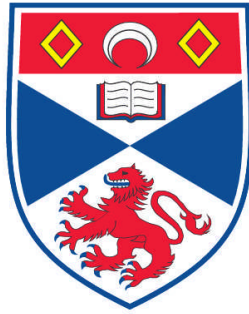


**ECOLOGICAL AND ACOUSTIC INVESTIGATIONS OF JELLYFISH  
(SCYPHOZOA AND HYDROZOA)**

**Christopher Philip Lynam**

**A Thesis Submitted for the Degree of PhD  
at the  
University of St. Andrews**



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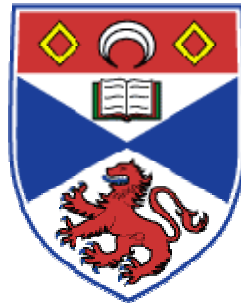
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*Ecological and acoustic investigations of  
jellyfish (Scyphozoa and Hydrozoa)*

*Christopher Philip Lynam*



Submitted in partial fulfilment of the requirements  
for the degree of Doctor of Philosophy

University of St Andrews

April 2006

*Ecological and acoustic investigations of  
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*Christopher Philip Lynam*

## Abstract

As the biomass of jellyfish (medusae of the Scyphozoa and Hydrozoa) has risen in numerous locations worldwide, awareness of their potential to exert a controlling influence on marine ecosystems and hinder the recruitment of fish stocks has increased. Medusae are capable of intensive, size-selective, predation on zooplankton, which may alter the composition of the plankton community. Jellyfish are often found in dense layers, up to hundreds of metres thick, which can extend horizontally for hundreds of kilometres. Such aggregations may benefit specialist feeders, such as turtles, that rely upon jellyfish for food and those fish that are able to find refuge under the jellyfish umbrellas. Nonetheless, the predominance of jellyfish in pelagic ecosystems is not generally viewed as desirable; in fact, this situation has been portrayed as the result of pollution and overexploitation of otherwise productive seas. However, jellyfish are sensitive indicators of environmental change, and their populations appear to respond to climatic fluctuations, so jellyfish warrant study for their intrinsic ecosystem role particularly given present concerns over climate change. With growing acceptance that fishery management should take an holistic ‘ecosystem approach’, knowledge of the interactions between jellyfish, fisheries and climate may be vital in progression towards the goal of ecosystem-based sustainable management of fisheries. Unfortunately, due to their gelatinous nature, medusae are difficult to sample using conventional netting techniques and data on changes in distribution and abundance are consequently sparse. Recent studies have demonstrated that medusae can be detected acoustically and that this technique could provide a rapid and cost-effective estimate of their biomass and distribution. This thesis reports my endeavour to demonstrate the ecosystem role of medusae and to develop acoustic techniques to monitor their biomass. Through regression analyses, I link the abundance of medusae (*Aurelia aurita*, *Cyanea lamarckii*, and *Cyanea capillata*) in regions of the North Sea to climatic fluctuations, as quantified by the North Atlantic Oscillation Index, and show that medusae may be important indicators of regional ecosystem change. The mechanisms linking climatic fluctuations to ecosystem changes are explored via a correlative modelling approach using General Additive Models; I show that the mechanisms are location dependent and explainable in terms of direct,

rapidly responding (intra-annual) influences (surface warming, river run-off, and wind-driven mixing and advection) and longer-term (interannual) oceanographic responses (changes in circulation currents i.e. the northward extent of the gulf stream and relative strength of inflow into the North Sea of the North Atlantic current, Continental Shelf Jet and Arctic waters). I present correlative evidence for a detrimental impact by *Aurelia aurita* on herring 0-group recruitment, once the influence of interannual change in herring spawning stock biomass on recruitment is factored out through modelling with a Ricker stock-recruitment relationship. Similarly, a commensal relationship between whiting and *Cyanea* spp. medusae is shown to improve North Sea whiting survival to the 1-group. In progress towards the automated acoustic identification of species, I have developed an *in situ* discrimination tool that can distinguish between echoes from: *Aequorea aequorea*; *Chrysaora hysoscella*; clupeid fish (sardine, anchovy and round herring); and horse mackerel/Cape hake. The technique relies upon characteristic differences in echo strength between frequencies, which are determined for each jellyfish species and finfish group using combined multifrequency acoustic and pelagic trawl samples. This method has facilitated the world's first acoustic-based estimate of jellyfish biomass in the Namibian Benguela Sea. The 12.2 million tonnes of biomass of medusae (*Aequorea aequorea* and *Chrysaora hysoscella*) in the Namibian Benguela Sea was found to be greater than the combined biomass, 3.6 million tonnes, of commercially important fish (horse mackerel, Cape hake, sardines, anchovy, and round herring) in the same area. These results suggest that medusae may have an important role in the Benguela ecosystem that has previously been overlooked and that their biomass should be monitored.

## Declarations

I, Christopher Philip Lynam, hereby declare that this thesis, which is approximately 72,000 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

date ..... signature of candidate .....

I was admitted as a research student in October 2002 and as a candidate for the degree of PhD in October 2003; the higher study for which this is a record was carried out in the University of St Andrews between 2002 and 2005.

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# Chapter 1

## General introduction

*“Observations of vast concentrations of gelatinous organisms are not new: both Darwin and Huxley, on their respective voyages on the Beagle and Rattlesnake, sailed through areas of sea covered with salps, jellyfish, or siphonophores (Huxley 1859). Yet it is only within the past few decades that the importance of the role of gelatinous organisms in marine food webs has become widely recognised, and attention directed to the causes and effects of their episodic pulses. Growing acceptance of the key role of gelatinous organisms has largely been due to innovations in observational techniques and to growing interest in trophic interactions.” (CIESM 2001)*

## 1. General introduction

This thesis reports novel research into aspects of the ecology of jellyfish (Scyphozoa and Hydrozoa, Table 1.1), and the development of new multifrequency acoustic techniques that enable rapid surveying of medusae biomass at sea. In this chapter, I review the relevant scientific literature on gelatinous zooplankton ecology, in particular where it relates to my species of interest (Scyphozoa: *Aurelia aurita*, *Cyanea lamarckii*, *Cyanea capillata*, *Chrysaora hysoscella* and the hydrozoan *Aequorea aequorea*, Table 1.2) and survey areas (North and Benguela Seas). Much of the literature on jellyfish growth and reproduction refers to *Aurelia aurita*, a common neritic jellyfish with a worldwide distribution (Russell 1970; Båmstedt 1990; Lucas et al. 1997). However, recent genetic studies have suggested that there may, in fact, be four or more ‘cryptic’ (morphologically similar) subspecies of *Aurelia* (Dawson and Jacobs 2001). *Aurelia aurita* shares many aspects of its life history with other scyphozoans – and indeed with some species of the Hydrozoa – and is therefore a good model for a general description of jellyfish growth (Figure 1.1 and 1.2).

| Class     | Sub-Class                       | Order                           | Comment  | Included in this study |  |
|-----------|---------------------------------|---------------------------------|--|------------------------|--|
| Scyphozoa |                                 | Semaeostomae                    | 5 British species<br>Incl. <i>A. aurita</i>            | ✓                      |  |
|           |                                 | Rhizostomeae                    | 1 British species                                      |                        |  |
|           |                                 | Coronatae                       | Deep-water species incl.<br><i>P. periphyla</i>        |                        |  |
|           |                                 | Stauromedusae                   | All sessile  |                        |  |
| Hydrozoa  |                                 | Hydroida                        | Freshwater hydras and colonial hydroids                |                        |  |
|           |                                 | Actinulida                      | Microscopic hydrozoans.                                |                        |  |
|           |                                 | Chondrophora                    | 2 accepted genera:<br><i>Porpita</i> and <i>Vellea</i> |                        |  |
|           |                                 | Leptomedusae                    | Incl. <i>A. aequorea</i>                               | ✓                      |  |
|           |                                 | Milleporina                     | Hydrocorals, millepores                                |                        |  |
|           |                                 | Siphonophora                    | Complex colonial organisms, incl.<br><i>Physalia</i>   |                        |  |
|           |                                 | Stylasterina                    | Hydrocorals  |                        |  |
|           |                                 | Narcomedusae                    | Holo-planktonic and essentially deep-water species     |                        |  |
|           |                                 | Trachymedusae                   |  |                        |  |
|           | Cubozoa                         |                                 | Cubomedusae  | Tropical               |  |
| Anthozoa  | Alcyonaria<br>(or Octocorallia) | Stolonifera                     | Organ pipe corals                                      |                        |  |
|           |                                 | Telestacea                      | Branched Pipe Corals                                   |                        |  |
|           |                                 | Gorgonacea                      | Sea fans/whips   |                        |  |
|           |                                 | Alcyonacea                      | Soft corals  |                        |  |
|           |                                 | Helioporacea                    | Blue Corals  |                        |  |
|           |                                 | Pennatulacea                    | Sea pens, sea pansies                                  |                        |  |
|           |                                 | Ceriantipatharia                | Antipatharia   | Black Corals           |  |
|           |                                 | Ceriantharia                    | Tube Anemones  |                        |  |
|           |                                 | Actiniaria                      | Sea anemones, stony corals,                            |                        |  |
|           |                                 | Hexacorallia<br>(or Zoantharia) | Corallimorpharia                                       | Mushroom anemones      |  |
|           |                                 |                                 | Ptychodactiaria  | Cold water anemones    |  |
|           |                                 |                                 | Scleractinia   | Hard / stony corals    |  |
|           |                                 |                                 | Zoanthinaria   | Zonanthids             |  |

Table 1.1 The Cnidaria Phylum indicating those Orders included in this study

| Order        | Family                              | Genus                                    | Species                                  | Distribution  | Appearance  |
|--------------|-------------------------------------|--|--|---|---|
| Semaestomeae | Ulmaridae<br>(subfamily Aureliinae) | <i>Aurelia</i><br>Lamarck                | <i>aurita</i><br>Lamarck                 | Coastal<br>cosmopolitan                                   | slight blue<br>tinge                                |
|              | Cyaneidae                           | <i>Cyanea</i>                            | <i>capillata</i><br>Lamarck              | Northern<br>boreal  | red/brown   |
|              |                                     | Péron and<br>Lesueur                     | <i>lamarckii</i><br>Péron and<br>Lesueur | Southern<br>boreal  | blue/yellow   |
| Rhizostomeae | Pelagiidae                          | <i>Chrysaora</i><br>Péron and<br>Lesueur | <i>hysoscella</i><br>Lamarck             | Southern<br>North Sea<br>and west<br>coast of<br>Scotland | red/brown   |
|              |                                     | Rhizo-<br>stomatidae                     | <i>Rhizostoma</i><br>Cuvier              | <i>octopus</i><br>Lamarck                                 | Southern<br>boreal and<br>west coast of<br>Scotland |

Table 1.2 Jellyfish of the Phylum Cnidaria and Class Scyphozoa that are resident in the coastal waters of the British Isles

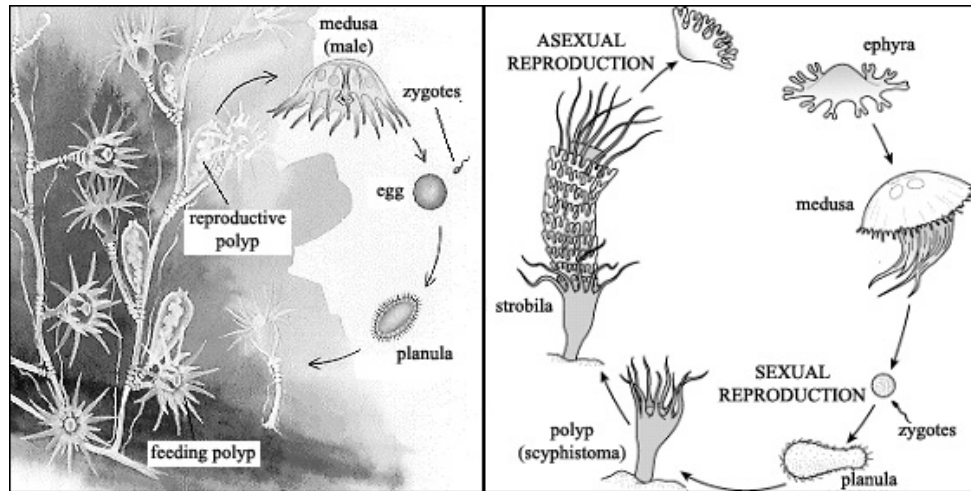


Figure 1.1 Life-cycle of meroplanktonic Hydrozoa (left) and Scyphozoa (right). Left diagram, from Aquascope (2000) [www.vattenkikaren.gu.se](http://www.vattenkikaren.gu.se) and right diagram, from NASA (1991) [http://lifesci.arc.nasa.gov/lis2/Chapter4\\_Programs/SLS/SLS\\_1.html](http://lifesci.arc.nasa.gov/lis2/Chapter4_Programs/SLS/SLS_1.html)

