and peaks associated with a significant high quantity of information (>4.2 bits; Ibañez 1982) as periods of population increase characteristic of local biological production.

4.3.4.3 Local environmental influence at the seasonal scale

To verify the influence of local environmental conditions on *M. atlantica* abundance at the Scottish sampling locations we identified significant associations with each of the local environmental parameters (SST, salinity and food availability). Associations were identified using quotient analysis (Van der Lingen et al. 2001). Abundance quotients were calculated as the percentage of the total abundance recorded within categories of local environmental parameters, divided by the percentage frequency of occurrence of each of the categories. Quotient values above 1 indicate a positive association of abundance with a specific environmental category, while quotients values below 1 indicate a negative association and quotient values of 1 indicate random association. To test the null hypothesis of associations occurring merely by chance, a permutation test with 10,000 repetitions was used to calculate confidence intervals with $\alpha = 0.05$. The quotient values were log transformed (to the base 2) to aid graphical representation of the negative quotients (that range only between 0 and 1); this transformation resulted in the test criterion diverging from 0 (instead of 1). For this analysis the log transformed ($\log_{10}$ [x+1]) monthly plankton data were used to limit the effect of extreme values. Only the months when *M. atlantica* was present were considered.

4.3.4.4 Source-sink processes at the annual scale

The ESC influences both plankton dispersal (Beaugrand et al. 2001) and the local environmental conditions in Scottish coastal waters (Inall et al. 2009). We used partial linear regression (Peres-Neto et al. 2006) to assess the respective contribution of endogenous (e.g. local demographic rates) and exogenous (e.g. immigration and emigration rates) processes to the interannual variability in the abundance of *M. atlantica*. This method of variation partitioning allows estimation of the amount of variation in a response variable that can be attributed exclusively to one set of explanatory variables, once the effect of the other set has been taken into account and controlled for (Legendre & Legendre 2012). This technique was used to test the null hypothesis that the Scottish sampling locations represent a source-habitat, against the alternative hypothesis that they represent a sink-habitat. In a source habitat local production outweighs immigration (Pulliam 2000) and therefore effects of local environmental variability on the species intrinsic (i.e. reproduction, fecundity, mortality) dynamics would be expected to explain the majority of the variability in the abundance of *M. atlantica*. Conversely, in a sink-habitat, immigration outweighs local production (Pulliam 2000) and therefore translocation would be expected to explain the majority of the variability. The steps of the method are briefly described below, following Legendre and Legendre (Legendre & Legendre 2012).

Let **y** represent the response variable (*M. atlantica* abundance), **X** one set of explanatory variables (local environmental factors: SST and food availability) and **W** (translocation factors: the ESC and source abundance, and an interaction variable represented by their product) the other set (also called 'the matrix of covariables'). First, the multiple linear regression of **y** against **X** and **W** together is computed. The corresponding adjusted coefficient of multiple determination (R^2_a) represents the fraction of the variation in y explained by both **X** and **W** (i.e. fraction [a + b + c] defined in Fig. 4.2). Next, the multiple linear regression of **y** against **X** is computed, with the corresponding R^2_a representing the fraction of variation explained by **X** (i.e. fraction [a + b]; Fig. 4.2). Similarly, the multiple linear regression of **y** against **W** is then computed, with its corresponding R^2_a representing the fraction of variation explained by **W** (i.e. fraction [b + c]; Fig. 4.2). Finally, the individual fractions [a], [b], [c] and the (residual) fraction [d] are calculated by subtraction. These individual fractions represent:

[a] The variation explained by **X** (local environmental factors) once the effect of **W** (translocation factors) has been removed;
[b] The common variation explained by both **X** and **W** (their intersection *not* interaction);
[c] The variation explained by **W** once the effect of **X** has been removed;
[d] The unexplained (residual) variation.

We considered the translocation factors as the matrix of covariables because the ESC influences both plankton dispersal and the local environmental conditions (Beaugrand et al. 2001; Inall et al. 2009). A stepwise selection procedure (with a probability-of-F-to-enter ≤0.05 and two-tailed p values) was applied separately to the sets of explanatory variables **X** and **W**. Provided the conditions of homoscedasticity, independence and normality of the residuals are satisfied, the significance of the fractions can be tested under the parametric framework; otherwise, p-values can be obtained using a permutation test (Legendre & Legendre 2012). Multicolinearity was evaluated using Belsley collinearity diagnostics (Belsley et al. 1980). The adjusted coefficient of multiple determination was used here because **X** and **W** contained random variables (Peres-Neto et al. 2006).

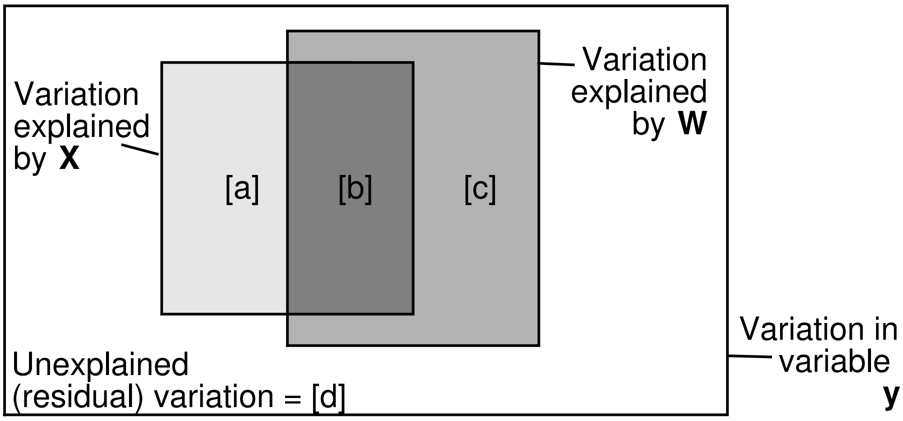


Fig. 4.2. Schematic Venn diagram representing the partition of variation of a response variable, y, among two sets of explanatory variables, X and W. The outer rectangle represents 100% of the variation in y. Fractions [a] and [c] represent the portion of variation attributed exclusively to X and W, respectively, while fraction [b] represents the intersection (not the interaction) of the variation explained by both X and W. The fraction [a + b + c] represents the total variability explained by both X and W together, while fractions [a + b] and [b + c] represent the exclusive and common variation explained by X and W, respectively.

4.4 Results

4.4.1 Loch Ewe: Seasonal variability and local production of *M. atlantica*

The seasonal occurrence of *M. atlantica* at Loch Ewe between 2003 and 2013 was ephemeral (Table 4.2), being present in only 33–39% of the monthly observations. The species was generally absent throughout the winter and much of the spring, with both stages typically appearing in early summer and remaining present until early autumn (Fig. 4.3). On average, the seasonal period of maximum *M. atlantica* density was from June–November. During 2006 and 2007 the seasonal distribution of *M. atlantica* was more restricted than observed during the other years analysed. This pattern was also apparent in 2013 for the polygastric stage. In 2012 both stages were absent from the loch. The monthly abundance of the two stages significantly covaried ($r = 0.94$, $p = < 0.001$), with the eudoxid stage typically attaining greater densities (Table 4.2).

During the periods 2003–2005 and 2008–2010 the abundance of both stages of *M. atlantica* increased in a manner characteristic of local biological production (Fig. 4.3). This local population development commenced immediately following their appearance in the loch and progressed for 2–4 month periods before culminating in peak population density in August–September. During the years characterised by a restricted period of occurrence, local population development was not recorded and the sporadic appearance of *M. atlantica* was related to abrupt fluctuations. Both stages typically displayed similar patterns of population development; however the eudoxid stage appeared and commenced development earlier than the polygastric stage in 2009 and it also peaked earlier in 2008. In 2011 and 2013 only the eudoxid stage of *M. atlantica* was identified developing *in situ*.

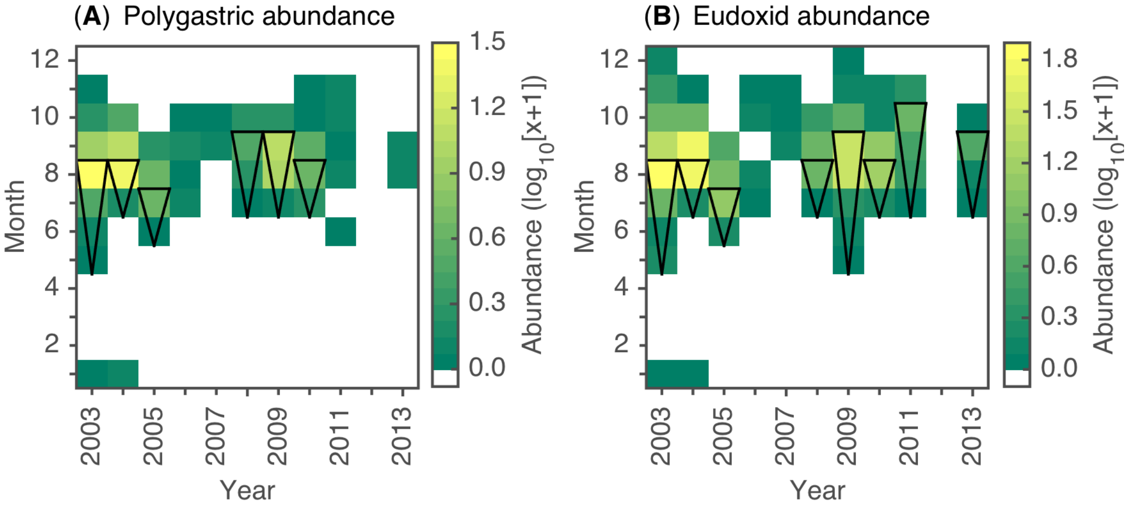


Fig. 4.3. Patterns of seasonal variability in the monthly time series of *Muggiaea atlantica* abundance ($\log_{10}$ [colonies $m^{-3}+1$]) at Loch Ewe between 2003 and 2013. (A) Polygastric stage and (B) eudoxid stage. Periods of population increase characteristic of local biological production are represented by black triangles.

Table 4.2. Mean, standard deviation and maximum abundance (colonies m^{-3}) and percentage of zero values in the monthly time series of *Muggiaea atlantica* polygastric and eudoxid stage abundance at the Scottish sampling locations: Loch Ewe (2003–2013) and Stonehaven (1999–2013).

	Mean	SD	Max	Zeros (%)
Loch Ewe				
Polygastric	0.9	3.7	3.4	67
Eudoxid	2.8	10.5	13.1	61
Stonehaven				
Polygastric	3.6	9.1	23.3	46
Eudoxid	8.5	32.7	33.1	63

SD: Standard Deviation; Max: 95th centile

4.4.2 Loch Ewe: Local environmental optima at the seasonal scale

The results of the quotient analysis were virtually identical for the polygastric and eudoxid stages of *M. atlantica* at Loch Ewe (Fig. A3.3) and therefore the species associations are described here in terms of the polygastric stage. The abundance of *M. atlantica* was positively related to Sea Surface Temperature (SST): occurring within the range 8.0–14.4 °C, high abundance of *M. atlantica* was significantly ($p < 0.05$) associated with temperatures between 12.8 °C and 14.4 °C, while a significant negative association was identified with temperatures in the range 9.5–11.2°C (Fig. 4.4A). *M. atlantica* was not recorded in the lowest temperatures range 6.3–7.9°C. The abundance of

M. atlantica was also significantly positively related to salinity (Fig. 4.4B). The species occurred within the salinity range 32.63–34.43, with high abundance significantly related to with the maximum salinity range of 34.20–34.43. When the salinity was low (~27.00–32.60) *M. atlantica* was not recorded. As observed for SST and salinity, *M. atlantica* displayed a positive relationship with food availability; high abundance of *M. atlantica* was significantly associated with the maximum calanoid copepod abundance, however, there was no significant negative association with low prey abundance (Fig. 4.4C).

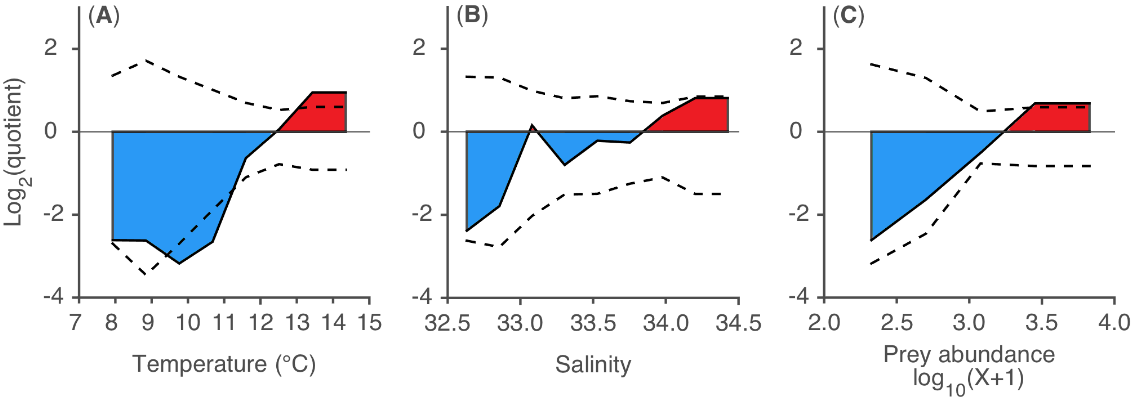


Fig. 4.4. Preferential ranges and critical thresholds of local environmental conditions associated with the abundance of *M. atlantica* at Loch Ewe between 2003 and 2013. Associations of polygastric abundance with (A) SST (Sea Surface Temperature), (B) salinity and (C) food availability (calanoid copepod abundance m^{-3}). Positive quotient values indicate a positive association (in red), while negative quotients values below 0 indicate a negative association (in blue) and quotient values of 0 indicate a random association. The dotted lines delimit 95% confidence intervals.