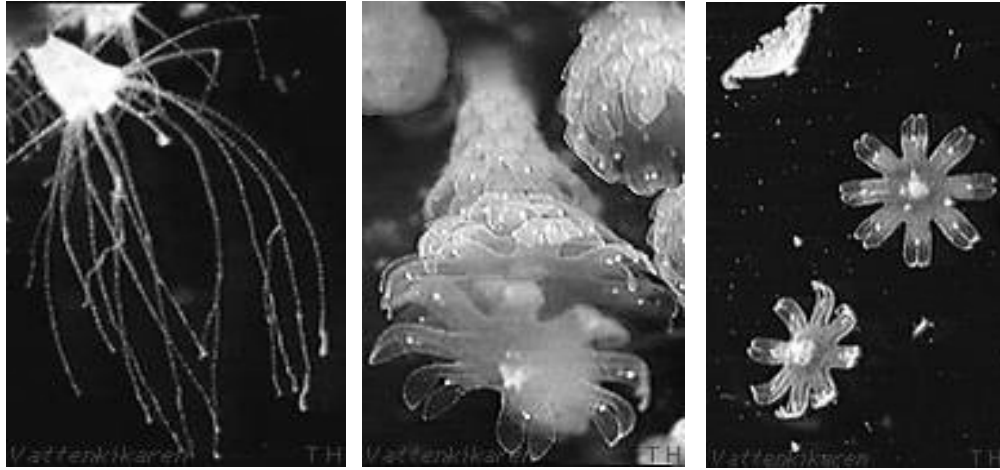


Figure 1.2: *Aurelia aurita* (left: a young polyp, middle: a strobila, right: ephyrae) (photographs reproduced from Aquascope 2000)

Seasonal environmental changes (in temperature, salinity, light and prey levels) are considered to be important cues for the production of medusae (through strobilation), and warm temperatures have been shown to increase the rate of growth of medusae (Sections 1.4 to 1.7 and references therein). I have studied the effect of climatic changes (as encapsulated by the North Atlantic Oscillation Index) on the abundance and distribution of jellyfish in the North Sea (Chapters 2 to 4); results from this work have been published in *Limnology and Oceanography* (Lynam et al. 2004) and the *Journal of the Marine Biological Association of the UK* (Lynam et al. 2005a) (Appendix A). Jellyfish have been implicated in suppressing fish stocks (Section 1.10 and references therein) and I have shown through a statistical analysis that *Aurelia aurita* and *Cyanea capillata* may reduce the survival of herring larvae (*Clupea harengus*) in the North Sea (Chapter 5); this study has been published in *Marine Ecology Progress Series* (Lynam et al. 2005b) (Appendix A). Gadoid fish are known to find refugia under the umbrella of, and among the tentacles of, medusae. The possible beneficial effect of this commensal relationship on the survival of North Sea cod, whiting, and haddock 0–group fish is explored in Chapter 6.

Chapter 7 describes the acoustic methods used to estimate the biomass of fish and of some zooplankton. Chapter 8 describes two methods that were used to determine the target strength (TS) of the common Namibian medusae: *Aequorea aequorea* and *Chrysaora hysoscella*. The results described in section 8.3 are

published in the co-authored publication in the *ICES Journal of Marine Science* Brierley et al. (2004). Section 8.4 reports a new TS–mass relationship for jellyfish that is independent of species. A multifrequency algorithm is developed in Section 8.5 (and described in my ICES report CM2004 R06, Appendix A) to enable the discrimination of echoes due to jellyfish from those echoes returned by other zooplankton and fish. Using the methods developed in Chapter 8, chapter 9 reports the results of the world’s first acoustic biomass survey of jellyfish in the Namibian Benguela Sea.

### **1.1. The pelagic food web**

The pelagic food web is commonly considered to comprise a four-tiered food chain: phytoplankton (mainly diatoms) → herbivorous plankton (largely copepods) → planktivorous fish → piscivorous fish and marine mammals. Gelatinous zooplankton have often been considered to form a separate ‘jelly food chain’: nano- and pico-phytoplankton → pelagic tunicates → herbivorous Cnidaria and Ctenophora → carnivorous medusae and ctenophores → specialist predators (e.g. turtles and some fish, Ates 1991; Purcell and Arai 2001). However, it has been proposed that, dependent on anthropogenic and environmental influences, the pelagic food web may switch production away from finfish and towards jellyfish or *vice versa* (Figure 1.3) (Parsons and Lalli 2002; Sommer et al. 2002). The basic processes of the ‘microbial food web’ describe the return of dissolved organic carbon to the food web through bacterivory by protozoa. If we are to gain a full understanding of ecosystem functioning, and of anthropogenic and climatic impacts on marine resources, we must take an ‘ecosystem perspective’ by which we consider all the components of the food web and their interactions (Pauly et al. 2002; Pikitch et al. 2004).



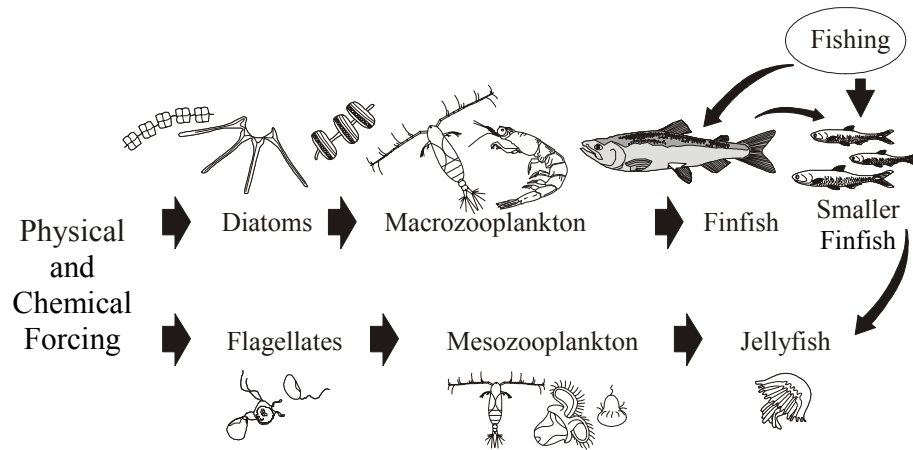


Figure 1.3 High (top row) and low (bottom row) energy food chains that may lead to ecosystem dominance by either finfish or jellyfish. The elimination of large quantities of fish by overfishing would cause an initial increase in the macroplankton followed by a decrease in the diatom population through grazing. As a result, more nutrients may then flow into the low energy food chain resulting in an increased jellyfish population. Adapted from Parsons and Lalli (2002).

## 1.2. Jellyfish species

Gelatinous zooplankton comprise the phyla Cnidaria (including siphonophores, corals, hydrozoans, and scyphozoans), Ctenophora ('comb jellies') and Chordata (pyrosomes, appendicularia, doliolids and salps). Of the phylum Cnidaria (Table 1.1), the 'true' jellyfish are those species of the class Scyphozoa. However, I will refer to the large medusae (adult stage reaching >10cm in umbrella diameter) of both the Scyphozoa and Hydrozoa classes as jellyfish. The majority of jellyfish species are found in shallow shelf seas and coastal areas due to their requirement for a suitable (warm and bright enough) substrate on which to settle. Nevertheless, some hydrozoan species and a few scyphozoan species are found in oceanic areas: for example in the north-east Atlantic *Pelagia noctiluca* and *Periphylla periphylla* (both Scyphozoa) are present and at least 27 species (17 Anthomedusae, 4 Leptomedusae, 5 Trachymedusae and 1 Narcomedusae) of the Hydrozoa have been reported (Russell 1970 and references therein).

This study will not be concerned with scyphozoan species of the order Stauromedusae, which are all sessile, nor with species of the Coronatae, which

are all deep-water species (Russell 1970). The remaining scyphozoan classes, Rhizostomeae and Semaestomae, both contain species that are found around the coast of the British Isles (Table 1.2). However, my climate and ecosystem studies are based on the central and northern North Sea, where the scyphozoan species *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* dominate and where Rhizostomeae are scarce (Chapters 2, 3, 5 and 6). *Rhizostoma octopus* is often highly abundant in the Irish Sea and occurs off the western coast of Scotland, yet in the North Sea this species appears restricted to the far south (off the coasts of Belgium, Denmark, in the German Bight and in the English Channel). Russell (1970 and references therein) report that pulsation rates of *Rhizostoma octopus* decrease with temperature and cease below 4 to 6°C: this cold intolerance may explain the absence of this species in the central and northern North Sea. *Pelagia noctiluca* are sometimes found in the North Sea; however, this medusa is not a permanent resident (Hay et al. 1990). The hydrozoan *Aequorea aequorea* (Order Leptomedusae), is also considered in this study as this species, in addition to the scyphozoan *Chrysaora hysoscella*, was the subject of an acoustic survey in the northern Benguela Sea (Chapters 8–9). The Cubozoa class (once included as a sub-class of Scyphozoa) are only found in tropical and subtropical oceans, while the Anthozoa does not contain any medusoid species. Therefore, neither the Cubozoa nor Anthozoa is included in this study.

### 1.3. Life history of jellyfish

Jellyfish (Scyphozoa and Hydrozoa) have a complex life cycle of alternating benthic and pelagic stages (Figure 1.1). The free-swimming adult medusae of most species, except the hermaphrodite scyphozoan *Chrysaora hysoscella*, are dioecious and reproduce sexually to produce larvae. Most jellyfish, including *Aurelia aurita*, are aggregated passively through current forcing and the local retention of medusae by topographic features leading to the regular appearance of ‘blooms’ in late summer. Jellyfish eggs are generally fertilized in the water column and develop into free-swimming larvae. However, the females of some species, e.g. *A. aurita* and *Cyanea capillata*, will capture the male zygotes with their oral arms and allow their eggs to develop in brood sacks before releasing them as planktonic planular larvae (Russell 1970).

Two scyphozoan species (*Pelagia noctiluca* and *Periphylla periphylla*) are accepted to reproduce without a sessile stage: *Pelagia noctiluca* (Semaestomeae) produces eggs which transform into planula larvae before metamorphosing into ephyrae (Russell 1970), while *Periphylla periphylla* (Coronatae) releases eggs which then metamorphose directly into small medusae (Jarms et al. 1999; Jarms et al. 2002). Some authors (Berrill 1949; Hirai 1958; Yasuda 1971, all cited in Hay et al. 1990) have also observed direct development of *Aurelia* spp. ephyra from pelagic larvae. Two orders of the Hydrozoa also contain species that develop directly from egg to medusae: Trachymedusae (*Liriope tetraphylla* and *Aglantha digitale*) and Narcomedusae (many species including the deep-water species *Solmissus incisa* that is found off the western coasts of Britain) (Russell 1970). However, in the majority of scyphozoan and hydrozoan species the larvae settle onto a substrate (including the seabed, cliff-faces, kelp or seaweeds and man-made structures such as oil rigs and harbour walls) to form polyps. The small plant-like benthic polyps of scyphozoans are known as scyphistomae (up to 3 mm tall), while hydrozoan polyp colonies are called hydroids and often measure many cm in length. Hydroids differ from scyphistomae in that hydroids are collections of specialist cells that perform separate processes (reproduction, feeding etc.), whereas the scyphistoma is a single fully functioning organism. Polyps are much more resistant to environmental fluctuations than medusae are, and in poor conditions (e.g. minimal prey levels and low temperature) polyps may encyst – a state similar to hibernation. Polyps feed on microscopic marine plankton and, at low prey levels, may reproduce vegetatively (asexually) by budding to form other polyps. However, once environmental conditions suffice, an hydroid's reproductive cells will mature and a scyphistoma will segment through the strobilation process (Figures 1.1 and 1.2). One by one the segments separate from the body of the scyphistomae (now known as the strobila) to become free-swimming ephyrae, which develop to the adult stage (the medusa). Similarly, when the hydroid colony is fully grown, a new generation of medusae will bud off from the polyp (Russell 1970 and Figure 1.1). However, jellyfish species are not all alike and some species may exhibit particularly unusual growth characteristics: the hydrozoan *Turritopsis nutricula*, for example, may

metamorphose from the medusa stage back into a polyp by inverting its umbrella and resettling on the seabed (Carla et al. 2003; Piraino et al. 2004).

#### 1.4. Seasonal phases of population growth

When food is in sufficient supply, jellyfish are capable of extremely rapid growth due to their low carbon density. For *A. aurita*, laboratory based measurements of the daily specific growth rate:  $\mu = (t_i - t_0)^{-1} \ln(W_i / W_0)$ , where  $W_i$  and  $W_0$  are the dry body weights at time  $t_i$  and  $t_0$  respectively, and the net growth efficiency:  $NGE = \mu / (\mu + R_s)$ , where  $R_s$  is the weight specific respiration rate, have shown that even at low prey densities medusae are able to double in weight every 3 to 5 days dependent on prey availability (Table 1.3) (Frandsen and Riisgård 1997). These calculations are supported by *in situ* measurements of the exponential increase in biomass of various scyphozoan populations where the daily growth rate has been calculated to be: 20% for *Rhizostoma octopus*, 30% for *Mastigias papua*, and between 10% and 30% for *Aurelia aurita* (Larson 1986, and references therein).

| Mean prey concentration (individuals per litre) | Daily specific growth rate, $\mu$ (%) per day) | Time (days) required to double weight | Net growth efficiency $NGE$ (%) |
|---|--|---------------------------------------|---------------------------------|
| 16 ± 8  | 15   | 4.6                                   | 77                              |
| 47 ± 8  | 14   | 5.0                                   | 68                              |
| 92 ± 7  | 19   | 3.6                                   | 83                              |
| 186 ± 5   | 24   | 2.9                                   | 82                              |
| 328 ± 16  | 21   | 3.3                                   | 78                              |

Table 1.3 The daily specific growth rate and the net growth efficiency for *Aurelia aurita* fed on the marine rotifer *Brachionus* sp. for 4 days. Table adapted from Frandsen and Riisgård (1997).