4.4.3 Loch Ewe: Interannual variability

No significant temporal trends were identified in the annual time-series (calculated using the months June–November) and therefore further analyses were conducted on the standardised annual anomalies.

Between 2003 and 2013 the long-term mean annual abundance (± standard deviation) of *M. atlantica* at Loch Ewe was 1.81±2.53 and 5.67±7.47 colonies m^{-3} for the polygastric and eudoxid stages, respectively. The abundance of the two stages was highly correlated (Table 4.3). Interannual changes in the species population density displayed a quasi-bimodal distribution characterised by two periods of high abundance in 2003–2004 and 2009 (maximum of ~1.7 standard deviations above the mean in 2003) flanked by periods of low abundance (maximum of ~1 standard deviation below the mean in 2012) (Fig. 4.5A).

Translocation factors. The long-term mean European Slope Current (ESC) anomaly and its standard deviation were −0.51±0.72 cm s^{-1}. Interannual variability in the magnitude of the ESC was significantly positively correlated with the population density of *M. atlantica* at Loch Ewe (Table 4.3), revealing a remarkable level of synchronicity (Fig. 4.5A&B; Table 4.3). The long-term mean annual abundance of *M. atlantica* and its standard deviation in the Western English Channel (L4) was 9.62±7.75 and 51.02±32.56 colonies m^{-3} for the polygastric- and eudoxid-stage, respectively. The population density of *M. atlantica* in Loch Ewe was not significantly linked to the species abundance in the Western English Channel (Fig. 4.5A&C; Table 4.3). Considering the interaction between the ESC and the species abundance in the Western English Channel (as their element-wise product) did not reveal any significant link with the local abundance of *M. atlantica* in Loch Ewe (Table 4.3; Fig. 4.5A&D).

Local environmental factors. The long-term means and standard deviations of local SST and salinity were 12.19±0.38 °C and 33.50±0.39, respectively. Concomitant with changes in the local abundance of *M. atlantica*, SST and salinity were maximal in 2003 and 2009/2010 and minimal in 2007 and after 2010 (Fig. 4.6A,B & C). Overall, both parameters were significantly positively related to the local abundance of *M. atlantica* (Table 4.3). The interannual abundance of calanoid copepod prey (3115±904 ind. m^{-3}) was remarkably stable from 2003 until 2007, after which it fluctuated above and below the long-term mean from year to year (Fig. 4.6D). However, this measure of food availability was not significantly related to the abundance of *M. atlantica* (Table 4.3).

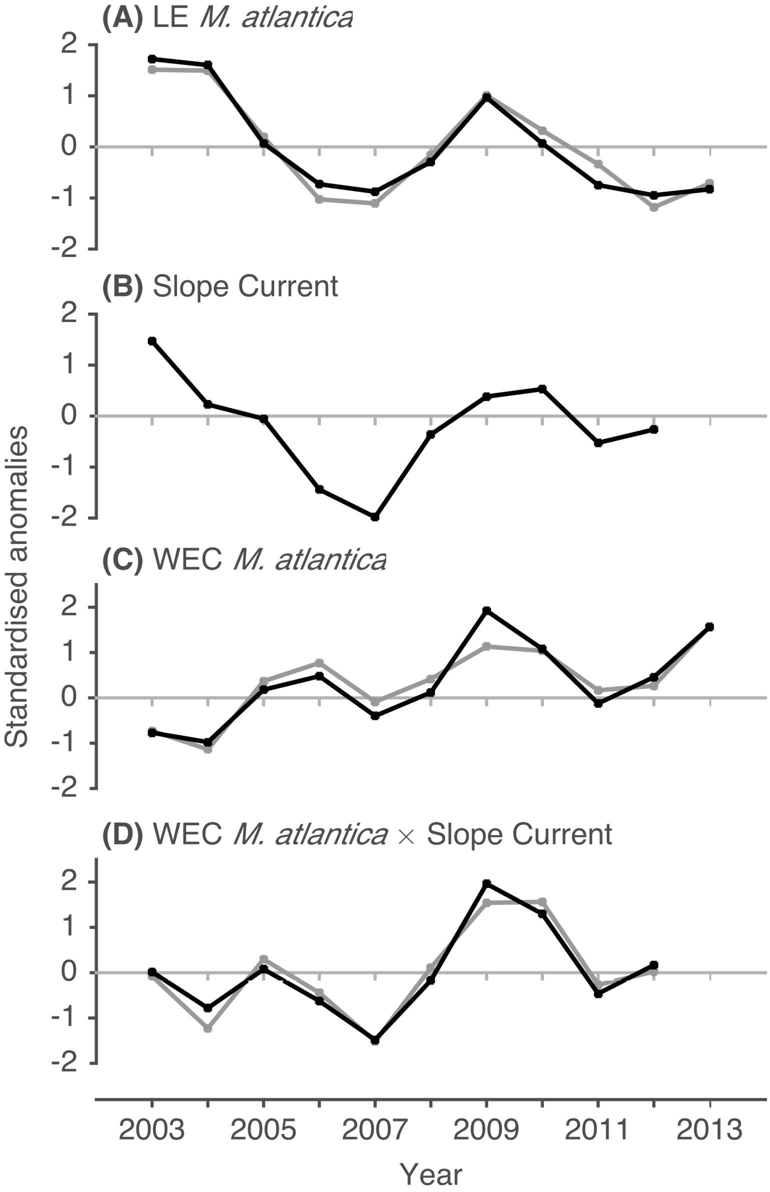


Fig. 4.5. Interannual variability in *Muggiaea atlantica* abundance and translocation factors conditions at Loch Ewe between 2003 and 2013. (A) The abundance of *M. atlantica* polygastric stage (black line) and eudoxid stage (grey line) at Loch Ewe (LE); (B) the strength of the European Slope Current; (C) the abundance of *M. atlantica* in the source habitat of the Western English Channel (WEC); (D) the ESC and source abundance interaction variable (their element-wise product). Values are represented by standardised annual anomalies calculated using the seasonal period of maximum *M. atlantica* population density (June–November).

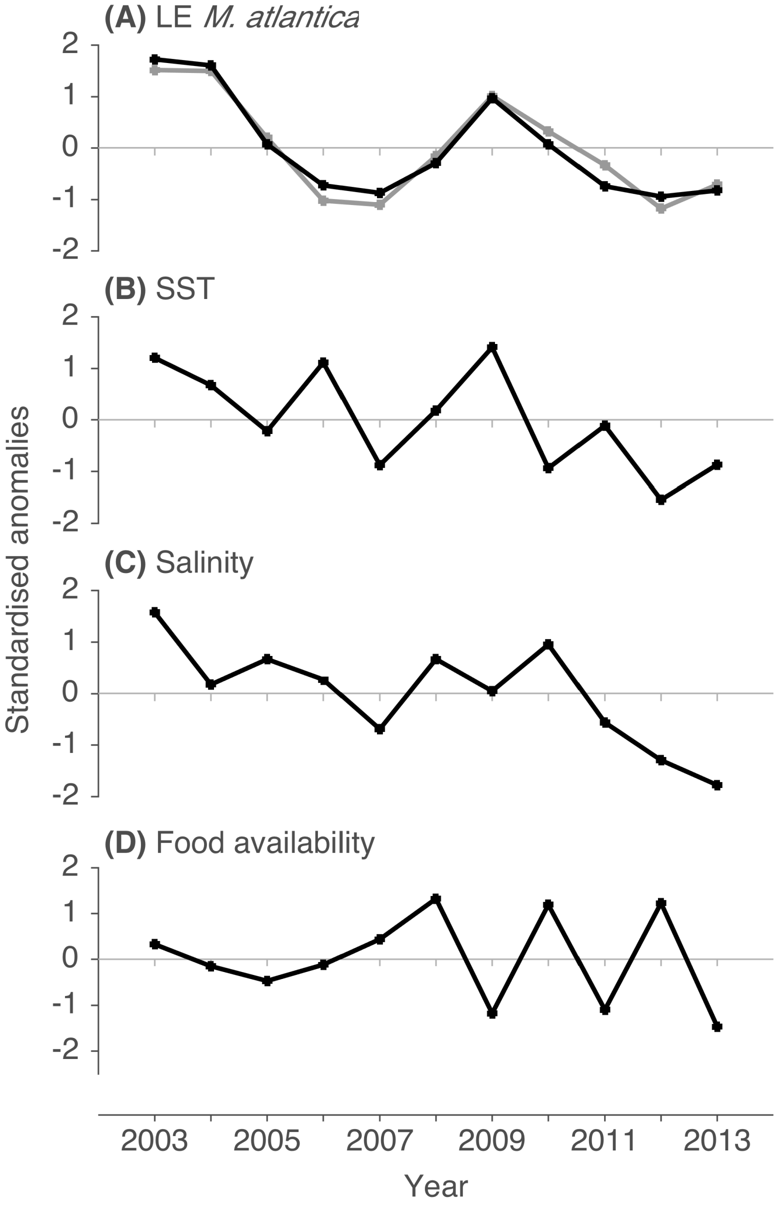


Fig. 4.6. Interannual variability in *Muggiaea atlantica* abundance and local environmental factors at Loch Ewe between 2003 and 2013. (A) The abundance of *M. atlantica* polygastric stage (black line) and eudoxid stage (grey line) at Loch Ewe (LE); (B) sea surface temperature (SST); (C) salinity; (D) calanoid copepod abundance (food availability). Values are represented by standardised annual anomalies calculated using the seasonal period of maximum *M. atlantica* population density (June–November).

Table 4.3. Correlation table of *Muggiaea atlantica* and environmental parameters at Loch Ewe between 2003 and 2013. Pearson's correlation coefficients were computed between standardised annual anomalies calculated using the seasonal period of maximum *M. atlantica* population density (June–November).

Variable	LEpg	LEex	SST	SAL	FA	ESC	WECpg	WECex
LEpg	1							
LEex	0.97***	1						
SST	0.63**	0.59*	1					
SAL	0.62*	0.65**	0.51	1				
FA	−0.23	−0.28	−0.55	0.08	1			
ESC	0.78***	0.82***	0.30	0.61*	0.00	1		
WECpg	−0.19	−0.12	0.01	−0.08	−0.12	0.04	1	
WECex	−0.46	−0.38	−0.11	−0.06	−0.02	−0.18	0.92***	1
WECpg × ESC	0.30	0.38						
WECex × ESC	0.14	0.25						

LE: Loch Ewe; PG: polygastric stage; EX: eudoxid stage; SST: Sea surface temperature; SAL: salinity; FA: food availability; ESC: European Slope Current; WEC: Western English Channel;

* p = < 0.1

** p = < 0.05

*** p = < 0.01

4.4.4 Loch Ewe: Source-sink dynamics at the annual scale

The results of the variation partitioning analysis were highly similar for both the polygastric and the eudoxid stages of *M. atlantica*; the results are described here in terms of the polygastric stage only (See Fig. A3.4 & Table A.3.2 for the eudoxid stage results).

A stepwise selection procedure statistically excluded ($\alpha > 0.05$) food availability from the local environmental factors (explanatory set X); salinity was also excluded from this set because it exhibited multicolinearity with the ESC. The stepwise selection procedure also excluded the source (Western English Channel) abundance of *M. atlantica* and the interaction of source abundance and the ESC from the translocation factors (explanatory set W). The residuals derived from the regression models were not normally distributed and therefore a permutation test with 10,000 repetitions was used to test the significance of the fractions of variation.

Together, the local environmental factor and the translocation factor (i.e. SST and the ESC, respectively) (fraction [a + b + c]) explained a large proportion of the total variation in the annual abundance of *M. atlantica* (~72%; Table 4.4). Alone, the local environmental factor (SST; fraction [a + b]) accounted for ~32% of the total variation, while the translocation factor (the ESC; fraction [b + c]) accounted for 56% (Table 4.4). However, these two fractions contain the common variation explained by both local environmental and translocation factors (fraction [b]). When this common variation was removed, only approximately half of the variation associated with fraction [a + b] (~16% of the total variation) was attributed exclusively to SST (fraction [a]). In contrast, approximately three-quarters of the variation associated with fraction [b + c] (~40% of the total variation) were attributed exclusively to the ESC (fraction [c]) (Fig. 4.7).

Table 4.4. Results of variation partitioning of interannual abundance of *M. atlantica* amongst the local environmental (SST) and translocation (ESC) factors at Loch Ewe between 2003 and 2012. Fraction [a + b + c] represents the variation explained by both explanatory factors, fraction [a + b] the variation explained by SST and fraction [b + c] the variation explained by the ESC

Fraction of variation	Explanatory variables	R^2_a	d.f.	F	Beta
[a + b + c]	SST	0.72	7	12.4***	1.15**
	ESC				0.67***
[a + b]	SST	0.32	8	5.27**	1.67
[b + c]	ESC	0.56	8	13.6***	0.80

SST: Sea surface temperature; FA: food availability; ESC: European Slope Current; WEC: Western English Channel

*** p = <0.01

** p = <0.05

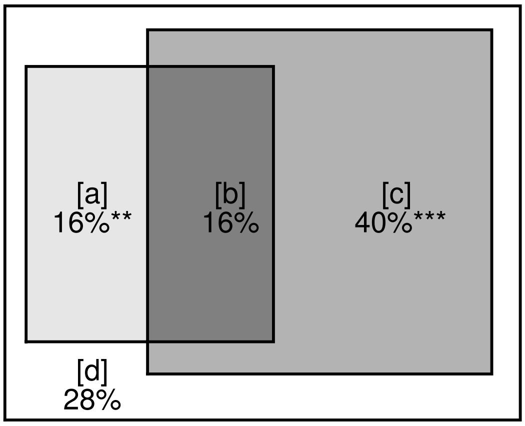


Fig. 4.7. Loch Ewe 2003–2012. Proportional Venn diagram representing the fractions of variation in the annual abundance of *Muggiaea atlantica* attributed exclusively to: [a] the local environmental factor (Sea surface temperature); [c] the translocation factor (strength of the European Slope Current); [b] the common variation explained by both factors; and [d] the unexplained (residual) variation. Numbers represent the percentage of the total variability. ** p = <0.05, *** p = <0.01.