In general, medusoids (ephyrae and medusae) show three phases of growth:

1. slow growth during late winter and early spring;
2. exponential growth once temperature and food availability have increased in mid-spring;
3. shrinkage, or ‘degrowth’, in diameter and mass (Hamner and Jenssen 1974; Frandsen and Riisgård 1997) in summer and autumn during gamete release or when resources are scarce.

These phases are evident in the growth of *Aurelia* and have been shown by populations in the Kiel Bight (Germany), Tomales Bay (USA), Kagoshima Bay (Japan) and Kertinge Nor (Denmark) (Miyake 1997 and references therein). The substantial variability in the maximum umbrella diameter, from <50 mm in Kertinge Nor to >200 mm Kagoshima Bay, is likely to depend on the particular environmental conditions at the specific location during the period of study. For example, *A. aurita* was present over a wide range of salinities, from a low of 10 ppt in Kiel fjord to a high of 32 ppt in both the Gullmar fjord and Kagoshima Bay, and temperatures, from a low of -1 °C in the Gullmar fjord to a high of 29°C in Kagoshima Bay (Miyake 1997).

### **1.5. Density dependent growth**

Schneider and Behrends (1994) and Lucas (2001) suggest inverse density dependence between maximum bell diameter and medusa abundance in *Aurelia aurita*. From the published values for North Sea *A. aurita* (Hay et al. 1990) the maximum mean bell diameter was indeed found at lowest *A. aurita* abundance, i.e. during 1981. However, in 1973 the mean bell diameter was also high while the abundance was not abnormally low. Thus density dependence is likely modified by environmental factors, such as temperature and prey availability, and will depend upon the scale over which measurements are made. The growth rates of *A. aurita*, and subsequently the maximum bell diameter, have been shown to depend on food availability in two contrasting U.K. populations: Southampton Water (a productive, partially-mixed coastal plain estuary, characterized by abundant plankton) and Horsea Lake (an enclosed, brackish, man-made body of water situated 30 km to the east of Southampton Water with a sparse plankton community) (Lucas and Williams 1994; Lucas 1996; Lucas et al. 1997).

### **1.6. Development and maturation**

The development of ephyrae (young medusoids) by polyps is dependent on environmental stimuli (such as decreasing temperature and prey density). Open populations of scyphomedusae (e.g. in Southampton Water) often show a single generation of medusae maturing in synchrony, while enclosed populations (e.g.

in the man-made Horsea Lake) may show multiple generations with summer and autumn blooms (Lucas and Lawes 1998). These multiple generations could be explained by either over-wintering ephyrae or over-wintering adult medusae (Hernroth and Grondahl 1985a).

The onset of maturation is usually concurrent with increases in temperature; the largest medusae (although there is no predetermined maturation size) are first to mature and are closely followed in time by all others, with no apparent minimum maturation size (Lucas 2001). The size of adult medusae at maturation will vary annually and spatially, and depends upon a number of factors (including: the date that the ephyrae were released; prey availability; and temperature during growth) (Lucas and Lawes 1998).

### **1.7. Over-wintering and post-spawning survival of medusae**

Most research indicates that *Aurelia aurita* individuals persist in the water column for between four and eight months (Veer and Oorthuysen 1985, cited in Lucas 2001; Schneider and Behrends 1994), with death following spawning. However, *A. aurita* populations are present throughout the year in the following locations: Urazoko and Tokyo Bays, Japan (Miyake 1997); the enclosed Horsea Lake, U.K. (Lucas and Lawes 1998); and Gullmar Fjord in western Sweden (Gröndahl 1988). Spangenberg (1965, cited in Lucas 2001) attributed the death of the medusae to the extrusion of gastric filaments during gamete release, resulting in morphological degradation and susceptibility to parasitic invasion. In contrast, Russell (1970) suggested that the deterioration of the medusae and hardening of the mesoglea (the 'jelly') during spawning, when the animal ceases to feed, may result in its increased buoyancy and hence stranding. However, some studies indicate that this may not be so for all populations of *Aurelia* spp.. Miyake (1997) suggested that the female *Aurelia aurita* of Kagoshima Bay may release planulae twice, proposing a life span of up to two years with the release of planulae in each of two summer periods. In the laboratory, Zahn (1981, cited in Schneider and Behrends 1994) kept three North Sea *Aurelia aurita* medusae for about two years. Hamner and Jenssen's (1974) study of *A. aurita* in Tomales Bay, California, found that not only could medusae survive spawning but that they could grow and reproduce continually for another full year. Hela (1951, cited in Russell 1970) recorded the clogging of fishing nets in the Baltic during

the winter by *Aurelia* medusae that had collected in bottom waters, implying that adult *Aurelia* do not necessarily die in the autumn. Russell (1970) stated that *Aurelia*, *Cyanea* and *Rhizostoma* species may all retreat to deeper waters during the winter months. Perhaps this explains the inconsistency in opinion on post-spawning survival as over-wintering medusae may be simply unnoticed. The hydrozoan *Aequorea aequorea*, however, is believed to be present in the Namibian Benguela throughout the year (Gibbons et al. 1992).

As reproduction in scyphomedusae may be triggered by environmental factors regardless of medusae size/age, it is possible that the condition of individual medusae prior to reproduction may influence post-spawning mortality. When starved, both adult and sexually immature medusae may shrink and, provided that they have not regressed disproportionately (with the bell becoming smaller than the oral arms), they are able to recover normally once food is again available (Hamner and Jenssen 1974). Therefore, factors such as medusa body size, prey abundance and associated consumption rates may influence the survival of over-wintering scyphomedusae.

### **1.8. Predation on jellyfish**

Medusae and ephyrae may be consumed by many predators, including:

- Other cnidarians, such as *Cyanea capillata*, *Aequorea victoria*, *Phacellophora camtschatica* and *Metridium senile*. In fact, *C. capillata* may be dependent on gelatinous zooplankton for its early (up to 85 days) development (Båmstedt et al. 1997).
- Birds, which prey on medusae at sea and when stranded onshore, including the sanderling (*Crocethian alba*) that has been recorded eating *Aurelia aurita*. Unidentified medusae have been found in the stomach contents of seagulls, kittiwakes, fulmars, puffins and shearwaters (Ates 1991).
- Various fish species, which prey on larvae, ephyrae and medusae, including: the Sunfish (*Mola mola*) whose diet consists largely of gelatinous zooplankton; spiny dogfish (*Squalus acanthias*) whose stomachs have been recorded to contain between 30 and 40% by volume of jellyfish; lumpfish (*Cyclopterus lumpus*) that prey upon the

ctenophore *Pleurobrachia* sp; chum salmon (*Oncorhynchus keta*) and Atlantic mackerel (*Scomber scombrus*) that may prey upon the hydrozoan *Aglantha digitale* (Ates 1991; Welch 1997; Purcell and Arai 2001).

- Turtle species, including the leatherback (*Dermochelys coriacea*) that are seasonal visitors to British waters and thought to be attracted by the high biomass of *Rhizostoma* found in coastal waters.
- Benthic scyphistomae (including polyps of *A. aurita*) and hydroids, which may prey on the ephyrae.
- Parasites including larval trematodes, cestodes, and Hyperiid amphipods (e.g. *Hyperia galba* M.), commonly are found in medusae.

Although predation on the benthic stage has been little documented, the nudibranch *Coryphella verrucosa* has been reported to consume *Aurelia aurita* polyps (Hernroth and Grondahl 1985b).

### **1.9. Commensal/symbiotic relationships with medusae (Scyphozoa)**

Fish-medusa symbioses have been reported between scyphozoan medusae and fish from nine families: four essentially pelagic fish families (*Carangidae*, *Stromateidae*, *Centrolophidae*, and *Nomeidae*); three relatively demersal families (*Gadidae*, *Girellidae*, and *Centriscidae*); and two abyssal families (*Tetragonuridae* and *Zaproridae*) (Mansueti 1963). The associations often exist for a limited period and may change over time. For example, young harvestfish (*Peprilus alepidotus*) and butterfish (*Poronotus triacanthus*) have both been reported to have a commensal and ectoparasitic existence with the scyphozoan *Chrysaora quinquecirrha* in Chesapeake Bay (Mansueti 1963). Yet in the harvestfish–*Chrysaora* symbiosis, the association is initially commensal during summer, becomes ectoparasitic as the fish feeds upon the host, and finally as its ecological requirements change, the fish becomes non-symbiotic, but continues to feed through autumn as a predator upon jellyfish.

For scyphozoan species found in British waters, commensal associations have been described between medusae of *Cyanea* spp., *Rhizostoma octopus* and *Chrysaora hyscoscella* and gadoid fish (cod, haddock, Norway pout, pollock, saithe and whiting), whereby young fish shelter among the jellyfish tentacles so avoiding predation. In addition, the gadoids may steal prey from the medusa and



feed on crustaceans (Hyperideida) that are parasitic on jellyfish (Russell 1970; Hay et al. 1990; Purcell and Arai 2001). Evidence of this behaviour by young whiting associated with *Rhizostoma octopus* was collected by Nagabhushanam (1959, cited in Russell 1970), who found up to 46 live fish, many with *Hyperia* sp. in their stomachs, among the tentacles of the parasitized medusae (for a summary of results see Table 1.4).

| Date                    | <i>Rhizostoma</i><br>umbrella<br>diameter (mm) | Whiting ( <i>Gadus merlangus</i> )  |                    | <i>Hyperia</i> sp. |                    |
|-------------------------|--|-------------------------------------|--------------------|--------------------|--------------------|
|                         |  | Number                              | Size range<br>(mm) | Number             | Size range<br>(mm) |
| 25/05/57                | 380  | 27                                  | 21-40              | 18                 | 2-6                |
| 29/05/57                | 430  | 46 (+14 in<br>stomach of<br>medusa) | 25-46              | 22                 | 2-18               |
| 17/06/57                | 410  | 11                                  | 30-51              | 16                 | 3-14               |
| 28/05/58                | 340  | 1                                   | 212                | 3                  | 4-10               |
| 28/05/58                | 420  | 2                                   | 21, 25             | 16                 | 4-15               |
| 02/06/58                | 340  | 1                                   | 31                 | 19                 | 2-12               |
| <b>Total<br/>number</b> | 6  | 88                                  | 21-51              | 94                 | 2-18               |

Table 1.4 Reported catches of parasitized *Rhizostoma octopus* in the Irish Sea with live whiting among their tentacles, from Nagabhushanam (1959, cited in Russell 1970). Larger (size not specified) *Hyperia* sp. were generally found on the surface of the medusae while smaller parasites were often within the umbrella canals. Three young cod (*gadus morhua*), one of which had ingested *Hyperia*, were also caught with a *Rhizostoma* during May 1958.

Recent observations of associations between fish and medusae have been provided by analysis of images taken by remotely operated vehicles: evidence of a close symbiotic relationship between the medusa *Stygiomedusa gigantea* and the fish, *Thalassobathia pelagica* has been reported (Drazen and Robison 2004), and Age-0 walleye pollock (*Theragra chalcogramma*) have been observed in association with medusae (up to 30 fish per medusa) of *Chrysaora melanaster* in midwater in the Bering Sea (Brodeur 1998).

A commensal association has also been reported between the mucus-feeding copepod *Paramacrochiron maximum* and the large (bell diameter up to 35 cm) edible medusa *Catostylus mosaicus* of the east Australian and Malay coastal waters (Browne and Kingsford 2005). Up to 5675 copepods were found on the oral arms of *C. mosaicus*. Possible associations between fish and this

particular medusa have been reported for: harvest fish (*Peprilus alepidotus*); bumper fish (*Chloroscombrus chrysurus*); shrimp (*Latreutes anoplonyx*); and horse mackerel (*Trachurus* spp.) (Browne and Kingsford, 2005).

#### **1.10. Predation by medusae on plankton**

Scyphozoans and hydrozoans are generalist predators and the composition of their diet (including crustaceans, ichthyoplankton, chaetognaths and cnidarians) is dependent upon prey availability. Behrends and Schneider (1995) report that *Aurelia aurita* has a predation potential of 10,000 copepods per medusa per day. Jellyfish are capable of intensive, size-selective, predation, which can shift the plankton community composition and affect the interactions between other members of the community. *Aurelia aurita* swims while feeding, using its oral arms and short tentacles to capture prey, and may select passively for small, slow prey (Costello and Colin 2002; Graham and Kroutil 2002; Purcell 2003). At high jellyfish densities, predation on copepods, the main prey of many fish species, can reduce copepod populations and have a knock-on effect for fish populations (Purcell 1997). Both Fancett (1988) and Purcell (1989; 1994) found a positive selection for fish eggs and larvae by scyphomedusae predators, based on a comparison of jellyfish stomach contents and the local prey availability as determined by net hauls. In Port Philip Bay, Australia, Fancett and Jenkins (1988) found that *C. capillata* could directly remove up to 20% of fish eggs and yolk-sac larvae.