4.4.5 Stonehaven: Seasonal variability and local *M. atlantica* production

At Stonehaven (1999–2013), the frequency of occurrence of *M. atlantica* (54%) was greater than observed at Loch Ewe (Table 4.2). However, the species still displayed a restricted period of occurrence, remaining absent throughout most of spring and summer. The period of maximum population density was from August–December, revealing a delayed phenology compared to Loch Ewe (Fig. 4.8). In 2005 and 2013 the occurrence of the polygastric stage was more sporadic than observed during the other years; the available data showed that the eudoxid stage displayed the same pattern in 2005. During the period of coincident data coverage (2001–2006) the monthly abundance of the polygastric stage and the eudoxid stage significantly covaried ($r = 0.92$, $p = < 0.001$) and the eudoxid stage was typically more abundant (Table 4.2).

The polygastric stage of *M. atlantica* displayed characteristic *in situ* population development during all of the years analysed except 2005 and 2013 (Fig. 4.8). Available data showed that population development of the eudoxid stage matched that of the polygastric stage, except in 2006 when its occurrence was irregular. As was observed at Loch Ewe, population development initiated immediately following the appearance of the stages. Population growth progressed for 2–4 months, reaching peak densities in September–October. In general, *M. atlantica* appeared approximately 2 months later, and peaked 1 month later, than observed at Loch Ewe. However, the species attained greater peak abundance (Table 4.2), and the patterns of occurrence and population development were more regular, than was observed at Loch Ewe.

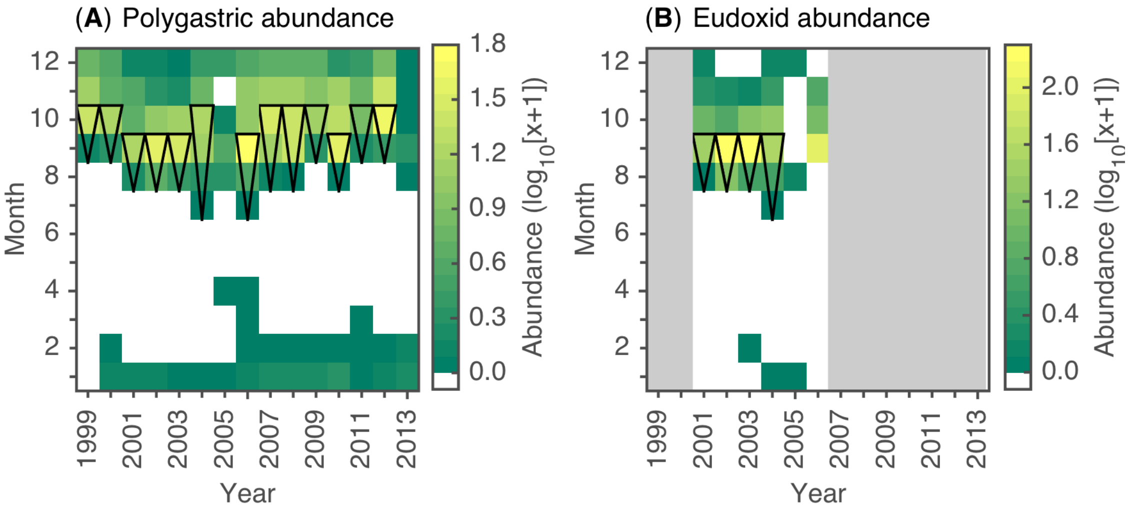


Fig. 4.8. Patterns of temporal variability in the monthly time series of *Muggiaea atlantica* abundance ($\log_{10}$ [colonies m^{-3}+1]) at Stonehaven between 1999 and 2013. (A) Polygastric stage and (B) eudoxid stage. Periods of population increase characteristic of local biological production are represented by black triangles. The grey areas in (B) represent periods with no data coverage

4.4.6 Stonehaven: Environmental optima at the seasonal scale

Due to the limited number of observations on the abundance of the eudoxid stage of *M. atlantica* at Stonehaven, quotient analysis was only performed on the polygastric stage. The abundance of *M. atlantica* was positively related to SST: occurring within the range 5.6–14.7°C, high abundance of *M. atlantica* was consistently significantly ($p < 0.05$) associated with the maximum temperature range of 13.1–14.7°C, while a significant negative association was identified with the temperature range of 5.6–7.4°C (Fig. 4.9A). *M. atlantica* was not recorded at the minimum SST range (4.9–5.6°C). The polygastric stage also displayed a positive relationship with salinity (Fig. 4.9B). Occurring in the range 33.70–34.85, high abundance of the polygastric stage was significantly associated with the maximal recorded salinities (34.50–34.85). There was no consistent negative association with salinity. High abundance of the polygastric stage was significantly associated with high food availability and a significant negative association was apparent with low food availability (Fig. 4.9C).

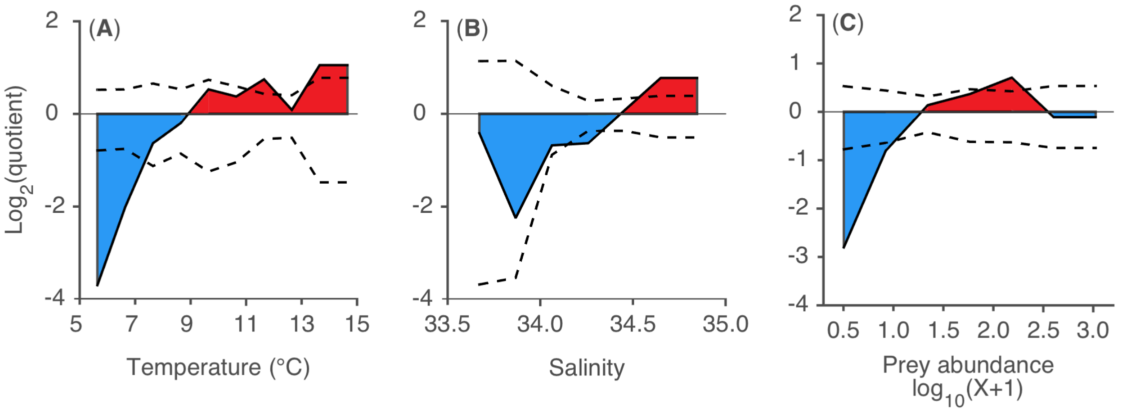


Fig. 4.9. Preferential ranges and critical thresholds of local environmental conditions associated with the abundance of *M. atlantica* at Stonehaven between 1999 and 2013. Associations of polygastric abundance with (A) SST (Sea Surface Temperature), (B) salinity and (C) food availability (calanoid copepod abundance m^{-3}). Quotient values above 0 indicate a positive association (in red), while quotients values below 0 indicate a negative association (in blue) and quotient values of 0 indicate a random association. The dotted lines delimit 95% confidence intervals. *M. atlantica* and food availability data were back-transformed to their original linear scale (number m^{-3}) prior to the calculation of the quotients

4.4.7 Stonehaven: Interannual variability

No significant temporal trends were identified in the interannual time-series (calculated using the months June–November) and therefore further analyses were conducted on the standardised annual anomalies.

At Stonehaven, the long-term (1999–2013) mean annual abundance (± standard deviation) of the polygastric stage of *M. atlantica* was 8.49±5.58 colonies m^{-3}. For the eudoxid stage it was 20.42±17.60 between 2001 and 2006. When data on both the polygastric and eudoxid stages was available, the abundance of the two stages co-varied (Fig. 4.10A). The pattern of interannual variability in the abundance of *M. atlantica* involved a relatively stable period from 1999 to 2004, with abundance around the long-term mean. In 2005 the abundance was particularly low, while from 2006 to 2008 it was stable above the long-term mean. From 2009 onwards the annual abundance of *M. atlantica* fluctuated above and below the mean, with the minimum abundance recorded in 2013 (Fig. 4.10A).

Translocation factors. No significant relationships were found between the local abundance of *M. atlantica* and interannual variability in the strength of the ESC or the species abundance in the source habitat of the Western English Channel (Table 4.5 & Fig. 4.10).

Local environmental factors. The long-term mean abundance of calanoid copepods (food availability) and its standard deviation were 193.6±93.6 ind. m^{-3}. Changes in the local abundance of

M. atlantica were significantly positively related to this measure of food availability (Table 4.5; Fig. 4.11D). The long-term means and standard deviations of SST or salinity were 11.71±0.40 °C and 34.52±0.13, respectively. Neither of these parameters displayed any significant relationship with *M. atlantica* (Table 4.5; Fig. 4.11B,C).

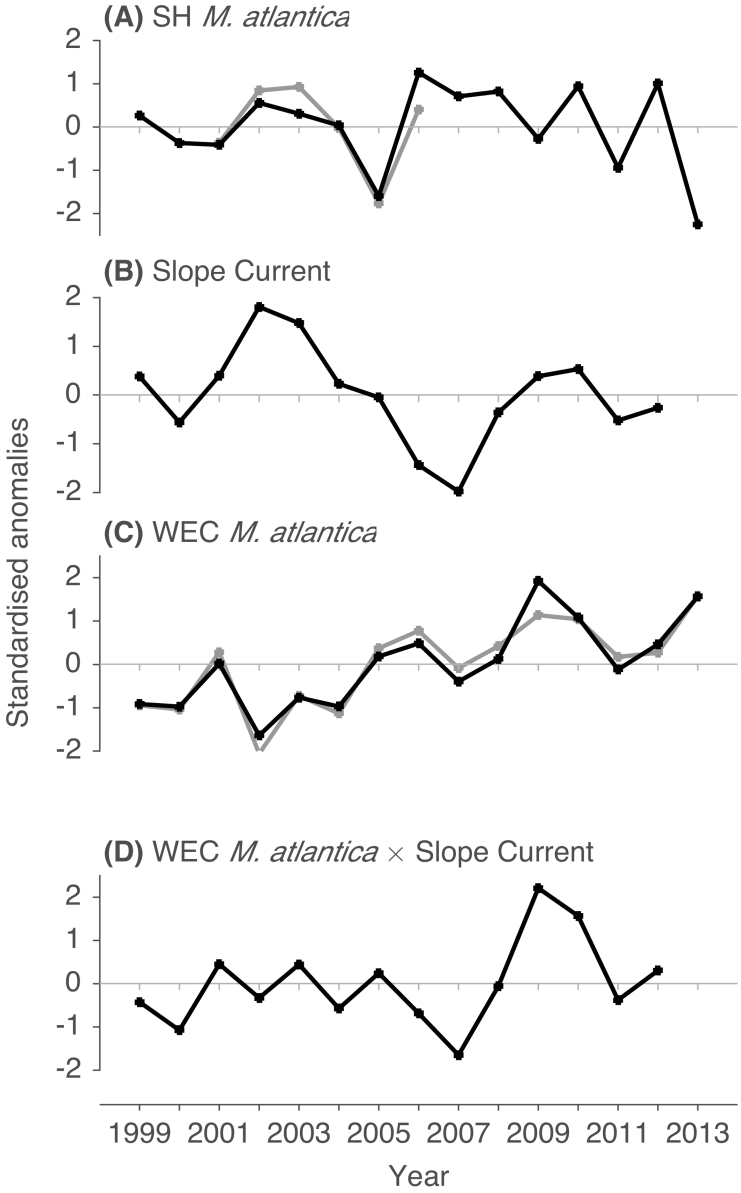


Fig. 4.10. Interannual variability in *Muggiaea atlantica* abundance and translocation factors at Stonehaven between 1999 and 2013. (A) The abundance of *M. atlantica* polygastric stage (black line) and eudoxid stage (grey line) at Stonehaven (SH); (B) the strength of the European Slope Current; (C) the abundance of *M. atlantica* in the source habitat of the Western English Channel (WEC); (D) the ESC and source abundance interaction variable (their element-wise product). Values are represented by standardised annual anomalies calculated using the seasonal period of maximum *M. atlantica* population density (August–December)

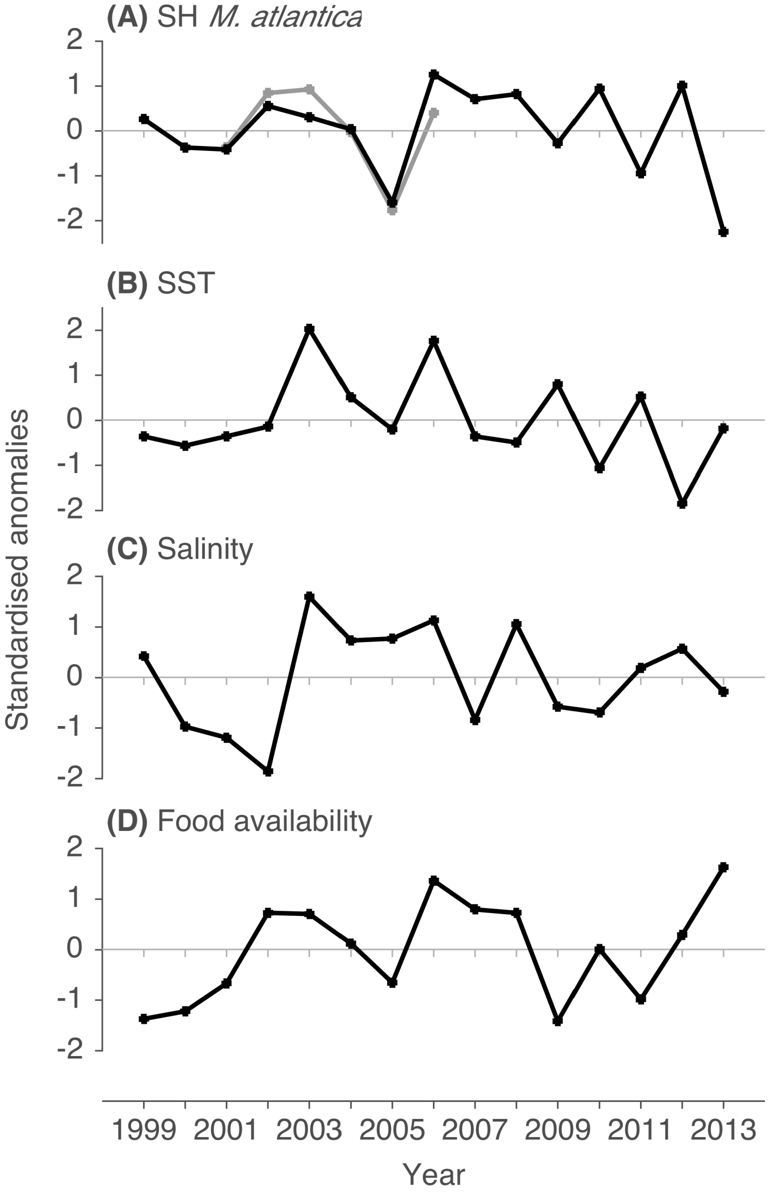


Fig. 4.11. Interannual variability in *Muggiaea atlantica* abundance and local environmental factors at Stonehaven between 1999 and 2013. (A) The abundance of *M. atlantica* polygastric stage (black line) and eudoxid stage (grey line) at Stonehaven (SH); (B) sea surface temperature (SST); (C) salinity; (D) calanoid copepod abundance (food availability). Values are represented by standardised annual anomalies calculated using the seasonal period of maximum *M. atlantica* population density (August–December)

Table 4.5. Correlation table of *Muggiaea atlantica* and environmental parameters at Stonehaven between 1999 and 2013. Pearson's correlation coefficients were computed between standardised annual anomalies calculated using the seasonal period of maximum *M. atlantica* population density (August–December)

Variable	LEpg	SST	SAL	FA	ESC	WECpg	WECex
LEpg	1						
SST	−0.08	1					
SAL	0.07	0.40	1				
FA	0.53**	0.06	0.25	1			
ESC	−0.11	0.09	−0.14	0.48*	1		
WECpg	0.04	−0.04	0.10	−0.21	−0.23	1	
WECex	0.03	−0.03	0.21	−0.23	−0.41	0.94***	1
WECpg × ESC	−0.08						
WECex × ESC	−0.11						

SH: Stonehaven; PG: polygastric stage; EX: eudoxid stage; SST: Sea surface temperature; SAL: salinity; FA: food availability; ESC: European Slope Current; WEC: Western English Channel.

* p = < 0.1

** p = < 0.05

*** p = < 0.01

4.4.8 Stonehaven: Source-sink dynamics at the annual scale

Due to the limited number of observations on the abundance of the eudoxid stage of *M. atlantica* at Stonehaven, only the polygastric stage was considered for this step of the analysis.

A stepwise selection procedure statistically excluded ($\alpha > 0.05$) all of the translocation factors and all of the local environmental factors except food availability (calanoid copepod abundance). These exclusions resulted in the analysis amounting to a simple linear regression model of annual *M. atlantica* abundance against food availability. This model explained only a relatively small proportion (23%) of the total variability in the annual abundance of *M. atlantica* (Table 4.6).

Table 4.6. Simple linear regression model details for *Muggiaea atlantica* abundance and food availability (calanoid copepod abundance) at Stonehaven between 1999–2013

Explanatory variable	r^2_a	d.f.	F	Beta
FA	0.23	13	4.81**	2.19

FA: Food Availability

** = $p < 0.05$

4.5 Discussion

The absence of strict physical barriers to the horizontal transport of plankton means that the limits of their spatial distribution are diffuse across wide transitional areas (Beaugrand et al. 2002). These limits may shift in space and time in response to seasonal changes in habitat suitability and the hydrographic processes that modulate species translocation (Beaugrand et al. 2001). These factors make it challenging to delimit the biogeographic range of plankton species. Whilst Mapstone (Mapstone 2014) defined the latitudinal range of *Muggiaea atlantica* as 59°N–53°S, records of the species' occurrence this far north in the Atlantic Ocean are exceptional (Totton & Fraser 1955; Fraser 1967; Heath et al. 1999). Pugh (Pugh 1999) was more conservative, considering the species' maximum latitudinal distribution in the Atlantic Ocean as 55 ºN. In contrast to these earlier findings, our study shows that *M. atlantica* is now a regular constituent of the Scottish (~57–58 ºN) coastal plankton, indicating that a northward expansion of the species' normal distribution has taken place.

Jellyfish populations have an innate propensity to fluctuate in space and time (Lucas & Dawson 2014). The opportunistic life history traits of jellyfish, including high fecundity, rapid growth rates, and short generation times, enable them to respond to local suitable conditions with dramatic population increase (i.e. true blooms sensu Graham et al. 2001). Conversely, their inability for long-distance horizontal volitional swimming means that jellyfish populations are readily dispersed in ocean currents and may aggregate in areas that do not normally support a population (i.e.

apparent blooms sensu Graham et al. 2001). However, this classification represents opposite ends of a continuum (Graham et al. 2001); these biological and physical factors can often combine, resulting in the formation of opportunistic blooms when jellyfish are translocated to areas where suitable conditions exist temporarily (e.g. Costello et al. 2012). Considering these factors, we investigated the biogeographical expansion of *M. atlantica* demonstrated in the present study in the context of source-sink dynamics (Pulliam 2000).

We employed several criteria to categorise the two Scottish sampling locations as either source- or sink-habitats for *M. atlantica*. Indirect evidence of sink habitats has been defined as the absence of reproduction—or insufficient local production to account for recruitment—coupled with the observation of frequent immigration (Pulliam 2000). To assess the contribution of local production to recruitment, we used a validated statistical procedure to identify patterns of seasonal population increase that were characteristic of reproduction. This local production accounted for the bulk of polygastric and eudoxid recruitment during the majority of the years studied at both Loch Ewe (respectively 55% and 73% of the total abundance occurring during periods of local production) and Stonehaven (87% and 66%, respectively). However, during a minority of the years local production either did not occur, or occurred in only one of the two life stages, indicating that the species was not always able to complete its full life history, a prerequisite for a source habitat (Pulliam 2000). The observed patterns of local recruitment therefore reflect features of both source- and sink-habitats in different years.

Sink habitats are characterised by the absence of the conditions necessary for a species to carry out its full life history (James et al. 1984). Temperature and food availability have well documented effects on animal physiology (Schmidt-Nielsen 1997) and have been identified as key determinants of reproduction in *Muggiaea* (Purcell 1982; Carré & Carré 1991). We identified significant positive relationships between the seasonal abundance of *M. atlantica* and Sea Surface Temperature (SST) and food availability (as calanoid copepod abundance). The temperature optima identified in our study (~13.0–15.0°C) are in close agreement with results from other areas (Licandro et al. 2012; Blackett et al. 2014; Chapter 2), indicating that at least the upper limit of the thermal environment at the Scottish sampling locations was periodically suitable for the species to carry out its life cycle.

However, in a source habitat species must be able to exist indefinitely (Pulliam 2000). *Muggiaea* are holoplanktonic jellyfish with short-lived larval stages and no known resting stages (Carré & Carré 1991). Consequently, the adult life stages must persist locally in the water column (Boero et al. 2008). Experimental and field observations suggest that overwintering is facilitated by a small number of reproductively inactive polygastric stages (Carré & Carré 1991; Blackett et al. 2015; Chapter 3). At both Scottish sampling locations, the polygastric stage (and eudoxid stage) exhibited extended periods of absence during the winter and spring. It could be that these absences simply reflect the species overwintering at an abundance that is below the level of detection of our sampling methodology (e.g. Rodriguez-Ramos et al. 2013). However, synchronised production with seasonal environmental changes is common in pelagic cnidarians (Purcell et al. 2007); in the WEC, *M. atlantica* emerges from overwintering in response to the onset of a critical temperature threshold (10 °C) (Blackett et al. 2015; Chapter 3). It could be expected that local production would commence coterminous with the onset of a similar temperature if *M. atlantica* was successfully overwintering at the Scottish sampling locations. However, this did not occur and local production began in conjunction with a range of SST that was always in excess of this threshold (mean = 12.71 ± 0.9 °C; data not shown).

Alternatively, the seasonal periods of absence could represent local annual extinction (e.g. Costello et al. 2012). Greve (Greve 1996) postulated that low winter temperature prevented the establishment of *M. atlantica* in the German Bight. The minimum winter temperatures recorded at Loch Ewe and Stonehaven (6.3 °C and 4.9 °C, respectively) are lower than observed in the source habitat of the WEC (8.8 °C; Blackett et al. 2014; Chapter 2), and *M. atlantica* was never recorded when temperatures were below 5.6 °C. These low winter temperatures may be below a critical limit for the survival of *M. atlantica*, precluding the existence of an overwintering population. Another possibility is that the species is flushed out of the Scottish systems; this scenario could arise if the duration of the non-productive overwintering period exceeds the local water residence times (Costello et al. 2012). Blackett (Blackett et al. 2015; Chapter 2) suggested that in the WEC, the polygastric stage entered the dormant reproductive stage in response to low winter temperature (<9.5 °C). At both Scottish sampling locations SST was below this value during ~6 consecutive months of the year (data not shown). Estimates of the surface water residence times of most Scottish lochs (Rydberg et al. 2003) and the North Sea sub-region that includes Stonehaven (Skogen 1993) are typically only ~50 days, supporting the proposition that *M. atlantica* could be flushed out. If *M. atlantica* cannot over-winter locally, then it must rely on immigration, a defining feature of sink-habitats (Pulliam 2000).

In the absence of direct evidence for immigration, we used the strength of the European Slope Current (ESC) as an index of potential immigration of *M. atlantica* into Scottish coastal waters. Flowing from the Bay of Biscay to the Faroe-Shetland Channel, the ESC is a major section of the poleward flow of warm and saline water in the Northeast Atlantic Ocean (Pingree & Garcia-Soto 2014; Xu et al. 2015). Although the ESC is typically confined to the continental slope, direct intrusions onto the Scottish Continental Shelf occur in winter (Burrows & Thorpe 1999; Souza et al. 2001). The ESC also has an indirect influence on the Scottish Continental Shelf via periodic flow instabilities and the effects of near surface winds (reviewed in Inall et al. 2009). Exceptionally occurrences of *M. atlantica* in the Scottish Continental Shelf region have been consistently associated with strong indicators of intrusions of the ESC (Fraser 1967). In the light of these complex interactions the annual time series of the ESC is the most appropriate index of potential immigration.

Although the ESC influences plankton dispersal in the region (Beaugrand et al. 2001), it also influences the physical environmental conditions of the Scottish Continental Shelf (Inall et al. 2009). Therefore, any relationships between the abundance of *M. atlantica* and the ESC may reflect both the direct effects of dispersal on immigration and emigration rates, and the indirect effects of consequent local environmental changes on demographic rates. Our variation partitioning analysis allowed us to disentangle the effects of these two processes, providing an estimation of the total, exclusive and combined contributions of local environmental conditions and the ESC on interannual variability in the abundance of *M. atlantica.*

For Loch Ewe, our partial linear regression model combining demographic variability (as indexed by SST) and immigration (as indexed by the ESC) explained a large proportion (~72%) of the interannual variation in the abundance of *M. atlantica*. The ESC explained 56%, while SST explained 32% of this total variation, confirming the importance of both biological and physical factors. However, these portions of the variation contain a degree of shared variation due to the effect of the ESC on local SST. The partitioning revealed that the exclusive contribution of SST (i.e. without the variation that was also explained by the ESC) was minimal, at only 16%. The other half of the potential contribution of SST could be attributed to either the effects of SST on demography, or the effects of increased immigration associated with the ESC. In contrast, the exclusive contribution of the ESC (40%) was a key determinant of the annual abundance of *M. atlantica*. Our results show that interannual variability in the abundance of this species is determined by, in order of increasing importance: (1) the availability of suitable local environmental conditions (16%); (2) the role of the ESC in modulating these environmental conditions (16%); and (3) the immigration of *M. atlantica* via the ESC (40%). In summary, these results reveal that whilst *M. atlantica* is capable of local production during some years, this local production is ultimately dependent upon the arrival of the species via immigration.

The high correlation of local salinity with the ESC provided indirect evidence for the inflow of waters transported by the ESC into Loch Ewe. This coupled with the significant association of high seasonal abundance of *M. atlantica* with maximum salinity provides further evidence for translocation via the ESC. Whilst food availability was shown to be an important factor at the seasonal scale, its influence on interannual variability was not significant. This could be due to high food availability combined with low year-to-year variability during many of the years, suggesting food availability was not a limiting factor.

These results provide compelling indirect evidence that Loch Ewe represents a sink habitat for *M. atlantica*. However, it is necessary to consider other possible explanations. Pseudo-sinks are habitats that are capable of sustaining low-level local production, but where this local production is masked by much higher levels of immigration (Watkinson & Sutherland 1995). However, if Loch Ewe was a pseudo-sink habitat, it could be expected that years with low immigration would still exhibit some population growth. This was not observed during several years that were characterised by low flow rates of the ESC. In summary the possibility remains that Loch Ewe could provide a pseudo-sink habitat in some years, but suffer periodic local extinctions due to unsuitable local conditions (e.g. Boero 2002) or elimination as a result of flushing (e.g. Costello et al. 2012). This is the likely cause of the recorded absence of *M. atlantica* in 2012. These results provide strong support for our classification of Loch Ewe as a sink habitat.