Purcell (1997) presented two groups of factors that can affect prey selection, namely encounter and capture events. In general, the number of prey captured by medusae increases directly with prey density, resulting in clearance rates (i.e. the volume of water equivalent to that which would be cleared of zooplankton given typical zooplankton densities and predation rates by jellyfish on zooplankton) that tend to be constant, even at extremely high prey densities (Reeve et al. 1978; Purcell 1992; Purcell and Nemazie 1992, all cited in Purcell 1997, de Lafontaine and Leggett, 1988). Based on *in situ* experimentation in 3.2 m<sup>3</sup> enclosures, de Lafontaine and Leggett (1988) found a type I functional response (a non-satiating linear relationship between prey abundance and consumption by medusae) for *A. aurita* (2.24 to 9.00 cm umbrella diameter) and *C. capillata* (7.54 to 15.00 cm umbrella diameter) preying on yolk-sac larval

capelin (*Mallotus villosus*) even at larval densities exceeding the 400 larvae m<sup>-3</sup> (the mean density found in Bryant's Cove, Newfoundland, Canada). The type I response was unchanged in experiments with or without the presence of alternate zooplankton prey. De Lafontaine and Leggett (1988) hypothesised that the primary regulating mechanism of larval capelin survival would be the shifting in the timing of larval emergence period relative to periods of medusae abundance.

In the Kiel Bight of the Baltic Sea, *Aurelia aurita* medusae may consume up to two thirds of daily secondary production (i.e. herbivorous zooplankton), and therefore exert a controlling influence over the ecosystem (Schneider and Behrends 1994; Behrends and Schneider 1995). Möller (1984) suggested that *A. aurita* in the Kiel Bight was a major factor regulating the abundance and body size of herring yolk-sac larvae during 1981–1983 (Section 4.2).

Medusae have the potential to exert predation pressure on zooplankton that may outstrip the zooplankton production rates, indicating that jellyfish populations may often be food limited (de Lafontaine and Leggett 1988; Båmstedt 1990). In the Black Sea, the major anchovy fishery collapsed after a rise in abundance of the resident jellyfish species (*Aurelia aurita* and *Rhizostoma pulmo*) and an invasion of the ctenophore *Mnemiopsis leidyi* in the late 1980s. It is widely believed that the consumption of zooplankton by the ctenophore, and the consequent depletion of food available for fish, was the principal cause of the collapse of the anchovy (*Engraulis encrasicolus*) stock in the Black Sea (Kideys 2002). However, the long-term decline of the ecosystem during the 1970s and 1980s is attributable to effects of eutrophication (decrease in oxygen, phosphates, silicates, and water transparency) and a possible trophic cascade caused by overexploitation and removal of the top predators (dolphins, Bluefish *Pomatomus saltator*, horse mackerel *Trachurus mediterraneus*, bonito *Sarda sarda*, and mackerel *Scomber scombrus*) (Daskalov 2002). In summary, overfishing of the anchovy stock, in combination with changes in phytoplankton and zooplankton composition, made it possible for *Mnemiopsis leidyi* to compete successfully for food, and also to overwhelm the early life stages of the anchovy stock (Bilio and Niermann 2004). The spread of *Mnemiopsis leidyi* continued into the ecologically sensitive Caspian Sea, where it was first noted in

1999 (Stone 2005). Overfishing and environmental degradation have already crippled the stocks of kilka/anchovy (*Clupeonella engrauliformis*) and the three species of sturgeon found there (Beluga *Huso huso*, Russian/Oscietra *Acipenser gueldenstaedti*, and the Stellate/Sevruga *Acipenser stellatus*) (Stone 2005). As a result of the invasion of *M. leidy*, zooplankton biomass has reportedly reduced tenfold, while phytoplankton have bloomed and Iran's kilka fishery fell from 85,000 tons in 1999 to 15,000 tons in 2004 (Stone 2005).

By 2001, the biomass of *M. leidy* in the Black Sea was reduced to negligible levels by the invasion of a second ctenophore *Beroe ovata*, which preyed almost exclusively upon *M. leidy*. However, this second invader is not able to reproduce in the saltier waters of the Caspian and it is feared that the outbreak of *M. leidy* will persist there indefinitely (Stone 2005).

### 1.11. Ecosystem control

At the simplest level, there are two contrasting hypotheses for ecosystem control (Gliwicz 2002):

- Bottom-up: primary phytoplankton production and nutrient availability control the zooplankton population and thus the higher trophic levels (i.e. fish and other predators) (Reid et al. 1990; Cury and Shannon 2004).
- Top-down: carnivores (including medusae) may exert control over ecosystems through predation on zooplankton, triggering a trophic cascade whereby the phytoplankton population benefits from a reduction in grazing pressure (Lindahl and Hernroth 1983; Carpenter et al. 1985; Verity and Smetacek 1996; Reid et al. 2000).

Schneider and Behrends (1998) studied the effects of gelatinous zooplankton predation on the neritic plankton community in the Kiel Bight. They found a pronounced shift in the zooplankton composition as a result of medusae predation. Herbivorous copepods and raptorial feeders (e.g. *Oithona similis*) were nearly absent in years of high *A. aurita* abundance, and omnivorous species dominated, lowering the grazing pressure on primary producers.

An investigation into nutrient input into the Spanish Mar Menor (a hypersaline coastal lagoon with a surface area of about 135 km<sup>2</sup>), discovered that when nutrient levels increased, planktonic biomass (in the 2 to 1000 µm

diameter size range) decreased (Pérez-Ruzafa et al. 2002). The authors attributed this apparent paradox to the top-down control mechanisms of the ecosystem and suggested that the scyphomedusae, *Rhizostoma pulmo* and *Cotylorhiza tuberculata*, were the responsible agents. The total population of the latter species has been estimated to number 46.98 million individuals, during 1997, with densities of up to 40 per 100 m<sup>3</sup>. These jellyfish grazed heavily on large diatoms, tintinnids, veliger larvae and copepods. Removing the large diatoms from the plankton reduced the uptake of nutrients, and removing the ciliates and copepods reduced the grazing pressure on smaller phytoplankton, allowing them to flourish (Pérez-Ruzafa et al. 2002). In this case, jellyfish appear to have altered the community composition, allowing smaller phytoplankton to dominate when increased nutrient loads alone would lead to dominance by larger cells (Awagin et al. 2000, cited in Pérez-Ruzafa et al. 2002).

Contrasting effects on phytoplankton densities have been shown by mesocosm studies, in which the density of herbivorous copepods was reduced through predation by jellyfish (the hydrozoan *Sarsia gemmifera* and the ctenophore *Bolinopsis infundibulum*) (Stibor et al. 2004). The change in total algal biomass during the experiments depended on the initial algal size distribution: if large algae dominated the community then predation by jellyfish on copepods resulted directly in reduced predation pressure on large algae, therefore the biomass of algae increased as the copepod population reduced; if small algae dominated the phytoplankton initially, then copepods would prey heavily on ciliates, who in turn would prey on small algae, so a reduction of copepods in this circumstance resulted in an increase in ciliates and a decrease in phytoplankton biomass.

It has been suggested that the overfishing of commercial finfish may result in more prey becoming available to unexploited species, such as jellyfish and squid, that may be in competition for prey with the exploited finfish species (Pauly et al. 1998; 2002). A rise in the abundance of jellyfish may also result through a trophic cascade, whereby the food web shifts to produce beneficial conditions for filter and tentacular feeders (Figure 1.3) (Parsons and Lalli 2002; Sommer et al. 2002; Stibor et al. 2004). Once jellyfish become dominant they

may also exert a controlling influence over the ecosystem because they consume the same zooplankton species as are prey for finfish. Since medusae have rapid life cycles and much lower metabolic demands than fish, once the ecosystem has switched it may quickly produce a biomass of jellyfish that exceeds the potential total fish biomass. As jellyfish have few natural predators the environmental conditions will largely control the biomass of these species through bottom-up processes.

### **1.12. Medusae distribution, abundance and biomass**

This section provides background information on the ecology of jellyfish in the locations focused upon in this project: the North Sea (Chapters 2–6) and the northern (i.e. Namibian) Benguela Sea (Chapters 8–9).

#### **1.12.1. Jellyfish in British coastal waters and the North Sea**

Of the four scyphozoan orders (Stauromedusae, Coronatae, Semaestomae, and Rhizostomeae), three (Coronatae, Semaestomae, and Rhizostomeae) occur in the British Isles; however, only the Semaestomae and Rhizostomeae contain species that are resident in British coastal waters (Table 1.2, Russell 1970). In St. Andrews Bay, for example, *Aurelia aurita*, *Cyanea capillata* and *Cyanea lamarckii* medusae are often found, particularly during June, July, and August (McIntosh 1885; 1926; 1927b; pers. obs. 2001-2005, Barnes 1964, cited in Russell 1970). The ephyrae of each species were found in St. Andrews Bay during May (2005) (pers. obs. 2005); however, *A. aurita* have been sighted as early as January (Laverack and Blackler 1974). This supports the expectation of Russell (1970) that ephyrae will appear around the British Isles anytime between January and April with the adult stages appearing during late April to August and then disappearing from coastal waters by late September or early October.

The only major survey of jellyfish abundance in waters of the British Isles was that reported by Hay et al. (1990) for sampling in the North Sea; however, a recent study (2002–2005) in the Welsh Tremadoc and Carmarthen Bays has used aircraft to monitor the abundance of *Rhizostoma octopus* in ‘superaggregations’ (extending over many km at densities of up to 1 per m<sup>3</sup>), which appear to attract leatherback turtles in search of prey (Hays et al. 2003). Since 2002, the Marine

Conservation Society of the U.K. has been coordinating a national survey, whereby volunteers record sightings of jellyfish in British coastal waters throughout the year, with the aim to identify hotspots of jellyfish that may be important areas for turtles.

Hay et al. (1990) identified the distribution and abundance of *Aurelia aurita*, *Cyanea capillata* and *Cyanea lamarckii* in the North Sea using bycatch data from pelagic trawls of 0–group gadoid fish during 1971–1986. A general trend of increasing abundance was found in the late 1970s and early 1980s, with high variability between years. The following observations on the distribution and abundance of jellyfish species were made:

- i. *Aurelia aurita* was the most abundant scyphozoan of the northern North Sea, particularly off the eastern coast of Scotland.
- ii. *Cyanea capillata* medusae were found over a wide distribution, mainly north of 58°N. *Cyanea capillata* was commonly found along the coast, although less so than *A. aurita*. Offshore (i.e. approx. >90 n.mi offshore), however, *C. capillata* was frequently more abundant than either *A. aurita* or *C. lamarckii*.
- iii. *Cyanea lamarckii* was more abundant in the southern than the northern North Sea. The species generally had a coastal distribution, although medusae were found further offshore relative to those of *A. aurita*.
- iv. *Rhizostoma octopus* were common along the continental coast of the southern North Sea.
- v. *Periphylla periphylla* was found in deep water to the west of Scotland.
- vi. *Pelagia noctiluca* medusae were rarely found and were not considered residents of the North Sea.

As the sampling bias of the survey was to the northern North Sea, very few *C. hysoscella* were recorded. Over the survey period the median abundance of medusae and their median size was observed to fluctuate dramatically; the median size of *C. capillata* (between 5 and 25 cm umbrella diameter) and the abundance of *Aurelia aurita* (between 1 and 22000 medusae per 1 hour trawl) were particularly variable. Catches of *A. aurita* were found frequently at >1000

medusae per hour, while those of *C. capillata* seldom exceeded 100 individuals per hour. However, regional variation did exist: north of Scotland and east of Shetland, the biomass of *C. capillata* was much greater than that of *A. aurita*, while the opposite prevailed east of Scotland. Hay et al. (1999) stated that, in some years, distributions of medusae off the eastern coast of Scotland and south of 58°N were found roughly parallel to the coast. They hypothesized that these concentrations were attributable to the weak frontal systems that develop between vertically mixed and stratified waters in that area (Hay et al. 1990).

### 1.12.2. Jellyfish in the northern Benguela Sea

There are twenty species of medusae in the Namibian Benguela Sea, the three most abundant species of which being the scyphozoan *Chrysaora hysoscella* (also found west of Scotland and in the English Channel), the hydrozoan *Aequorea aequorea*, and the tiny transparent trachymedusan *Lirope tetraphylla* (Pagès 1992). The two larger species were first reported in the 1970s (Venter 1988; Fearon et al. 1991 and references therein) and their abundant populations have persisted, becoming of concern to local fishermen and diamond mining operators during the last few decades (Brierley et al. 2001). Pagès (1992) identified three planktonic assemblages in which jellyfish were found namely:

1. Coastal/upwelling: cold, weakly saline surface waters carrying a high concentration of ephyrae and juvenile *Chrysaora hysoscella*.
2. Oceanic water: relatively warm, highly saline water, where *Lirope tetraphylla* are most abundant.
3. Shelf fauna: intermediate waters from mixing of assemblages 1 and 2 and supporting *Aequorea aequorea* and adult *Chrysaora hysoscella*.

Sparks et al. (2001), in agreement with Pagès (1992), reported a spatial segregation between *A. aequorea* and *C. hysoscella*. From surface observations, *A. aequorea* was found to be more abundant offshore than *C. hysoscella*, which occurred along the shelf and inshore in great numbers relative to *A. aequorea*. Although both *A. aequorea* and *C. hysoscella* appear to be somewhat exclusive in their relative distributions, as a unit they occur across the shelf to exert a consistently high predation pressure upon the zooplankton. There is anecdotal evidence to suggest that this was not the case prior to the 1970s (Hart and Currie 1960; Kollmer 1964; Stander and de Decker 1969), and that these jellyfish have



become established as a major component of the Benguelan ecosystem over a relatively short period of time due to the overexploitation of fish stocks in the region and subsequent increase in prey for jellyfish (Venter 1988; Fearon et al. 1991). The diets of *C. hysoscella* (Scyphozoa) and *A. aequorea* (Hydrozoa) may differ through passive selection; in Prince William Sound, Alaska, for example, *A. aequorea* showed relatively weak but significantly negative selection for copepods at 45% of the stations analysed, and significantly positive selection for larvaceans at 20% of the stations (Purcell 2003). The same study found that selection by *Aurelia labiata* (Scyphozoa) was significantly positive for small copepods at 60% of the stations. Jellyfish consume an enormous biomass of zooplankton and feed on similar items as do commercially important pelagic fish, therefore knowledge of the distribution and dynamics of the jellyfish is essential to understand the ecosystem and ultimately to manage fisheries and other exploitative activities.

As the recorded increase in jellyfish and Cape horse mackerel (*Trachurus trachurus capensis*) abundance off Namibia appears to have coincided with a period of decline of commercial catches of sardine (*Sardinops ocellatus*, “pilchard”) and the collapse of anchovy (*Engraulis capensis*) stocks (Shannon et al. 1992; Boyer and Hampton 2001), these phenomena might be linked (Brierley et al. 2001). Despite the potential ecological and economic importance of jellyfish in Namibian waters, relatively little of their biology or population dynamics is known (Gibbons et al. 1992; Buecher et al. 2001; Sparks et al. 2001; Heymans et al. 2004). Some information on the distribution and abundance of *A. aequorea* and *C. hysoscella* is available from BONGO net surveys (Fearon et al. 1991; Pagès and Gili 1991; Pagès 1992), but these studies used small nets (50–57 cm mouth opening) that are unlikely to provide unbiased data, particularly for adult *C. hysoscella* that may attain umbrella diameters exceeding 50 cm. Fearon et al. (1991) provide the first estimates of the total biomass of *Chrysaora hysoscella* ( $29.7 \times 10^6$  tons) and *Aequorea aequorea* ( $10.8 \times 10^6$  tons) in the northern Benguela ( $17^{\circ}15' - 24^{\circ}15' S$ , from 0 to 70 miles offshore) based on sampling of the upper 50 m only during January–March 1982-1989.

### **1.13. Changing populations of gelatinous zooplankton**

Jellyfish abundance is increasing in numerous marine ecosystems worldwide (Graham 2001; Mills 2001; Sparks et al. 2001). Medusae reproduce rapidly so that their populations are able quickly and opportunistically to exploit newly available environmental niches (Alldredge 1983, cited in Purcell and Arai 2001), which may be created through anthropogenic disturbance (Arai 2001), increased fishing pressure (Mills 1995; Brierley et al. 2001; Cury et al. 2005), climate change (Chapters 2 and 3)(Goy et al. 1989; Brodeur et al. 1999; Sullivan et al. 2001; Purcell 2005) and/or regime shift (Brodeur et al. 2002; Pérez-Ruzafa et al. 2002; Hunt and Drinkwater 2005).

Blooms of gelatinous zooplankton (i.e. transient, often periodic, localised and highly dense aggregations) occur seasonally in the natural environment and are prominent during the summer months. Sumich (2001, cited in Benovic and Lucic 2001) has defined a planktonic bloom as “*a dense concentration of plankton individuals which occurs in response to optimum growth conditions*”. However, in many regions where jellyfish blooms are a regular occurrence, sustained interannual increases in medusa biomass have been reported (Table 1.5). Invasions of non-indigenous species (Cnidaria and Ctenophora), resulting in jellyfish ‘outbreaks’ (i.e. unusual blooms of greater biomass than would normally occur in the ecosystem), have had dramatic effects on ecosystem functioning (Table 1.6).

| Region                   | Increasing species  | Comment  | Reference  |
|--------------------------|---|--|--|
| North Sea                | <i>Aurelia aurita</i><br><i>Cyanea capillata</i><br><i>Cyanea lamarckii</i>   | General trend of increasing abundance, from the late 1970s to the early 80s linked to climate variability.   | Hay et al. (1990), Chapters 2, 3 and 4.            |
| Mediterranean            | <i>Pelagia noctiluca</i><br><i>Liriope tetraphylla</i><br><i>Solmundella bitentaculata</i><br><i>Rhopalonema velatum</i><br><i>Pleurobrachia rhodopis</i> | Increasing overall abundance from 1966 to 1999 linked to climate variability.  | Molinero et al. (2005).                            |
| Northern Benguela        | <i>Aequorea aequorea</i><br><i>Chrysaora hysoscella</i>   | Speculated rise since early 1970s. Negative impact on diamond mining and fisheries.  | Sparks et al. (2001).                              |
| Yangtze Estuary<br>Japan | <i>Cyanea capillata</i><br><i>Sanderia malayensis</i>   | Population rise followed damming of the Yangtze River in 2003. Problematic for fishermen. In contrast, the edible species, <i>Rhopilema esculenta</i> has been depleted through overfishing. | Xian et al. (2005).                                |
| Tokyo Bay<br>Japan       | <i>Aurelia aurita</i>   | Population rise began in the 1960s following a shift in zooplankton composition, possibly due to eutrophication.   | Omori et al. (1995).                               |
| Bering Sea               | <i>Aequorea aequorea</i><br><i>Cyanea capillata</i><br><i>Chrysaora melanaster</i>  | Ten-fold increase in biomass in the area of an important fishery between 1990-2000. Fall from 2001 to 2003 but still at greater biomass than during 1975-1990                                | Brodeur et al. (2002), Hunt and Drinkwater (2005). |
| Black Sea                | <i>Rhizostoma pulmo</i><br><i>Aurelia aurita</i>  | Overfishing (1970s) followed by eutrophication (1980s).  | Kideys and Romanova (2001).                        |
| Northern Gulf of Mexico  | <i>Aurelia aurita</i><br><i>Chrysaora quinquecirrha</i>   | Increase in abundance from 1985 to 1997. Threat to fisheries, rise linked to climate change.   | Graham (2001).                                     |

Table 1.5 Examples of long-term rises in jellyfish (Scyphozoa and Hydrozoa) abundance.

| Region  | Invasive species   | Comment  | Reference   |
|---|--|--|---|
| Mediterranean                                     | Scyphozoa<br><i>Rhopileme nomadica</i><br><i>Phyllorhiza punctata</i>                        | Environmental hazard to bathers and fishermen.   | Galil et al. (1990), Lotan et al. (1994), Kideys and Gucu (1995), Pérez-Ruzafa et al. (2002). |
| San Francisco Bay and Chesapeake Bay (N. America) | Hydrozoa<br><i>Blackfordia virginica</i><br><i>Maeotias marginata</i><br><i>Moerisia sp.</i> | Effect on ecosystem unknown.   | Mills and Rees (2000), Rees and Gershwin (2000).  |
| Northern Gulf of Mexico                           | Scyphozoa<br><i>Phyllorhiza punctata</i>   | Up to \$10M lost by shrimp fishermen in 2000, through clogging of nets by medusae. Jellyfish also consumed anchovy eggs. | Graham et al. (2003).   |
| The Black Sea                                     | Ctenophora<br><i>Mnemiopsis leidyi</i><br>followed by<br><i>Beroë ovata</i>                  | Population rise of <i>M. leidyi</i> with subsequent collapse of commercial fishery.                                      | Kideys et al. (2000), Weisse and Gomoiu (2000), Kideys and Romanova (2001).                   |

Table 1.6 Examples of recent invasions by gelatinous zooplankton.

With ever declining world fish stocks (Hutchings 2000; Pauly et al. 2002) and concomitant increases in jellyfishes (Tables 1.5 and 1.6), it is important to be able to understand the mechanisms of ecosystem variability (Brodeur et al. 1999; O'Brien et al. 2000; Attrill and Power 2002; Hunt and Drinkwater 2005). Many hypotheses for increasing jellyfish abundance exist (reviewed by Mills 2001; Purcell 2005):

a) Overfishing: Many medusae and fish species share similar diets (Purcell 1997; Purcell and Arai 2001); therefore, over-exploitation of fisheries may release medusae from the population control previously imposed through competition with fish, thus raising the carrying capacity for jellyfish in the ecosystem (Brodeur et al. 2002; Cury et al. 2005). Mills (1995) presents evidence that in overfished or disturbed ecosystems energy may be transferred from fish production to the production of Cnidaria and Ctenophora (Parsons and Lalli

2002; Sommer et al. 2002). This transfer may explain the tenfold rise in gelatinous zooplankton biomass observed over a single decade (1990–2000) in the Bering Sea, where the biomass of forage fishes (juvenile herring *C. pallasi*, Age-1 pollock *Theragra chalcogramma*, and capelin *Mallotus villosus*) has decreased fivefold (Brodeur et al. 2002). Jellyfish may directly inhibit fisheries recovery due to high consumption rates of copepods and fish larvae/eggs (Purcell 2003). However, some fish, such as 0–group whiting (Hay et al. 1990), seek refuge amongst the tentacles of *C. capillata* and may benefit from their presence.

- b) Zooplankton composition change: e.g. In Tokyo Bay, the dominant copepod species shifted (during the 1960s) from the relatively large *Acartia omori* and *Paracalanus spp.* to the smaller *Oithona davisae* (Omori et al. 1995). Omori et al. (1995) suggested that this might have improved conditions for *A. aurita* since planktivorous fish find the smaller copepod species harder to catch. In many seas and oceans, particularly in coastal habitats, activities such as fishing, mining, sewage treatment, shipping and tourism are degrading the ecosystem and altering the relative zooplankton composition. As a result, some jellyfish populations may benefit in the altered state, sometimes at the expense of other gelatinous species and/or local fisheries.
- c) Eutrophication: Many eutrophic marine waters have been found to contain high abundance of jellyfish, although eutrophication is rarely the only factor causing change in jellyfish populations (reviewed by Arai 2001). Sommer et al. (2002) suggested that at low nutrient levels, or where there is a high supply of N and P, but a low supply of Si, energy flow will be diverted, through changes in the phytoplankton, from finfish to jellyfish production. Increased nutrient inputs to the Black Sea during the 1970s and 1980s modified the ecosystem, producing favourable conditions for a jellyfish ‘bloom’ and poor conditions for finfish (see Section 1.9). Damming of the Yangtze River has altered the conditions downstream, particularly in the estuary, such that the fisheries bycatch of *Cyanea capillata* in the Yangtze estuary increased from <1% of the total catch in

1998 to 85% in 2003, while in 2004 *Sanderia malayensis* bloomed for the first time composing 98% of the total catch.

- d) Climate Change: Outbreaks of *Pelagia noctiluca* in the Mediterranean Sea have occurred at intervals of about 12 years over the past 200 years and have been linked to a combination of low rainfall, high temperature and high atmospheric pressure from May to August (Goy et al. 1989). Jellyfish (*Aequorea aequorea*, *Cyanea capillata*, and *Chrysaora melanaster*) biomass increased dramatically in the Bering Sea between the 1980s and the 1990s, concurrent with changes in atmospheric pressure patterns reflected in the North Pacific Decadal Oscillation Index (Brodeur et al. 1999). These atmospheric changes resulted in an alteration in the extent and persistence of sea-ice cover. However, a direct mechanism linking the jellyfish aggregations to the sea-ice remains unclear. Brodeur et al. (2002) proposed that the increase in jellyfish might be due to a release from competition with planktivorous forage fishes. They established that a climatic 'regime shift' occurred in 1976, with temperature being cooler prior to the shift. In the cooler years before the shift they hypothesized that competition may have been more important than predation in ecosystem control, and suggested that the jellyfish could outcompete the fish. In the warmer situation, after 1975, abundant food levels then facilitated rapid population growth of the already dominant jellyfish. Since 2001 the jellyfish population has crashed with no apparent explanation; however, the last published biomass estimate (for the year 2003) was circa  $60 \times 10^9$  tonnes, greater than any estimate between 1975 and 1990 (no sampling between 1976 and 1978) (Hunt and Drinkwater 2005).

Despite increases in abundance, in some locations jellyfish diversity has been found to be falling, perhaps indicating that some species may outcompete others when ecosystems are disturbed. Benovic et al. (1987) report the loss of 31 species of hydromedusae, from an initial total of 42 known species in the northern Adriatic between 1910-84. Buecher and Gibbons (2000) noted a trend showing the loss of half the gelatinous fauna in St. Helena Bay (West coast of S.

Africa) over the years 1988-97. Mills (1995) also reported a population and biomass decrease of *Aequorea victoria* in and near Friday Harbour, Washington.