At Stonehaven, the results of our study are less conclusive. Only food availability had a significant influence on the annual abundance of *M. atlantica*, explaining a small proportion of its interannual variability (23%). Whilst SST was an important determinant at the seasonal scale, its influence on interannual variability was not significant. This could indicate that the relatively low food availability during the seasonal occurrence of *M. atlantica* was an important limiting factor, potentially masking the influence of SST variability. The lack of any significant relationship with the ESC may be attributable to its relative remoteness, compared to Loch Ewe, which is more directly influenced due to its proximity. At the Fair-Isle Channel the ESC bifurcates, with one stream entering the North Sea along the east coast of Scotland (Burrows & Thorpe 1999). Lynam (Lynam et al. 2010) found that the abundance of a scyphozoan jellyfish population in the Northern North Sea east of Scotland was significantly related to this inflow and not to hydroclimatic variability. As these waters represent a more variable mix of the ESC and Scottish coastal waters compared to Loch Ewe (Inall et al. 2009), this could potentially explain the lack of any clear link between *M. atlantica* and the ESC at Stonehaven. Our analysis at the annual scale did not provide any clear evidence on the source-sink status of Stonehaven. However, in light of the patterns of local production and recruitment previously discussed we tentatively classify it as a sink habitat.

We had hypothesised the translocation of *M. atlantica* from the source habitat of the WEC into the Scottish sampling locations via the ESC. However, our analysis of the data covering the whole study period did not show a clear link between the abundance in the source habitat of the WEC and either of the Scottish sampling locations. This applied even when the effect of the interaction of the strength of the ESC and the abundance in the WEC were used to indicate potential magnitude of translocation. Despite this, it is interesting to note that after 2005 the abundance of *M. atlantica* in the WEC increased from predominantly below the long-term mean, to predominantly above it. Chen (Chen et al. 2014) showed that potential sources might transition to active sources if productivity increases sufficiently. Consistent with these findings, after 2005 the relationship between the abundance of *M. atlantica* in the source habitat of the WEC and the sink habitat of Loch Ewe changed to a significant positive correlation (not shown). Therefore other source areas may have been important prior to 2005, but after this date the importance of the WEC as a source may have increased.

A number of different factors could be relevant to the relationship between sources and sinks. Whilst larval dispersal is common in marine planktonic organisms (Cowen & Sponaugle 2009), *Muggiaea* have short-lived larval stages and no known resting stages (Carré & Carré 1991). Therefore, the polygastric and eudoxid stages are the most likely dispersal propagules. These life stages may continue active reproduction in transit, provided that suitable conditions prevail. The ESC travels a distance ~1600 km (Pingree et al. 1999) at a mean speed of 10 cm s^{-1} (Xu et al. 2015), therefore the estimated transit time from source to sink is ~6 months. The life cycle of the congeneric *Muggiaea kochi* is in the order of weeks (Carré & Carré 1991), so theoretically the dispersing population could have completed several generations during transit. This process could have the effect of a progressive uncoupling of the link with the source abundance.

Our study confirms that *M. atlantica* is now a regular constituent of the Scottish coastal plankton. This apparent biogeographical shift was associated with the formation of sink habitats, indicating that the occurrence of the species does not represent the establishment of permanent resident populations, but rather the formation of transient opportunistic populations that are dependent on immigration. We showed that on the west coast of Scotland the translocation mechanism was the inflow of Atlantic water associated with the poleward flow of the ESC. However the translocation mechanism associated with immigration to the east coast of Scotland was not identified. The hypothesis that the Western English Channel was the source of this immigration was not definitively proven, perhaps indicating the importance of a network of as yet unidentified source populations.

We previously demonstrated the establishment of a resident population of *M. atlantica* in the WEC in the 1960s (Blackett et al. 2014; Chapter 2). Subsequently, an increase in the frequency of occurrence of the species in Irish coastal waters was reported (Jeal & West 1970). The recent expansion of *M. atlantica* into Scottish coastal waters (present study) indicates that a progressive expansion of the species northern distributional limits in the coastal waters of the United Kingdom has taken place since the 1960s. These results are consistent with published studies that have demonstrated concurrent northward shifts in the biogeography of other species of plankton (Beaugrand et al. 2002; Hays et al. 2005). While the increasing trend in Northern Hemisphere temperature has been demonstrated as an important driver of these changes (Beaugrand et al. 2002), changes in path or strength of currents along the European Continental Shelf could have had dramatic impacts on changes in the distribution of plankton around the United Kingdom (Beaugrand et al. 2001). As a result, increased habitat suitability coupled with increased translocation may have facilitated the biogeographical shift of *M. atlantica*. Further research combining field sampling, genetic markers and oceanographic modelling are required to develop our understanding of these processes (e.g. Decker et al. 2013; Lee et al. 2013)

Chapter 6

Synthesis and conclusions

5. Synthesis and conclusions

Jellyfish are a ubiquitous component of pelagic ecosystems (Lucas et al. 2014b). The opportunistic ecology of most jellyfish (i.e. metagenic life cycles, short generation times, and high feeding rates) enables them to 'bloom', i.e. to rapidly and dramatically proliferate (Hamner & Dawson 2009; Lucas & Dawson 2014). Historically perceived as ecologically unimportant, jellyfish received little scientific attention. Consequently, jellyfish are enigmatic and relatively poorly understood, despite their ubiquity (Pugh 1989; Haddock 2004). However, over recent decades dramatic increases in the spatio-temporal distribution and abundance of jellyfish (e.g. Brotz et al. 2012) have fuelled greater scientific interest. In many regions these changes appear to be occurring in response to the progressive anthropogenic degradation of the marine environment (Purcell 2012). To some, a paradigm has developed where the structure of the global ocean is changing to a state dominated by jellyfish (Richardson et al. 2009). However, to others this paradigm lacks foundation because there are too few long-term data to exclude the role of long-term oscillations (Condon et al. 2012; Condon et al. 2013). Irrespective of extent or persistence of recent changes, the increased scientific interest in jellyfish has greatly improved our understanding and recognition of their biology and ecology (e.g. Pauly et al. 2009). However, the current focus on global-scale changes in jellyfish populations has led to a tendency to neglect the vast ecological and physiological diversity of jellyfish, limiting our understanding of how individual species and populations function and respond to change (Condon et al. 2012). Furthermore, jellyfish blooms occur both as a direct result of growth and reproduction and also as an indirect effect of physical translocation and aggregation (Graham et al. 2001; Hamner & Dawson 2009). A failure to discriminate between these two fundamental processes can obscure our understanding of the specific factors that drive changes in jellyfish populations. To further develop our understanding of these mechanisms, a greater focus on the biology and ecology of jellyfish and how they interact with their environment at the species level is required (Mills 2001).

The aims of this thesis were to address these specific knowledge gaps by (1) assessing recent changes in the abundance and distribution of the neritic siphonophore, *Muggiaea atlantica* in the coastal waters of the United Kingdom, and (2) to investigate the influence of environmental variability on both the biological (i.e. demography) and physical (i.e. dispersal) processes that drive these changes.

The specific objectives of the thesis were to address the following research questions:

1) Have the abundance and distribution of *Muggiaea atlantica* in UK waters changed?
2) Are these distributional changes associated with the establishment of resident populations or alternatively are these transient populations that are dependent on immigration from other areas?
3) What are they key environmental parameters that affect the species population dynamics and abundance; and how does this affect its distribution?

The main findings that are relevant to these research questions are addressed within the scientific chapters (2, 3, and 4). In this section I will provide a synthesis of these findings and draw general conclusions regarding their implications.

(1) Have the abundance and distribution of Muggiaea atlantica in UK waters changed?

From a historic perspective (1900–1979), *M. atlantica* was not frequently recorded further north than the southwest coasts of the UK and Ireland (Chapter 1, section 1.4.4.2). At this northerly extreme of its distribution the species arrived sporadically and at low abundance, associated with the influx of southerly waters from the Bay of Biscay region (Chapter 2). In agreement with these early findings, a meta-analysis of historic records (since 1900) of the abundance of *M. atlantica* in the northeast Atlantic revealed that the species' centre of distribution was within the Bay of Biscay and Iberian coast region, with only sporadic excursions into the coastal waters of the UK (Chapter 1, section 1.4.4.2).

From the late 1960s, the occurrence of *M. atlantica* in the Western English Channel (WEC) entered a state of change. The species became an increasingly common component of the Channel plankton, with a progressive increase in the frequency and period of occurrence, and dramatic increase in abundance. These changes were particularly pronounced from the 1980s, after which the species occurred recurrently, throughout the seasons of every year and attained abundances several orders of magnitude higher than before (Chapter 2). This northern spread was subsequently followed by an increase in the prevalence of *M. atlantica* in Irish coastal waters (Jeal & West 1970), suggesting a continued northward extension of the species range. This continued extension was confirmed by the recurrent appearance of *M. atlantica* in Scottish coastal waters since the late 1990s, a region where it had previously been extremely rare (Chapter 4). These results reveal that in the northeast Atlantic, there has been a dramatic progressive northward extension of this species' distribution from its centre of population in the Bay of Biscay and Iberian Coast region since the late 1960s (Fig. 5.1). This represents a substantial northward latitudinal shift of approximately 10°.

(2) Are these distributional changes associated with the establishment of resident populations or alternatively are these transient populations that are dependent on immigration from other areas?

Jellyfish populations are modulated both by processes that influence demography (i.e. production and mortality) and also by processes that influence dispersal (i.e. immigration and emigration). It is essential to discriminate between these two processes in order to fully understand the true extent of species distribution. Source-sink dynamics provides a framework to understand how dispersal and demography influence species distribution (Pulliam 2000). Source-sink dynamics differentiates source habitats, where local reproduction outweighs mortality from sink habitats where local mortality exceeds local reproduction. Source habitats are self-sustaining, whilst sink habitats must rely on immigration to balance local mortality.

Before the late 1960s, the WEC represented a sink habitat for *M. atlantica*, as its occurrence was dependent upon immigration and not local production. The changes that occurred from the late

1960s onwards represented the establishment of a resident population—sustained by local production—and the transition of the WEC from a sink to a source habitat (Chapter 2). This transition was demonstrated using a numerical procedure that showed that the occurrence of *M. atlantica* was the result of local production and not immigration. Experimental observations have suggested that overwintering of the congeneric *Muggiaea kochi* in the Mediterranean is facilitated by a dormant polygastric stage (Carré & Carré 1991). In the case of *M. atlantica* in the WEC, modelling the functional relationship between the abundance of the polygastric and eudoxid stages of *M. atlantica* in the WEC confirmed this hypothesis also applied to this species (Chapter 3). This result revealed the capacity for *M. atlantica* to persist indefinitely in the WEC, providing compelling evidence for the range extension of the species as a persistent resident population.

This is in contrast to the occurrence of *M. atlantica* in Scottish coastal waters (Chapter 4). On both the west and east coasts of Scotland the dynamics of the occurrence of *M. atlantica* indicated characteristics of both source and sink habitats. Local production was often sufficient to account for recruitment during some years, but insufficient during other years, indicating the development of opportunistic populations dependent on immigration from other areas. Extensive periods of absence, and the species' sporadic appearance suggested that local annual extinction occurred as a result of the species inability to overwinter in the area. To definitively categorise an area as a sink habitat it is necessary to provide evidence of immigration. On the west coast of Scotland the European Slope Current (ESC) was identified as the source of immigration. Variability in the strength of the ESC was the dominant factor modulating the abundance of *M. atlantica*, confirming the categorisation of the west coast of Scotland as a sink habitat. However, on the east coast of Scotland a clear link with immigration via the ESC was not apparent, probably due to the less direct proximity of the ESC. These results indicate that the range extension of *M. atlantica* into the west coast of Scotland was not associated with the establishment of a resident population, rather an opportunistic population that is dependent on immigration via the ESC. The evidence for the east coast of Scotland was not definitive and this is an area that merits further research.

I hypothesised that a source-sink relationship existed between the WEC and Scottish coastal waters, modulated by the ESC. However, this relationship was not clearly demonstrated, perhaps indicating the importance of a network of source populations, or a progressive de-coupling of the source-sink relationship as a result of continued reproduction during transit.

These changes in the distribution of *M. atlantica* in UK coastal waters could have significant implications for marine ecology and the ecosystem services they provide. These implications could involve impacts on the structure and function of pelagic ecosystems and the productivity of local fisheries and aquaculture. Affects on aquaculture could be particularly pronounced in Scottish waters, where this industry is economically important.

(3) What are they key environmental parameters that affect the species population dynamics and abundance; and how does this affect distribution?

Identification of local production by *M. atlantica* confirmed the specific environmental factors that drive reproduction. In the WEC and Scotland, local production of *M. atlantica* was consistently associated with a specific range of temperature (Chapters 2, 3, 4). At all locations high local production was significantly associated with the optimal thermal conditions of ~13–15°C. These results are in close agreement with preferential temperature conditions identified in the Mediterranean (e.g. Licandro et al. 2012), thus supporting the identified optimum thermal requirements of this species. In the WEC, the commencement of local production in spring was associated with the onset of a critical thermal threshold of 10 °C, which initiated eudoxid release by the overwintering polygastric stage (Chapter 3). In support of this finding, local production of the polygastric stage of *M. atlantica* was not detected when the Sea Surface Temperature (SST) was below 9 °C (Chapter 2), providing information on the lower thermal requirements for successful local production. The proposed inability for *M. atlantica* to overwinter in Scottish waters provides an estimation of the lethal thermal limits of *M. atlantica*; the species was not recorded when temperatures were below ~6–7 °C. The thermal limits of species represent essential information that can help facilitate the inclusion of species in ecosystem models, information that is lacking for most species of jellyfish (e.g. Pauly et al. 2009).