#### **1.14. Local jellyfish aggregations and major factors affecting them**

Jellyfish are often found in dense layers that vary from a few centimetres to hundreds of metres in depth. The horizontal dimension may be tens of metres to hundreds of kilometres (Graham et al. 2001). Purcell and Arai (2001) and Purcell et al. (2000, cited in Graham et al. 2001) suggested that large aggregations might be an effective defence against predation by other medusae and fish. However, dense aggregations of *Rhizostoma octopus* in British coastal waters do attract leatherback turtles that migrate from the Atlantic Ocean in order to feed on these medusae (Hays et al. 2003). Highly concentrated aggregations of jellyfish may also exclude potential competitors for prey, perhaps through exudation of chemical ‘scents’ or unfired nematocysts (Bullard and Hay 2002). Physical gradients and discontinuities have been implicated in affecting aggregations of gelatinous zooplankton (Graham et al. 2001). Gradients and variation of physical properties in the sea are far more pronounced in the vertical dimension than the horizontal. The following variables are key:

- a) Light:
  - i. Diurnal Vertical Migrations (DVM), which often correlate with changes in ambient illumination, have been documented for scyphomedusae (Yasuda 1973; Mackie et al. 1981, both cited in Graham et al. 2001).
  - ii. The ‘sun-compass’ hypothesis for oriented swimming is supported by *Aurelia sp.* (Hamner et al. 1994).
- b) Winds: e.g. After several days of strong winds, large aggregations of medusae form near to coasts: in St Andrews Bay *Aurelia aurita* are often found (personal observations 2003 and 2004), while in the Mediterranean Sea *Pelagia noctiluca* reaches typical offshore densities of about 20 per m<sup>3</sup> (1984–1985), with near–shore accumulations of up to 600 medusae per m<sup>3</sup> (Zavodnik 1987). Jellyfish may also become

trapped within Langmuir circulation cells, which develop under sustained winds of between 2 and 10 ms<sup>-1</sup> (Kingsford et al. 1991, cited in Graham et al. 2001).

- c) Local tidal fronts: Coyle and Cooney (1993, cited in Graham et al. 2001) conducted an acoustic study of zooplankton abundance and found Cnidarian assemblages dominated around surface frontal features. In addition to increased fertilization, accumulation of medusae within near-shore fronts may aid in the retention of aggregations close to shore and near the hard substrata required for successful larval settlement (Purcell et al. 2000).
- d) Temperature: Jellyfish may aggregate in warmer waters (e.g. at the surface) to take advantage of the favourable conditions for growth and feeding. Graham (1994, cited in Graham et al. 2001) showed that *Chrysaora fuscescens* medusae exhibited layering along a thermocline. However, *C. hysoscella* was able to swim unimpeded through steep thermal gradients (Pagès and Gili 1991).
- e) Haloclines: May result in the passive accumulation of small jellyfish (Arai 1997, cited in Graham et al. 2001). However, *in situ* observations have shown larger medusae transiting sharp haloclines without difficulty (Graham et al. 2001).
- f) Topography: e.g. the entrainment of upwelled water by coastal prominences in northern Monterey Bay, California, results in high jellyfish abundance (Graham et al. 1992, cited in Graham et al. 2001).

### **1.15. Jellyfish blooms: economic and social issues**

Native jellyfish species have been observed to be increasing in abundance and/or in importance to local economic activities.

#### **1.15.1. Detrimental impacts**

Blooms of jellyfish may have a detrimental effect on fisheries, tourism, power stations and the Namibian inshore diamond mining industry. For example:

- Jellyfish may impede fishery activities through clogging and bursting of purse-seine and trawl nets (*Cyanea sp.* (Kramp 1937, cited in Russell 1970), *Rhizostoma sp.* (Netchaeff and Neu 1940, cited in Russell 1970),



*Aurelia* sp. (Hela 1951, cited in Russell 1970), *Chrysaora hysoscella* and *Aequorea aequorea* (Venter 1988; Brierley et al. 2001), *Phyllorhiza punctata* (Graham et al. 2003)).

- Gelatinous predators may affect fish stocks, either directly through predation on fish larvae or indirectly through competition for food resources (Möller 1984; Fearon et al. 1991; Purcell and Arai 2001).
- Abundant medusae may deter or sting bathers (Russell 1970 and references therein), therefore jellyfish may be detrimental to tourism (CIESM 2001).
- Dense jellyfish blooms in Japan (Matsueda 1969), the Baltic (Möller 1980) and the Philippines (The Economist, Dec 18, 1999, pp36-37) have resulted in unexpected shutdowns of power stations due to medusae clogging seawater intake screens and compromising the power plants' coolant mechanisms (Russell 1970 and references therein).
- The Namibian inshore diamond mining industry has been affected by the jellyfish *Chrysaora hysoscella* and *Aequorea aequorea*, which block the suction devices used to mine alluvial sediments (Brierley et al. 2001).

### 1.15.2. Food industry and mangement of jellyfish stocks

Jellyfish are largely composed of water (between 75% and 99%) with the remainder comprising mainly protein, of which the edible component is largely collagen, and some lipid (Nagai et al. 1999). Some species of jellyfish are commercially harvested and many of the order Rhizostomeae (including *Rhizostoma octopus*) are edible once dried (Table 1.7) (Ozer and Celikkale 2001). The largest market for jellyfish is to be found in Southeast Asia, where the average annual catch of jellyfish between 1988 and 1999 was estimated to be  $\approx$  169 000 tonnes in wet weight, approximately half of the worldwide catch ( $\approx$  321 000 tonnes) (Omori and Nakano 2001). However, non-asian fisheries do exist: in the U.S. *Stomolophus meleagris* is landed and much of the catch is exported to Asia (Hsieh et al. 2001), while *Catostylus mosaicus* is commercially harvested in New South Wales, Australia.

Jellyfish stocks may be vulnerable to intensive fishing because most species are short-lived (<1 year), highly fecund, with considerable interannual fluctuations in abundance and often a large proportion of the stock is aggregated. This vulnerability poses great problems for managers, especially given that the value of jellyfish fisheries is often low compared with other fisheries (e.g. fishes, prawns and lobsters). For example, overfishing of *Rhopilema esculenta* in the Yangtze Estuary, coupled with local environmental change (possibly a result of the operation of the Three Gorges Reservoir), has resulted in the gradual replacement of the edible species by the inedible *Cyanea capillata* (Xian et al. 2005). To reduce the risk of overexploitation of jellyfish fisheries it has been proposed (Kingsford et al. 2000; Pitt and Kingsford 2000) that

- geographic entities (such as estuarine populations) be treated as whole stocks until proved otherwise
- fisheries be based only on the known biomass of medusae: i.e. it should not be assumed that perennial benthic reserves of polyps and podocysts will buffer over-exploitation.

| <b>Family</b>   | <b>Species</b>                     |
|-----------------|------------------------------------|
| Cepheidae       | <i>Cephea cephea</i>               |
|                 | <i>Catostylus mosaicus</i>         |
| Catostylidae    | <i>Crambione mastigophora</i>      |
|                 | <i>Crambionella orsisi</i>         |
| Lobonematidae   | <i>Lobonema smithii</i>            |
|                 | <i>Lobonemoides gracilis</i>       |
| Stomolophidae   | <i>Stomolophus meleagris</i>       |
|                 | <i>Rhizostoma octopus (=pulmo)</i> |
| Rhizostomatidae | <i>Rhopilema esculentum</i>        |
|                 | <i>Rhopilema hispidum</i>          |
|                 | <i>Neopilema nomurai</i>           |

Table 1.7 Identified species of edible (Scyphozoa, Rhizostomae) jellyfish in the world (Omori and Nakano 2001).

### 1.16. Conclusion

Jellyfish are able to bloom rapidly in abundance in response to favourable environmental conditions; these dense and extensive aggregations often hinder

coastal fisheries, diamond mining, and power generation operations. However, jellyfish may also be harvested and aggregations of large medusae may benefit fish through commensal association or even as a food source. The rapid development and complex life cycle of jellyfish allows these species to rapidly colonise newly available niches that may present themselves through the effects of overexploitation, pollution, eutrophication or the transport of jellyfish to new regions. Once dominant in a locality, jellyfish are able to exert a controlling influence on the ecosystem through high rates of predation on zooplankton. Relatively few predators consume medusae and therefore jellyfish are often resource limited. Jellyfish populations are, however, regulated by environmental influences (e.g. salinity, temperature, and stratification) and climatic changes have been proposed to influence the abundance of medusae. Increases in jellyfish biomass have been recorded in many locations and yet, despite their ecological importance, relatively little is known about their biology. For example: the link between climatic variables and *Pelagia noctiluca* abundance in the Mediterranean may be replicated by populations of jellyfish in other localities; the high predation rate of jellyfish on zooplankton have been suggested to influence the recruitment of fish populations, yet few studies have tested this impact statistically. The lack of research is partially attributable to the difficulties in sampling gelatinous organisms by traditional plankton netting techniques, which either damage the fragile animals or become clogged with them, but also due to a general lack of interest from the scientific community. Despite an extensive 15-year dataset of jellyfish abundances in the central and northern North Sea, little research has been focused on the ecological importance of these medusae there. I have taken this dataset and through statistical analyses I have studied: the effect of climatic fluctuations, as encompassed by the North Atlantic Oscillation Index, on jellyfish abundance (Chapters 2 and 3); the effect of oceanographic influences on the distribution of jellyfish in the North Sea (Chapter 4); the possible detrimental relationship between herring recruitment and *Aurelia aurita* abundance (Chapter 5); and the commensal relationship between gadoids and *Cyanea* spp. (Chapter 6). One major difficulty still facing jellyfish ecologists is the quantitative sampling of jellyfish over wide-ranging areas. So, in Chapter 7, I review the recent work in

the field of acoustics that has given rise to the opportunity for *in situ* sampling of medusae. I develop this technique in Chapter 8 in order to facilitate the world's first large-scale acoustic survey of jellyfish biomass the Benguela Sea (Chapter 9).

## Chapter 2

### Fluctuating abundance of medusae in the North Sea and hydroclimatic change

*“Due to limited data sets, there is unfortunately little statistical evidence firmly linking gelatinous massive events with climatic fluctuations. It will be most interesting to monitor the sensitivity of gelatinous outbreaks to global climatic change in years to come; such massive events may reveal pluri-annual trends in the state of the global environment.” (CIESM 2001)*

The work described here has been published as:

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I estimate that I contributed 75 % of the total effort towards the paper, which can be broken down into the following five equally weighted areas: Data collection/preparation 0 %, the jellyfish data were gathered by SJH and others at Marlab and the climate data is publicly available; Inspiration 100 %, which developed naturally from my literature review and previous NAO-related study during my M.Res; Analysis 90 %, where the remainder is attributable to suggestions from ASB; Conclusions 100 %; Publication 85 %, the paper was written by me but reviewed by ASB.

## **2. Fluctuating abundance of medusae in the North Sea and hydroclimatic change**

### **2.1. Abstract**

Jellyfish are important predators of zooplankton and may impact upon fish recruitment both directly (top-down control, see Section 1.10) and indirectly (through competition). Hydroclimatic forcing may be an important factor influencing the abundance of gelatinous zooplankton and thus may modulate the scale of any ecosystem impact by jellyfish. Abundances of *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* medusae (Scyphozoa) in the North Sea are considered here in relation to large-scale interannual climatic change, as quantified by the North Atlantic Oscillation Index (NAOI).

### **2.2. Introduction**

The seasonal bloom of jellyfish medusae is a characteristic of many marine environments, but there is also great interannual variability in medusa abundance. Environmental variation has been suggested to affect both the abundance (Goy et al. 1989) and distribution (Graham et al. 2001) of jellyfish and it has been shown that food availability, light, stratification, salinity and temperature are important to the strobilation of the scyphistomae and the survival of the medusae (Russell 1970; Omori et al. 1995; Lucas 2001). When conditions are favourable, the biomass of jellyfish may rise to unexpectedly high levels; for example, the population of *Aurelia aurita* in the Black Sea rose from a typical biomass of tens of millions of tons to a estimated peak of 300-500 million tons in the late 1980s (Mills 2001).

The North Sea is highly dependent on oceanic inflow for its supply of nutrients (Skogen et al. 2004) and, since the rate and composition of inflowing water has been linked to atmospheric variability (Becker and Pauly 1996; Planque and Taylor 1998), it is reasonable to assume that the suitability of the North Sea environment for a jellyfish bloom may be governed, at least to some extent, by climatic variability. The North Atlantic Oscillation (NAO) is the dominant mode of recurrent atmospheric variability over the North Atlantic and contributes greatly to the variability in the weather system over Europe and the North Sea. The NAO has been shown to affect both marine and terrestrial

systems (Beaugrand et al. 2000; Ottersen et al. 2001; Reid et al. 2001) and is quantified by an Index (NAOI) generated from the mean wintertime (December–March) difference in sea level pressure (SLP) between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (Figure 2.1) (Hurrell et al. 2003). The phase of the NAO (high/low) alters the prevailing wind field over northern Europe and influences atmospheric variables (i.e. wind speed and direction, air temperature, heat and moisture transport, and precipitation), leading to changes in sea temperature, salinity, river run-off, vertical mixing, and oceanic circulation. These factors, in turn, influence nutrient levels available for phytoplankton growth and zooplankton production (Drinkwater et al. 2003). In the period 1977 to 1979 the NAO was in a low phase (strongly negative index) and the North Sea suffered the coldest winters of the latter 20th century. This same period saw high abundances of scyphomedusae (*Aurelia aurita*, *Cyanea capillata*, and *C. lamarckii*) in the North Sea (Hay et al. 1990).

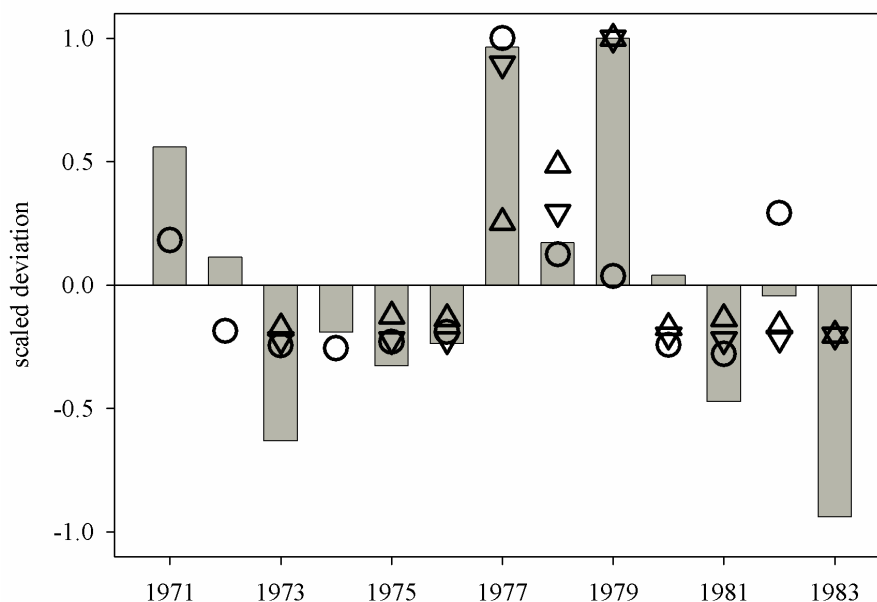


Figure 2.1 The normalized North Atlantic Oscillation Index (NAOI) (December - March) Index (bars) and jellyfish abundance in the North Sea (*Aurelia aurita*: triangles down - West of Northern Denmark and circles - East of Scotland, *Cyanea lamarckii*: triangles up - West of Northern Denmark). The NAO Index data was scaled and inverted for ease of visual interpretation by dividing by the minimum value of the time-series. The species abundance data was normalised by subtracting the mean and dividing by the maximum value of the remaining points for each series.

### 2.3. Methods

Jellyfish abundance data were collected over 15 years (1971-86, not 1984) during the routine summer ICES International 0-group Gadoid Surveys of the North Sea using the International Young Gadoid Pelagic Trawl (IYGPT) (Hay et al. 1990). Every year, trawls were conducted during June and July and for the years 1971 and 1972 additional hauls were made in August. The maximum number of trawls made in any one year was 215 (in 1979) and the minimum was 43 (in both 1985 and 1986). Jellyfish were a bycatch of these surveys. From 2,030 IYGPT trawls throughout the North Sea in this period, more than 430,000 jellyfish were caught, identified and measured. Three species of jellyfish, *A. aurita*, *C. lamarckii* and *C. capillata*, were particularly abundant. The IYGPT had mesh sizes of 100 mm in wings, bosom and belly, tapering through intermediate mesh size to 10 mm knotless meshing in the extension piece and codend. The mouth opening of the net was approx. 14 m<sup>2</sup>. When fished for one hour at a maximum speed of 2.5 knots, about 65,000 m<sup>3</sup> of water was filtered assuming 100% filtration efficiency (Hay et al. 1990).

The trawl was fished for one hour in a standard depth profile. For the first third (0-20 mins) of the trawl duration the net was fished close to the seabed. The net was then hauled to mid-water, or thermocline depth where known, and fished for a further 20 mins. The third period of the trawl was fished close to the surface (5-10 m). In depths >150 m, 125 m was taken as the bottom depth and in depths <30 m only the bottom and surface were fished for 30 mins each (Hay et al. 1990). Although the catches of jellyfish will give conservative estimates of abundance due to the variable mesh sizes and the variable sizes of jellyfish, and the stepped vertical haul profile may also lead to bias in estimations (Hay et al. 1990), the same method was used throughout the survey (leading to internal consistency) and a wide length range (1 to 47 cm) of jellyfish was present in the samples.

Hay et al. (1990) identified four areas of the North Sea (Figure 2.2) that were representative of the major areas of jellyfish abundance, however the regions were not sampled uniformly. The regions were sampled as follows: East of Shetland (ESh) 1971 to 1986 not 1984 (14 years); North of Scotland (NoS) in 1974 and from 1976 to 1986 excluding 1984 (11 years); East of Scotland (EoS)



from 1971 to 1983 (13 years) and the region West of Northern Denmark (WND) was sampled in 1972 and from 1975 to 1983 (10 years).

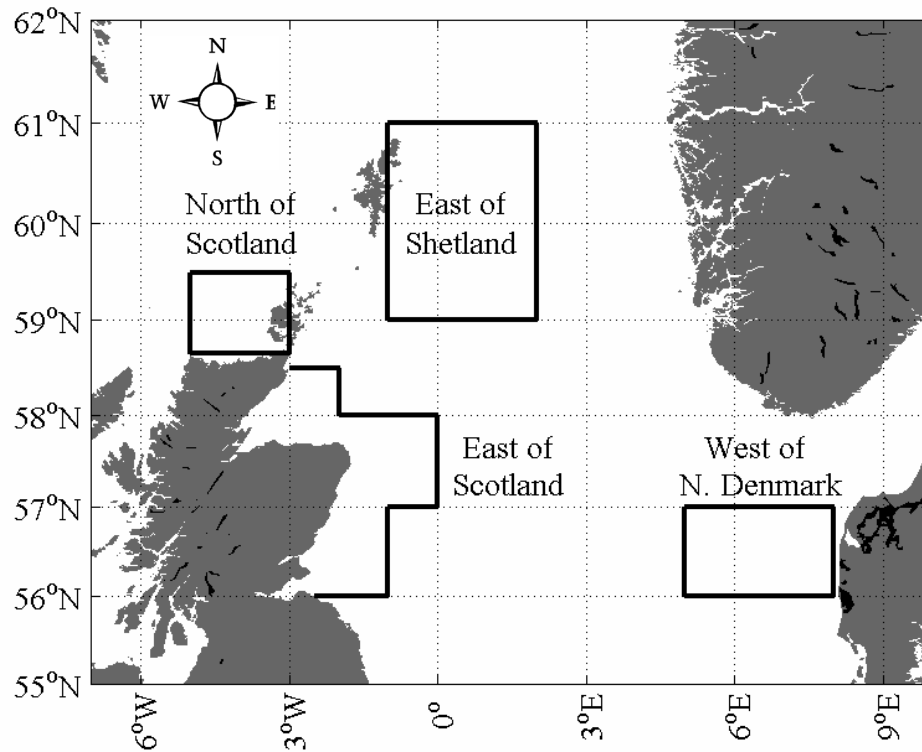


Figure 2.2 Map showing the four survey areas in the North Sea.

To test for links between jellyfish abundance and environmental variables, I investigated data for each species in each area separately through regression analysis. The winter (December–March) NAOI was obtained from the National Center for Atmospheric Research, Climate and Global Dynamics Division, Boulder, CO, USA. Where necessary, medusa abundance data were natural logarithm transformed to normalize the variance of the distributions prior to further statistical analyses. Medusa abundance and the NAOI were also assessed for linear temporal trends, the significance of which was judged at the 0.05 level with a standard Student's *t*-test of the estimated slope parameter. Linear trends were removed in order to compare interannual variability between time series. Linear regressions of abundance data against the NAOI were made, for each species in each area, to compute models of the form:

$$y_t = \beta_0 + \beta_1 x_t + e_t \quad (1)$$

where  $y_t$  was the natural logarithm of the medusa abundance value in year  $t$ ,  $x_t$  was the NAOI in year  $t$ ,  $e_t$  was an error term with unit variance and zero mean, and  $\beta_0$  and  $\beta_1$  were the intercept and slope parameters estimated using linear regression. Parameter significances for all models were assessed using a Student's  $t$ -test at the 0.05 level to minimize corresponding Type II errors. The model assumptions (linearity, homogeneity of variance, normality, and independence of residuals) were tested following procedures outlined in Krzanowski (1998). The Durbin–Watson (DW) statistic was used to assess residuals for first-order autocorrelation; the Breusch–Godfrey test was used for higher-order serial correlation; and the Shapiro–Wilk test was used to assess normality. Outliers were assessed using the mean shift outlier model: the largest absolute residual was tested using the  $t$ -distribution and the Bonferroni correction at the 0.05 significance level (Fox 1997).

## 2.4. Results

85% of all *A. aurita* and 32% of *C. lamarckii* medusae were caught in the region East of Scotland (EoS). However, per trawl, *C. lamarckii* was most abundant (300 medusae per trawl) West of Northern Denmark (WND), (Figure 2.3). *Cyanea capillata* was most abundant North of Scotland (NoS, 50 medusae per trawl). None of the species was abundant East of Shetland (all species <50 medusae per trawl).

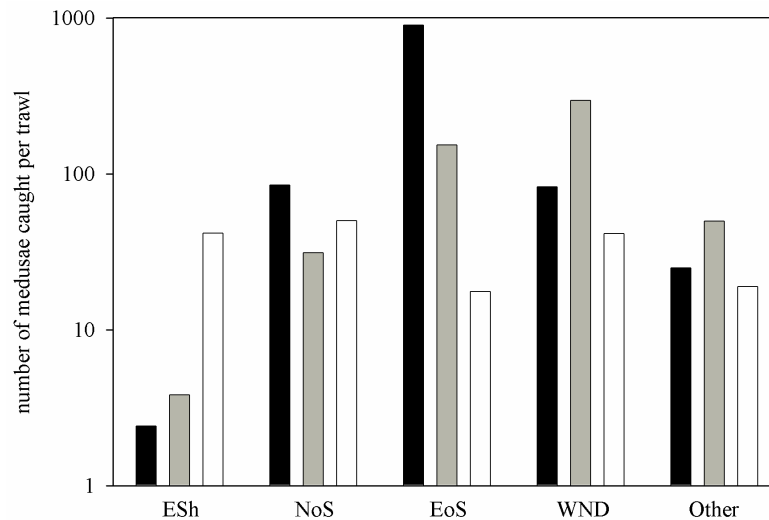


Figure 2.3 Jellyfish catch per trawl by region: *Aurelia aurita* (black bars), *Cyanea lamarckii* (grey bars) and *C. capillata* (white bars).

The  $\ln(\text{median abundance})$  (medusae caught per hour), as reported by Hay et al. (1990), of *A. aurita* significantly correlated with that of *C. lamarckii* in all regions analysed (WND,  $R^2 = 0.58$   $P = 0.011$   $N = 10$ ; EoS,  $R^2 = 0.34$   $P = 0.037$   $N = 13$ ; NoS,  $R^2 = 0.44$   $P = 0.026$   $N = 11$ ). One significant correlation was found between the regions EoS and WND for *A. aurita*  $\ln(\text{median abundances})$  ( $R^2 = 0.44$   $P = 0.048$   $N = 9$ ), where one outlier was identified and removed (year 1983, Bonferroni corrected  $P = 0.011$   $N = 10$ ). When the outlier year was included, the correlation between abundances failed the homogeneity of variance test. No other significant correlations ( $P < 0.10$ ) between medusae abundances were found.

The  $\ln(\text{median})$  medusa abundance during June to August in the North Sea was inversely related with the preceding December–March NAOI for both *A. aurita* (WND,  $R^2 = 0.70$   $P = 0.003$   $N = 10$  Figure 2.4A; EoS,  $R^2 = 0.53$   $P = 0.008$   $N = 12$  Figure 2.4B) and *C. lamarckii* species (WND,  $R^2 = 0.74$   $P = 0.002$   $N = 10$  Figure 2.4C). For *A. aurita* catches, in the EoS region only, the abundance value for the year 1983 was identified again as an outlier and removed (Bonferroni corrected  $P = 0.070$   $N = 13$ ). When the outlier was included, the regression of *A. aurita* abundance against the NAOI was not significant ( $R^2 = 0.13$   $P = 0.22$   $N = 13$ ). The assumptions of linearity, homogeneity of variance, normality and independence of residuals were upheld by all significant regressions. No significant ( $P < 0.05$ ) linear temporal trends were found in the NAOI data or the abundance of medusae (a positive trend was found in the ESh data for *C. capillata*; however, this data (raw or detrended) did not correlate with the NAOI). No autocorrelation or higher-order serial correlation was present in the data.