In addition to the importance of temperature, food availability was also identified as an important environmental factor in all three scientific chapters of this thesis. In agreement with the observations of Purcell (1981a) I showed that copepod prey were an important covariate of local production of *M. atlantica* (Chapters 2 and 4). However, in Chapter 3 I showed that other prey taxa were also important during different seasonal periods; Bivalvia emerged as an important covariate in the summer, when the abundance of copepods was scarce. In Chapter 2 I showed that copepod prey were particularly important at the onset of population growth in spring, suggesting that they represent an important food resource for the polygastric stages that are emerging from overwintering, and also for the subsequent development of the eudoxids. The results of Chapter 2 also revealed how the interactive effects of changes in temperature and food availability influence the phenology and abundance of *M. atlantica*. Cold conditions in spring caused a delay to the initiation of *M. atlantica* population development, which had the effect of disrupting the phasing of eudoxid production with food availability. This trophic mismatch was associated with the production of a single autumn *M. atlantica* cohort, rather than the summer and autumn cohorts produced during years with warmer conditions in spring.

This thesis has shown that temperature is a critical factor influencing the local production of *M. atlantica*. However, changes in temperature alone were not sufficient to explain the establishment of a resident population in the WEC (Chapter 2). Complex structural changes in the WEC ecosystem have occurred throughout the twentieth century with an apparent cyclical nature, referred to historically as the 'Russell cycle' (Southward 1980; Southward et al. 2005). A recent analysis (McManus et al. 2015) has shown that these cyclical changes are dominated by long periodicities (>50 y), which are not readily resolved within the 88 y time frame for which data are available. This result echoes the concerns of Condon et al. (2013) and suggests that continued observations are required to fully understand the mechanisms that have driven the establishment of *M. atlantica* in the WEC.

Nevertheless, the progressive extension of the northern distribution of *M. atlantica* since the late 1960s identified in this thesis has also been observed in other functional plankton groups. Beaugrand et al. (2002) demonstrated a northward biogeographical shift in the distribution of a copepod species association ('pseudo-oceanic temperate') with a similar general centre of distribution to that of *M. atlantica* identified in section 1.4.4.2 of this thesis (Fig. 5.1). This northward shift in the number of 'warm' species has occurred progressively since the 1960s, and seems to parallel the distributional extension identified for *M. atlantica* in this thesis. An updated map of the biogeography of *M. atlantica* is provided with the results of this thesis is presented in Fig. 5.1. Whilst the expansion in the copepod species was strongly correlated with increasing Northern Hemisphere temperature (Beaugrand et al. 2002), it has also been suggested that changes in the path and intensity of continental slope currents could elicit considerable changes in the structure of ecosystems to the north and west of the UK (Beaugrand et al 2001). My results from Chapter 4 support this suggestion, showing that changes in the strength of the ESC modulated the abundance of *M. atlantica* on the east coast of Scotland. The IPCC (2014) projections for future global climate change suggest a continued elevation of SST under a range of potential greenhouse gas emission scenarios (Representative Concentration Pathways). This continued increase in SST could result in the modification of additional habitats, increasing the thermal suitability for *M. atlantica*. Such changes could result in the further establishment of resident populations of *M. atlantica* in previously uninhabited locations. However, regional and local patterns of SST are modulated by the complex interaction of ocean currents. This thesis highlights the importance of current driven dispersal as well as suitable local environmental conditions for the establishment of populations of *M. atlantica*.

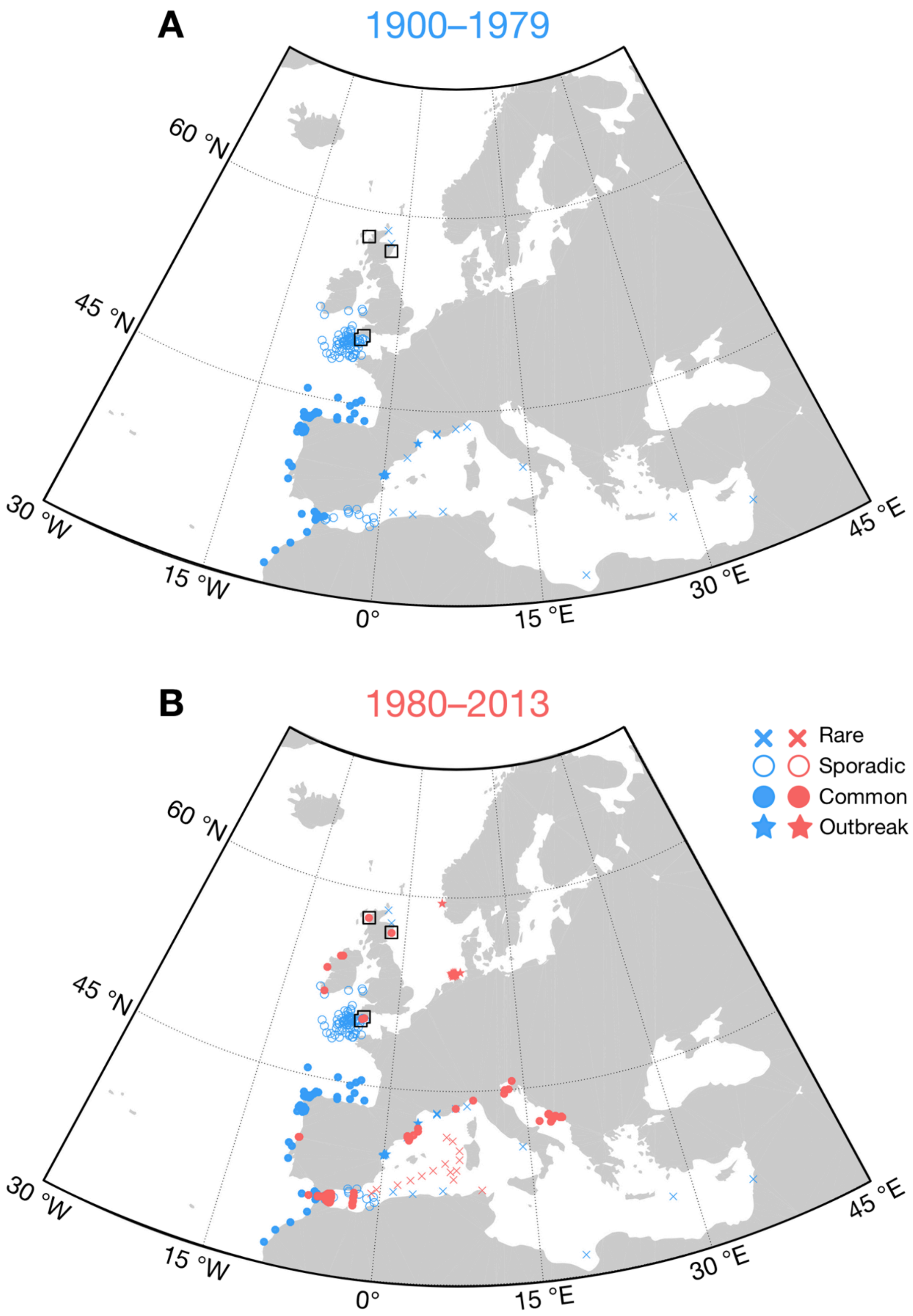


Fig. 5.1. Historic and contemporary distribution of *Muggiaea atlantica* in the northeast Atlantic. (A) Distribution of *M. atlantica* from 1900–1979. (B) Distribution of *M. atlantica* from 1980–2013. Rare records indicate very low abundance and highly sporadic occurrences; Sporadic records indicate low abundance with little temporal continuity; Common records indicate high abundance with temporal continuity; and Outbreak records indicate very high abundance with no temporal continuity. The black squares indicate the sampling locations that were utilised in this thesis.

Appendices

A1. Appendix for Chapter 1

A1.1 Biological and physiological laboratory observations

A1.1.1 Sample collection

Specimens of *Muggiaea atlantica* were collected during weekly routine zooplankton sampling at the L4 plankton station (50.25° N, 4.22° W) off the coast of Plymouth, UK, in the Western English Channel. Additional specimens were also collected from coastal structures along the coast of Plymouth.

Specimens were collected by hand pulling, at slow speed (<1cm s^{-1}), a specially designed plankton net with the following characteristics: 0.5m diameter, 95 μm mesh size, with a large (5l) non-filtering cod-end. A small mesh size was used to avoid abrasive damage to the fragile colonies (Raskoff et al. 2003) and the large non-filtering cod-end was used to prevent damage from turbulence and impaction (Reeve 1981). Preliminary trials with a larger (0.75 m diameter, 700 μm mesh size) plankton net hauled mechanically resulted in catastrophic damage to the delicate siphosome.

The contents of the cod-end were immediately transferred into large (20L) plastic containers. This large volume of water prevented oxygen depletion and the build up of metabolites. The plastic containers were opaque to prevent photo-excitation (Biggs 1977a). Plastic containers were also sealed with no air space to prevent the generation of air bubbles, which can become lodged within the delicate siphonophore tissues and cause lethal gas embolisms (Mackie & Boag 1963). When collected at sea the plastic containers were stood in large plastic trays on-deck, with running seawater to maintain a constant temperature.

A1.1.2 Sample processing

In the laboratory (SAHFOS, Plymouth, UK) the large plastic containers were stood in a large water bath maintained at the ambient collection temperature. Sub-samples (500ml) were carefully removed from containers and visually inspected for the presence of *M. atlantica* using a specialist viewing stage, which consisted of: a black concave background, directional LED lighting and a low power magnifying glass attached to an articulating arm. Once identified, siphonophores were carefully extracted using wide-bore plastic pipettes and transferred to 5l beakers of fresh filtered seawater (20 μm) that were stood in running seawater for the duration of sample processing. The isolated specimens were screened visually and those displaying evidence of physical damage were discarded; damaged colonies were evident due to the 'crinkling' of nectophores or deformation of the cormidia. Healthy specimens were separated into size classes and transferred into 5l beakers of fresh filtered seawater (as above) for an acclimation period of 4.5 h (sufficient for the digestion and egestion of any gastrozooid contents; see section 1.4.3.3). Following siphonophore removal, the sample remainder was filtered through successive mesh screens. Zooplankton retained within the size range 50–500 μm were isolated and sorted into broad taxonomic groups. Known prey taxa were retained as a source of food. If kept for prolonged periods the colonies were fed 1-day old *Artemia* nauplii or the natural zooplankton that were collected simultaneously with the siphonophores.

A1.1.3 Experimental conditions

Water was supplied from the aquarium system of the Marine Biological Association. This water is pumped into the building from the Plymouth Sound through a glass-lined pipe and then filtered mechanically to remove macroscopic particulates and sterilised with ultraviolet (UV) light. In the laboratory, water was treated using a two stage filtration process: water was filtered through a 20 µm mesh screen to remove any macroscopic particles, then filtered to 0.2 µm using a membrane filter and vacuum pump. Filtration was essential, as suspended particles tended to accumulate on the siphonophore appendages, causing irritation and impairing mobility (Mackie & Boag 1963). Filtered water was stored in sterile water drums and supplied with vigorous aeration provided by an electric air pump equipped with an in-line air filter. Water parameters (pH, salinity, ORP) were monitored using digital probes and water was refreshed every 2-3 days.

In the sea jellyfish only encounter the air-water and water-benthos interfaces, consequently their maintenance in relatively small laboratory vessels may produce adverse behavioural and physiological 'container effects' (Lafontaine & Leggett 1987). The feeding of ctenophores is significantly depressed when container to animal-volume ratios are less than 2500:1 (Sabatés et al. 2010); this critical ratio is 15000:1 for medusae (Toonen & Fu-Shiang 1993). I housed the polygastric colonies of *M. atlantica* individually in 3 L squat-form beakers that provided average water volumes that are in excess of 4×10^4 times the colony volume. Eudoxids were kept individually and/or in groups in 1 L squat-form glass beakers that provide a container- to animal-volume ratio of 2×10^5:1. These containers provided water volumes well in excess of the recommended volumes, mitigating container effects. Water and prey were refreshed every 24 h. All experimental vessels were covered with 10 µm mesh to limit the introduction of airborne material, particularly synthetic fibres that have been shown to cause mortality of *M. atlantica* in preliminary experiments (personal observation). Beakers were placed in a purpose built large water bath supplied with temperature-controlled water maintained at 15±1 °C.

The use of beakers results in the siphonophores experiencing static water conditions. Excepting the most quiescent, stratified waters this is not representative of conditions *in situ*. In addition to the effects of sinking, water movement hastens the dissolution of the siphonophores tentacle net and results in the colony having to periodically reset the net. Static water conditions therefore result in the siphonophores spending a disproportionate amount of time 'fishing' without needing to reset the tentacle array, which could result in inflated feeding rates. Furthermore static water does not effectively disperse the prey into homogenous distribution – one of the prerequisites for the clearance rate method of measuring predation rates.

To mitigate these caveats various methods of water mixing were investigated through preliminary experimentation. Introduction of an air stream is unsuitable as large bubbles can cause physical damage and small bubbles become lodged in gelatinous tissues potentially causing tissue embolisms (Raskoff et al. 2003). Mechanical stirring can cause physical damage, which can be prevented by the use of a subsurface mesh to prevent direct contact between the stirring paddles and the siphonophores. However, the stirring speeds need to be sufficiently low as to avoid excessive turbulence, whilst adequate to propagate to the bottom of the vessel (personal observations). The pseudo-plankton kreisel (Greve 1968) relies on biological filtration to maintain water quality avoiding the need for daily refreshment; however this design was impractical to fabricate the number of units required. The plankton kreisel (Hamner 1990) provided the most promising design and prototypes were constructed. However, due to the swimming behaviour of *M. atlantica* – escape swimming in response to adverse stimuli – they did not respond favourably to the flow regime within kreisels. When encountering outflow jets siphonophores would respond by swimming rapidly, colliding with vessel walls and suffering damage. A disproportionate amount of time-spent swimming also results in excessive energy expenditure and inhibits feeding.

A1.1.4 Feeding and digestion

For feeding experiments siphonophores were placed in individual beakers with a known concentration of prey (1-day old *Artemia* nauplii) for a 24 h period with a 12/12 photoperiod. After each 24 h period siphonophores were removed and transferred to previously prepared beakers. Remaining prey were filtered through a 20 μm mesh screen and fixed in 4% buffered formalin for subsequent enumeration. All experimental vessels were covered in black plastic to prevent phototactic responses of predators and prey (Purcell 1982).

For digestion experiments polygastric colonies were housed in 500 ml beakers and a single *Artemia* nauplius was carefully placed in close proximity to the tentilla. Following successful prey capture, the time taken to fully ingest the prey was record. The gastrozooid was then monitored every 15 minutes and the time taken until the prey was egested was recorded.

A1.1.5 Growth and development

During daily water refreshment, the number of functional polygastric cormidia was recorded using a dissecting microscope at a range of magnifications (4–200×). Liberated eudoxids were isolated from the polygastric host and housed separately. During subsequent water changes the development of the eudoxid gonophore was monitored.

A2. Appendix for Chapter 2

A2.1 The STATIS procedure

This section provides a detailed description of the STATIS procedure following the methodology of Abdi et al. (2012).

The STATIS procedure is used to analyse K data sets collected on the same observations. Each data set is stored as an $\mathrm{I} \times \mathrm{J}_k$ table denoted X_k, where I is the number of observations and J_k the number of variables in each of the K tables. The X_k tables are also concatenated into the complete $\mathrm{I} \times \mathrm{J}$ table X as:

$$\mathrm{X} = [\mathrm{X}_{[1]}| \ldots |\mathrm{X}_{[k]}| \ldots |\mathrm{X}_{[K]}].$$

A2.1.1 Preprocessing

The columns of each X_k table are centred (mean = 0) and normalised (sum of squared elements = 1) and then each X_k table is normalised (total variance = 1) to ensure all tables participate equally in the analysis.

A2.1.2 Interstructure

To assess the structural similarity of the set of K tables, the cross-product matrices of each $\mathrm{X}_{[k]}$ table, denoted $\mathrm{S}_{[k]}$, are computed as:

$$\mathrm{S}_{[k]} = \mathrm{X}_{[k]} \mathrm{X}_{[k]}^{\mathrm{T}}.$$

Where $^{\mathrm{T}}$ represents the transpose of a matrix.

The individual $\mathrm{S}_{[k]}$ matrices are then collected in a $\mathrm{K} \times \mathrm{I}^2$ matrix, denoted Z, defined as:

$$\mathrm{Z} = [\mathrm{vec}\{\mathrm{S}_{[1]}\}| \ldots |\mathrm{vec}\{\mathrm{S}_{[2]}\} \ldots |\mathrm{vec}\{\mathrm{S}_{[k]}\}]^{\mathrm{T}}.$$

Next, the inner products between all K matrices, denoted C, are computed as:

$$\mathrm{C} = \mathrm{Z}\mathrm{Z}^{\mathrm{T}}.$$

Matrix, C, is then eigendecomposed as:

$$\mathrm{C} = \mathrm{U}\Theta\mathrm{U}^{\mathrm{T}} \quad \text{with} \quad \mathrm{U}^{\mathrm{T}}\mathrm{U} = \mathrm{I}.$$

The eigendecoposition of C provides principal components that describe the similarity structure of the set of tables. The individual $\mathrm{X}_{[k]}$ tables are then projected onto the principal components using their factor scores (coordinates), computed as:

$$\mathrm{G} = \mathrm{U}\Theta^{1/2}.$$

This provides an ordination of the $\mathrm{X}_{[k]}$ tables, revealing similarities and dissimilarities in their structures.

A2.1.3 Compromise

The compromise represents the global structure shared by all $\mathrm{X}_{[k]}$ tables and is constructed by the linear combination of the individual tables.

The first eigenvector provided by the eigendecomposition of matrix C reflects the similarity of each of the tables to the other tables, the 'global' similarity. Consequently it is practical to use these values as weights for the linear combination of the tables into the compromise; enabling tables with similar structures to contribute more and distinctive tables to contribute less to the compromise.

Specifically, if u_1 denotes the first eigenvector of C, the optimal weights are computed by rescaling u_1 so that the sum of its elements is equal to one. These weights are collected in a $\mathrm{K} \times 1$ vector, denoted α, as:

$$\alpha = \mathrm{u}_1 \times \mathrm{sum}(\mathrm{u}_1)^{-1}.$$

Each variable is then assigned the weight corresponding to the table to which it belongs, this collection of weights are stored as the diagonal elements of the diagonal matrix, A, defined as:

$$\mathrm{A} = \mathrm{diag}\{[\alpha_{\mathrm{i}} 1_{[1]}^{\mathrm{T}}, \ldots, \alpha_{\mathrm{k}} 1_{[k]}^{\mathrm{T}}, \ldots, \alpha_{\mathrm{K}} 1_{[K]}^{\mathrm{T}}]\}.$$

Where $1_{[k]}$ represents a $\mathrm{J}_{[k]}$ vector of ones.

An equal mass, m_i, was then assigned to each observation by constructing the diagonal mass matrix M:

$$\mathrm{M} = \mathrm{diag}\{[\mathrm{m}_{[1]} = \frac{1}{\mathrm{I}}, \ldots, \mathrm{m}_{[i]} = \frac{1}{\mathrm{I}}, \ldots \mathrm{m}_{[I]} = \frac{1}{\mathrm{I}}]\}.$$

The Generalised Singular Value Decomposition (GSVD) of X is then computed under the constraints of M and A, expressed as:

$$\mathrm{X} = \mathrm{P}\Delta\mathrm{Q}^{\mathrm{T}} \quad \text{with} \quad \mathrm{P}^{\mathrm{T}}\mathrm{MP} = \mathrm{Q}^{\mathrm{T}}\mathrm{AQ} = \mathrm{I}.$$

The I by I matrix P represents the left generalised singular vectors, the J by I matrix Q the right generalised singular vectors and the I by I diagonal matrix Δ the generalised singular values. Each column of P and Q represent a principal component with Q describing the loadings (variables) and P being used to compute the factor scores F (describing the observations) as:

$$\mathrm{X} = \mathrm{FQ}^{\mathrm{T}} \text{ with } \mathrm{F} = \mathrm{P}\Delta.$$

The eigenvalues, denoted λ, are defined as:

$$\mathrm{diag}(\Delta^2).$$

The inertia (variance) they explain is computed as:

$$\frac{\lambda_{[i]}}{(\sum_i^I \lambda_{[i]}) \times 100}$$

The factor scores, F, describe the ‘compromise space’ – the best representation of the structure of the observations common to all of the tables. These factor scores are plotted in a biplot along with loadings that describe the contribution of the different variables to the dimensions of the compromise space. These variable loadings are computed as the correlation of the weighted mean of the original variables (weighted by α) with F.

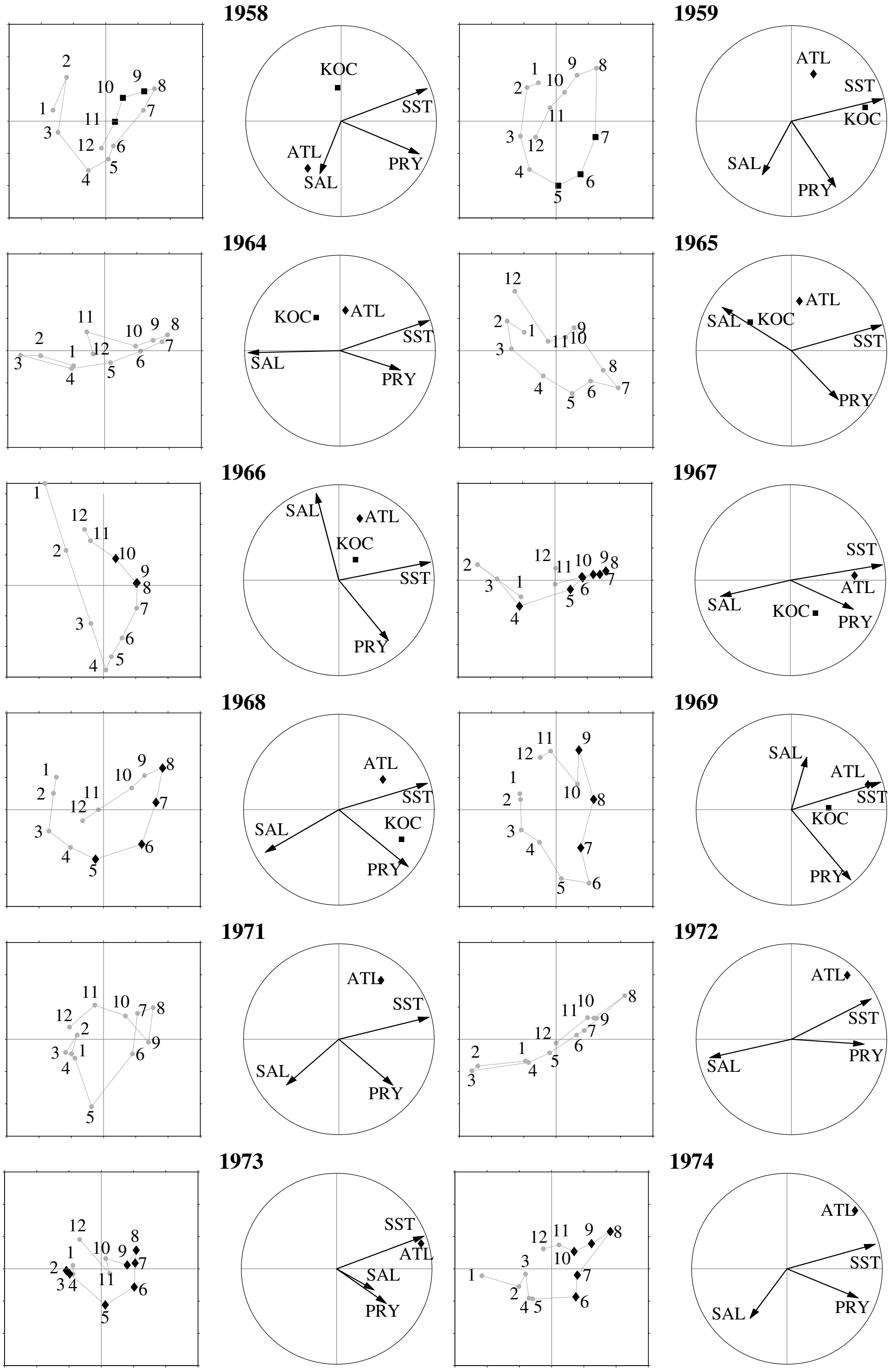
A2.1.4 Trajectories

As each column of Q corresponds to a principal component and each row a variable, the loadings for each individual table are easily extracted from the matrix Q. These loadings are used to calculate the partial factor scores F_k as:

$$\mathrm{F}_k = \mathrm{X}_k \mathrm{Q}_k.$$

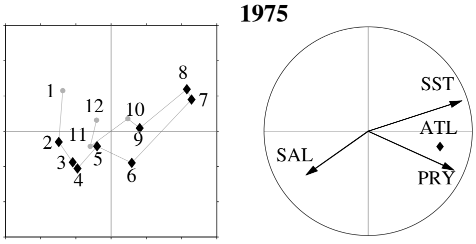
The partial factor scores represent the projection of the individual X_k tables’ observations in the compromise space. The partial factor scores are plotted in biplots along with the individual tables’ variable loadings computed as the correlation of the original J_k variables with F_k.

A2.2 Trajectories; supplementary results

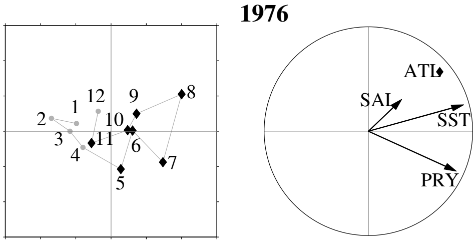


Legend overleaf

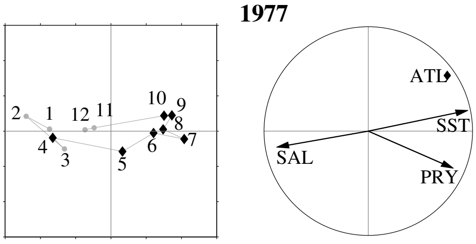
1975



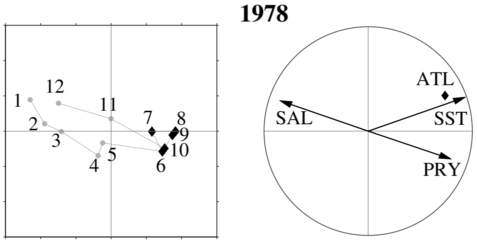
1976



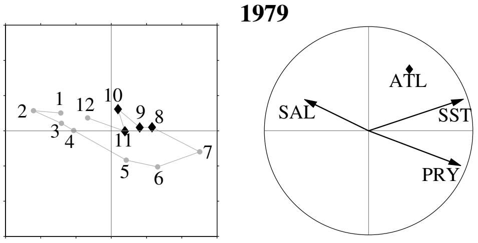
1977



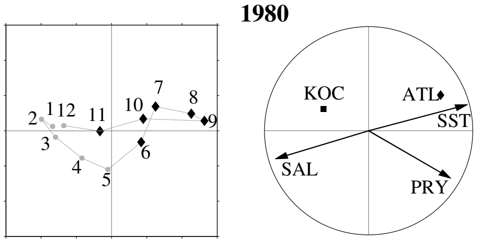
1978



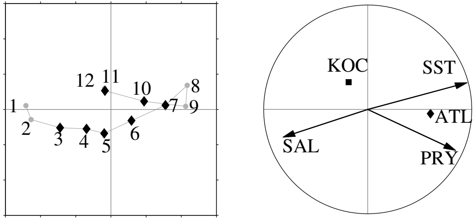
1979



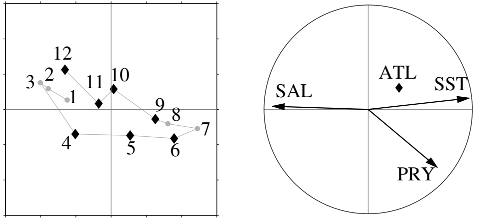
1980



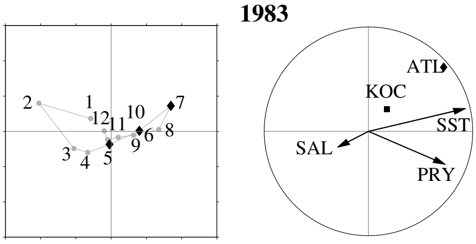
1981



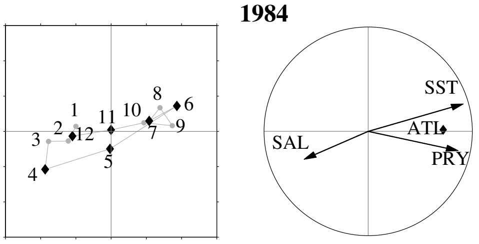
1982



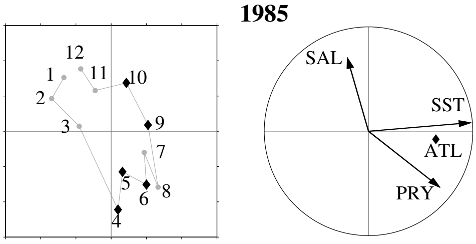
1983



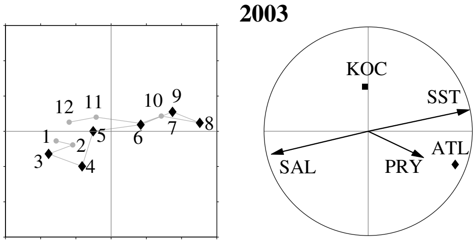
1984



1985



2003



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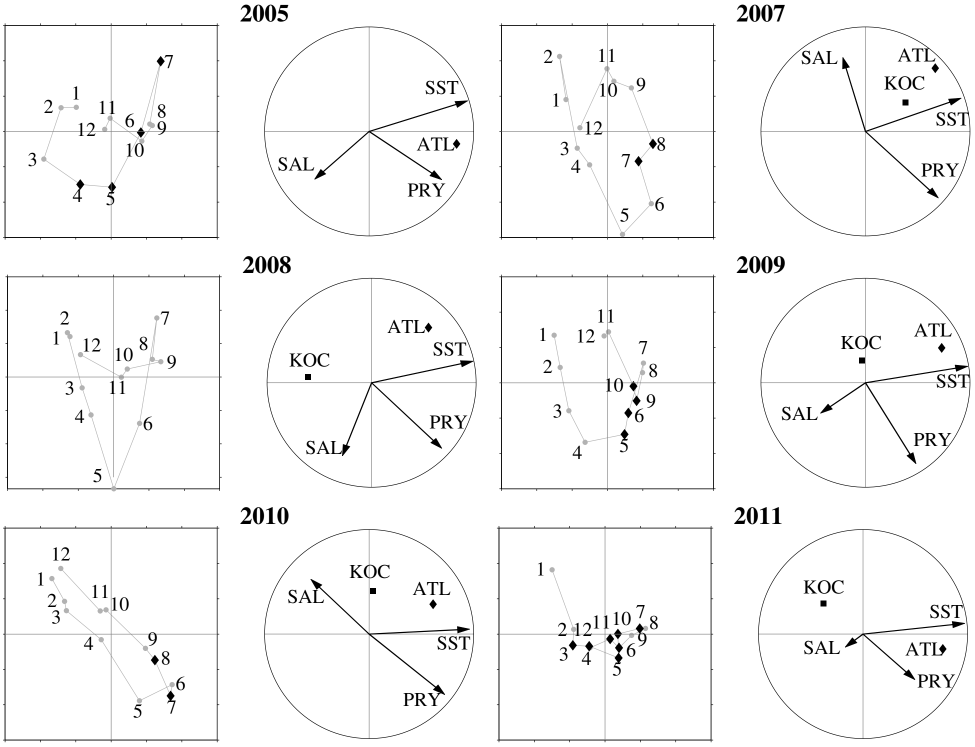

Fig. A2.1. Trajectories of the STATIS analysis. Plots show the environmental characteristics of the individual years, revealing similarities and differences amongst years. Months during which the *Muggiaea* populations were developing in situ are represented by black diamonds (*Muggiaea atlantica*) or squares (*Muggiaea kochi*).

A3. Appendix for Chapter 4

A3.1 Western English Channel *Muggiaea atlantica* abundance data extrapolation

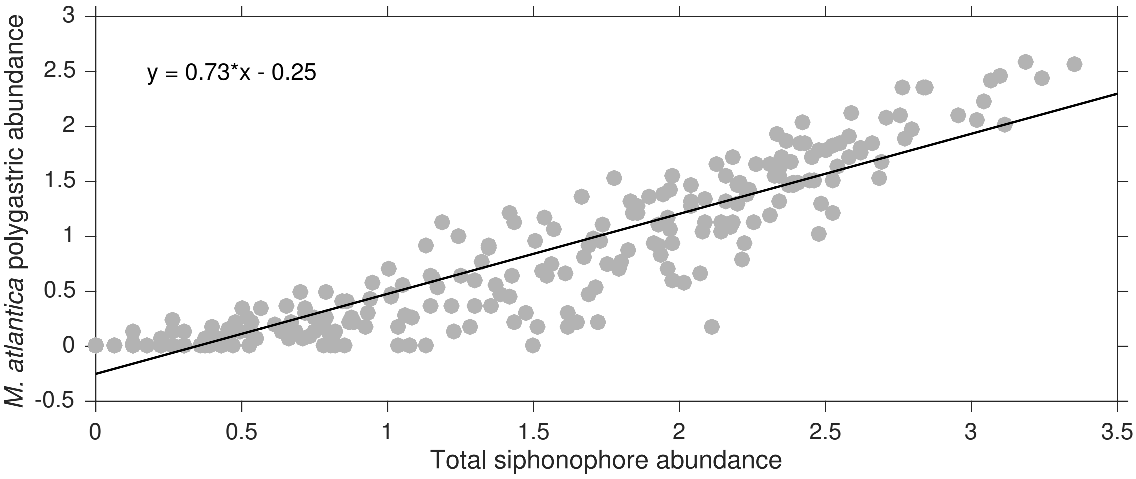

Fig. A3.1. Linear relationship between the abundance of the polygastric stage of *Muggiaea atlantica* (y) and total siphonophore abundance (x) at station L4 in the Western English Channel between 2009 and 2013. The regression equation (inset) was used to extrapolate polygastric abundance for the period 1999–2008. R_2 (adjusted) = 0.84; *F* = 1320; *p* = < 0.0001; RMSE = 0.29.

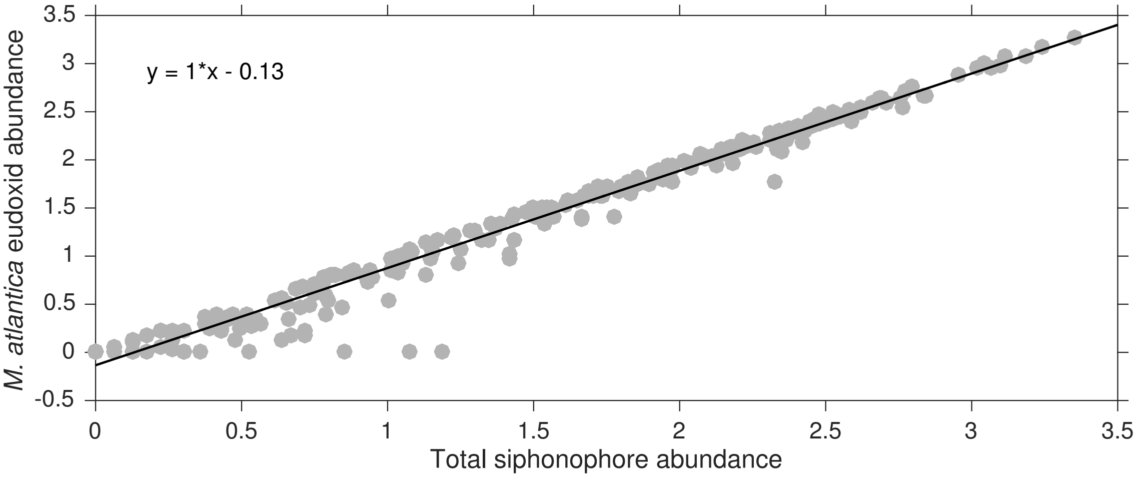

Fig. A3.2. Linear relationship between the abundance of the eudoxid stage of *Muggiaea atlantica* (y) and total siphonophore abundance (x) at station L4 in the Western English Channel between 2009 and 2013. The regression equation (inset) was used to extrapolate eudoxid abundance for the period 1999–2008. R_2 (adjusted) = 0.97; *F* = 9490; *p* = < 0.0001; RMSE = 0.15.

Table A.3.1. Results of Pearson's correlation analysis between the abundance of the polygastric stage of *M. atlantica* at the Western English Channel Stations L4 and L5/E1 during the period 2009–2012 (exclusive) and during the period 2005–2012 (inclusive). The extended period used to construct 'inclusive' was extrapolated using linear.

	r	p	t	d.f.$_a$
Exclusive	0.797	0.0002	4.9381	16
Inclusive	0.796	0.00008	5.2682	18

A3.2 Loch Ewe *M. atlantica* eudoxid environmental preferences

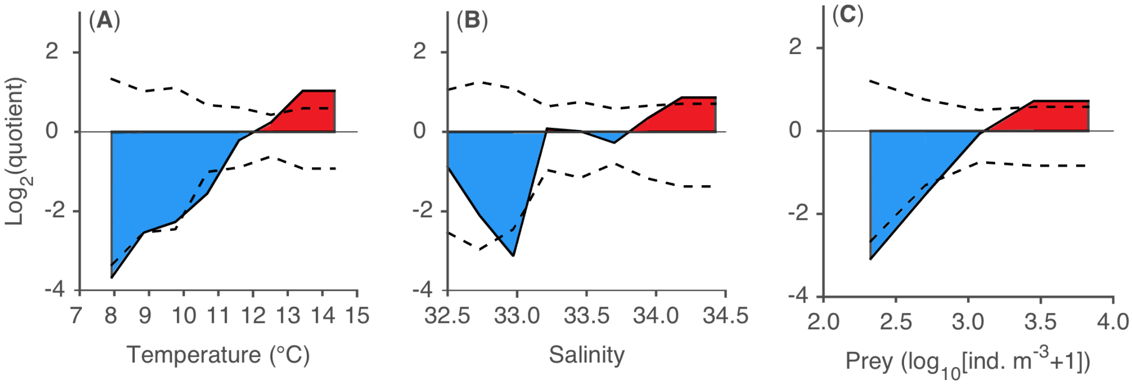

Fig. A3.3. Environmental preferences of the eudoxid stage of *Muggiaea atlantica* at Loch Ewe from 2003–2013 identified using quotient analysis: (A) Sea Surface Temperature; (B) Salinity; (C) Food availability (calanoid copepod abundance).

A3.3 Loch Ewe *M. atlantica* eudoxid source-sink processes at the annual scale

Table A.3.2. Results of variation partitioning of interannual abundance of the eudoxid stage of *M. atlantica* amongst the local environmental (SST) and translocation (ESC) factors at Loch Ewe between 2003 and 2012. Fraction [a + b + c] represents the variation explained by both explanatory factors, fraction [a + b] the variation explained by SST and fraction [b + c] the variation explained by the ESC.

Fraction of variation	Explanatory variables	R^2_a	d.f.	F	Beta
[a + b + c]	SST	0.75	7	14.7***	1.01**
	ESC				0.74***
[a + b]	SST	0.35	8	4.3**	1.58
[b + c]	ESC	0.68	8	16.9***	0.86

SST: Sea surface temperature; FA: food availability; ESC: European Slope Current; WEC: Western English Channel

*** p = <0.01

** p = <0.05

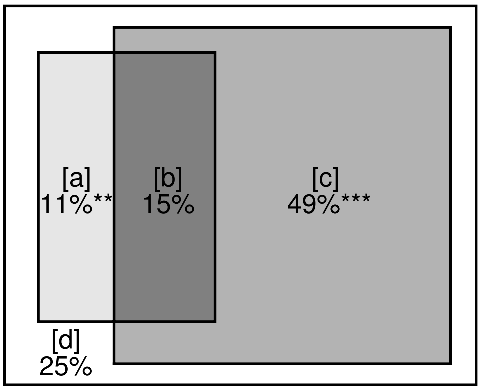

Fig. A3.4. Loch Ewe 2003–2012. Proportional Venn diagram representing the fractions of variation in the annual abundance of *Muggiaea atlantica* attributed exclusively to: [a] the local environmental factor (Sea surface temperature); [c] the translocation factor (strength of the European Slope Current); [b] the common variation explained by both factors; and [d] the unexplained (residual) variation. Numbers represent the percentage of the total variability. ** p = <0.05, *** p = <0.01.

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