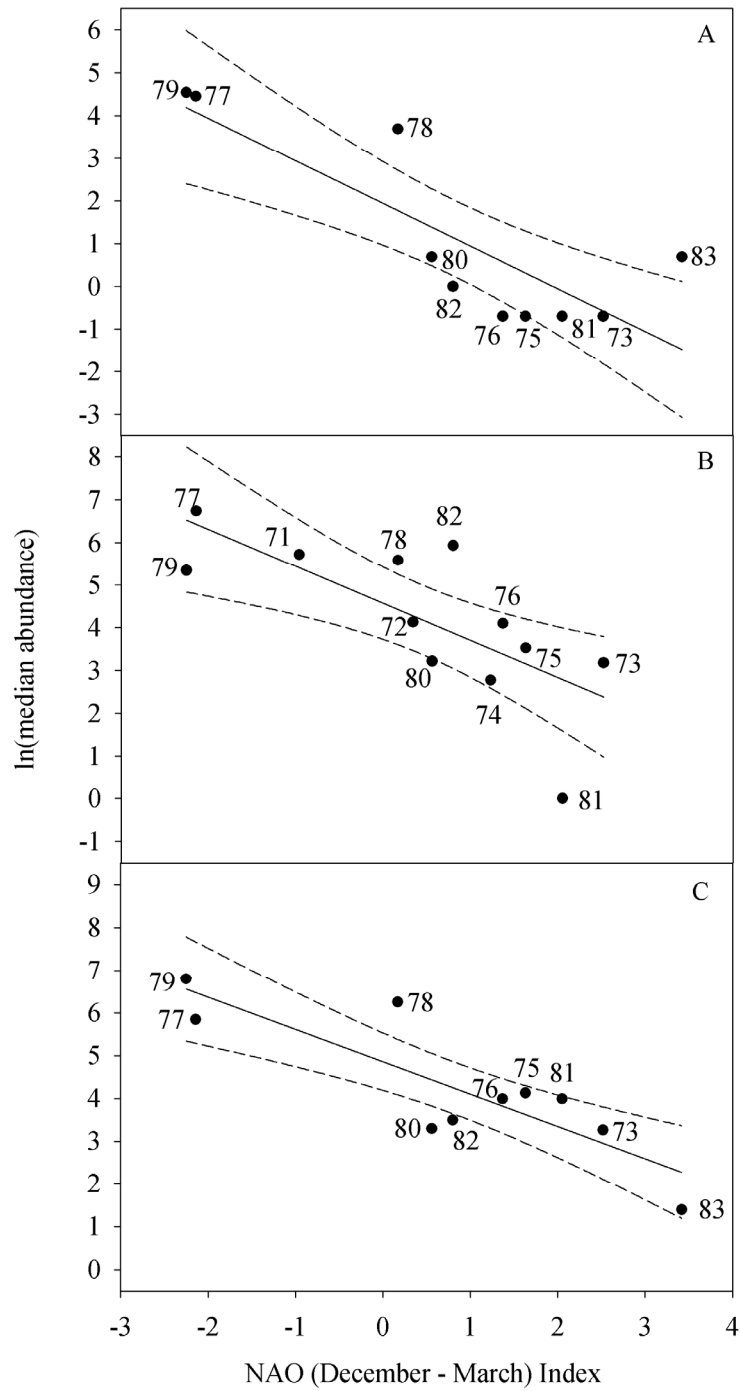


Figure 2.4 Linear regressions of jellyfish abundance against the NAO (December - March) Index. Solid lines show model fit, dashed lines indicate 95% confidence interval. A: *Aurelia aurita* West of N. Denmark  $R^2 = 0.70$ ,  $P = 0.003$ ,  $N = 10$ ,  $y = 1.9 - 1.0 x$ . B: *Aurelia aurita* East of Scotland  $R^2 = 0.53$ ,  $P = 0.008$ ,  $N = 12$ ,  $y = 3.0 - 0.6 x$ . C: *Cyanea lamarckii* West of N. Denmark  $R^2 = 0.74$ ,  $P = 0.002$ ,  $N = 10$ ,  $y = 5.0 - 1.0 x$ .

No relationship with the NAOI was found for *C. capillata* as an individual species. Significant ( $P < 0.05$ ) relationships between medusa abundance and the NAOI were found for: the summation of each species' median catch by each region and for all regions combined, as well as sums of median catches of pairwise combinations of species by region, and for all regions combined. However, all  $R^2$  values for these summations were low, relative to those reported for individual species by region, indicating that these combinations merely decreased the proportion of population variability that could be explained by the regression.

## 2.5. Discussion

For the first time, we have shown that interannual variation in the abundance of medusae in the North Sea may be driven by changes in the climate as quantified by the winter NAOI. A jellyfish/climate interaction has previously been proposed for the Bering Sea (Brodeur et al. 1999) and the Mediterranean Sea (Goy et al. 1989), but statistically significant links to an atmospheric oscillation such as the NAOI have not previously been demonstrated.

Numerous NAOI-related factors could influence fish and medusa abundance in the North Sea, where the NAOI is positively correlated with the west component of wind stress, sea surface temperature and changes in the influx of Atlantic and Norwegian water (Beaugrand 2003; Reid et al. 2003). NAOI-related effects of the hydroclimatic environment may be evident in the timing and abundance of the North Sea spring phytoplankton bloom, and changes in zooplankton community structure (Edwards et al. 2002; Reid et al. 2003). The rapid growth and short life-span (usually 8–10 months) of medusae suggest that jellyfish would show a same-year response to climatic changes, and thus no lag is to be expected in regressions of abundance against the NAOI. Our data are insufficient to elucidate the exact mechanisms by which the climate affects jellyfish populations, but we present two possible scenarios within the framework of a conceptual model (Figure 2.5). The NAOI-related mechanisms might act directly between the climate and jellyfish by altering advective dispersal/concentration of ephyra, juvenile medusoid, aggregations, or via changes in temperature, salinity, light and current strength to improve conditions for ephyra release and growth (Graham 2001; Lucas 2001; Purcell et

al. 1999). Alternatively, the mechanisms linking the climatic changes to interannual jellyfish population variation may be indirect, resulting in improved availability of prey to the growing jellyfish, either by altering the timing of the spring bloom to synchronize with the period of rapid ephyral growth, or by increasing the abundance of zooplankton or ichthyoplankton prey to juvenile medusae (Båmstedt et al. 2001; Edwards et al. 2002; Platt et al. 2003).

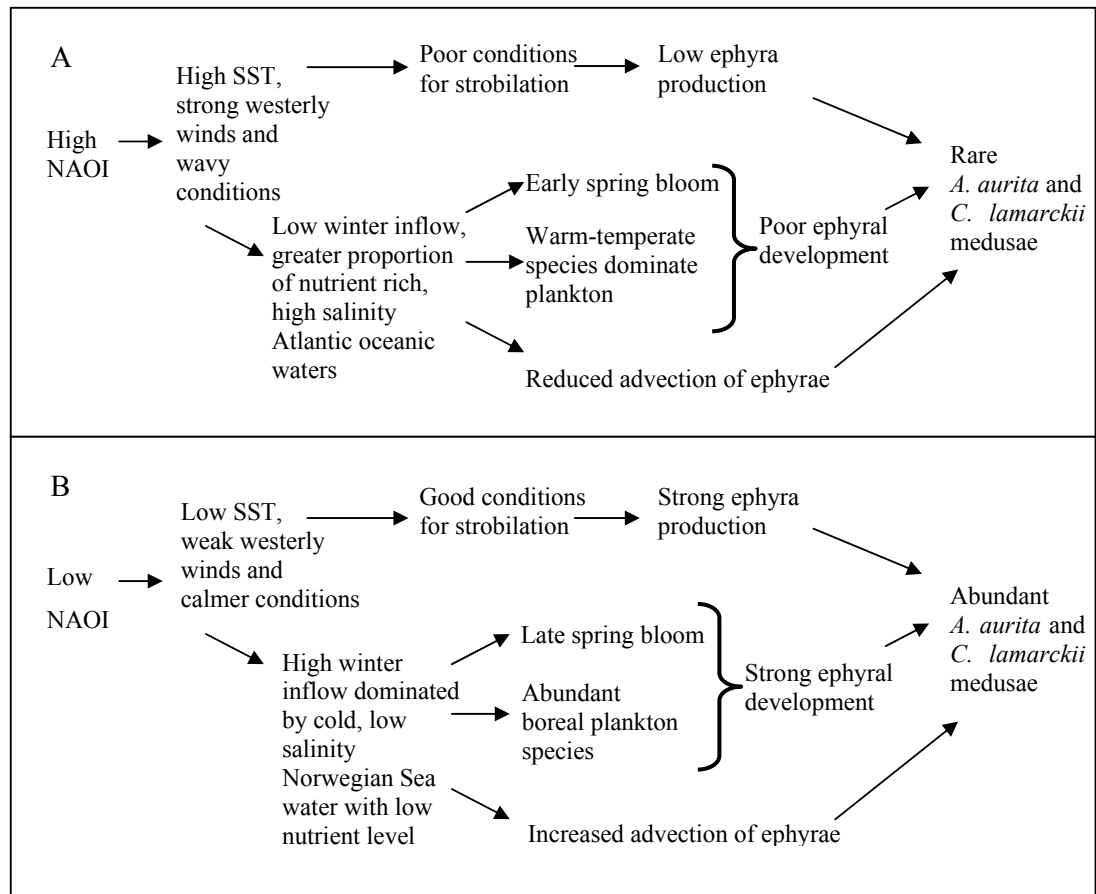


Figure 2.5 A conceptual model of the possible associations between the NAO (A: high/+ve index and B: low/-ve index) and the North Sea jellyfish *Aurelia aurita* and *Cyanea lamarckii*.

Although we found strong relationships between both *A. aurita* and *C. lamarckii* abundances and the NAOI, we found none for *C. capillata*. A number of factors may contribute to this absence of association. In contrast to the other species, over-wintering *C. capillata* medusae were found to contribute significantly to the summer biomass (Hay et al. 1990). So, *C. capillata* may exhibit multiple generations (although it is unlikely that this would extend to >2 generations)

and any single-year effects of changes in the NAOI on the population may be spread and confounded over a number of years. Hay et al. (1990) also noted that variable numbers of *C. capillata* and *A. aurita* had drifted westward each year from Norwegian coastal waters into the deep offshore waters outside the survey area. *Cyanea capillata* had a more northerly dispersed spatial distribution relative to the other species, and this species was found to be most abundant in the region NoS. Here, the NAOI appears to be less influential on sea surface temperature (SST) relative to the other regions, possibly due to variation in salinity through changes in the relative inflow of Atlantic and Norwegian waters. Becker & Pauly (1996) found the NAOI was significantly spatially correlated with SST anomalies in the North Sea with high correlation in the central North Sea and in the area covering the WND region, where regressions of medusa abundance against the NAOI were found to be most explanatory. So, the more complex hydrographical conditions found in the northern regions (ESH and NoS) may obscure any NAO-related impacts on the pelagic ecosystem.

Strobilation of scyphistomae in *Aurelia* and *Cyanea* spp. is triggered environmentally, following a change in sea temperature (Russell 1970; Brewer and Feingold 1991; Miyake et al. 2002). Therefore, SST anomalies may impact on the strobilation process and may partly explain the link between medusa abundance and the NAOI. Lucas (2001) suggested that the timing of initiation and the duration of the strobilation process might be dependent on both the winter minimum temperature and on food availability. Omori et al. (1995) proposed that environmental conditions during the polyp stage of *A. aurita* could govern mass occurrences of the medusae. In the North Sea, jellyfish ephyrae are produced and released during the winter/early spring months from sessile scyphistomae (Russell 1970), when the NAO has greatest influence on the North Sea. The NAO therefore may play an important role in mediating the environmental conditions that affect scyphistomae strobilation.

Planque and Taylor (1998) report on modelling work that shows significant ( $P < 0.01$ ) correlations between inflow of Atlantic water to the North Sea during the winter and the NAOI. However, it would appear that the study might have integrated both Norwegian and Atlantic influx. Recent work by Reid et al. (2003) suggests that a composite relationship may exist between the NAOI

and inflow: these authors found that during the first three months of the year the NAOI was positively correlated with inflow for an upper layer of water (0-150m) representing Atlantic influx, and negatively correlated with deeper water (150-500m) that they suggested derives from the Norwegian Sea via the Norwegian Trench. If we consider Planque and Taylor's (1998) study in this light, it appears that the negative correlations they found between inflow of water (East of Shetland and West of Norway) and the NAOI may represent dominance by Norwegian deep water, while the positive correlation between inflow through the passage between Orkney and Shetland may represent dominance by Atlantic water.

Even if the relationship between the NAOI and the abundance of medusae shown in the southern regions were to hold ESh and NoS, the effect may be masked by changes in advection. Assuming that ephyrae are present ESh and NoS, advection from these regions may result in a more southerly distribution of medusae during the summer and thus more concentrated aggregations EoS and WND. An extreme example of this process may explain the outlier year (1983) detected in the *A. aurita* data EoS. During 1983, Atlantic herring moved from their northern spawning grounds to Aberdeen Bank, a ground that had not been used for 16 years, and this reappearance has been attributed to an unusual late summer inflow of Atlantic water to the North Sea (Corten 1999). Advection to/from the Skagerrak, where medusae are often abundant, might also explain some of the variation in the abundance of medusae WND. However, the high abundance of medusae recorded WND in 1977, 1978 and 1979 coincides with an unusual negative salinity anomaly that was measured between 1977 and 1981 in the entrance of the Skagerrak and attributed, due to the presence of arctic-boreal species, to advection from the Norwegian trench rather than from the Skagerrak (Edwards et al. 2002).

Reid et al. (2003) describe a 'cold biological event' between 1978 and 1982 linked to decreased inflows of warm Atlantic water (evident in the reduced netflow of an upper water layer (<150 m) and increased inflows of colder, deeper (150 – 500 m) Norwegian water carrying boreal indicator plankton species (such as *Calanus hyperboreus*, *Euchaeta norvegica* and *Metridia longa*) into the North Sea. This cold biological event coincided in reduced copepod



diversity in the North Sea that was significantly correlated with the NAOI (Beaugrand 2003). In 1979, the year of highest recorded *A. aurita* and *C. lamarckii* medusa abundance WND, *C. hyperboreus* was recorded as far south as the entrance to the Skagerrak and the cold water dinoflagellate *Ceratium longipes* was found to be 5 standard deviations above its long-term mean abundance, while *Ceratium macroceros* experienced a population crash and other resident phytoplankton species were found in unusually low abundance in the North Sea (Edwards et al. 2002). Overall, the cold biological period coincided with low abundance of dinoflagellate, diatom, decapod larvae and copepods, with substantial declines in herring and western mackerel stocks, while arctic-boreal plankton species and both *A. aurita* and *C. lamarckii* medusae were particularly abundant.

The impacts on the North Sea ecosystem of pollution, overfishing and climatic change and the subsequent impact on jellyfish are difficult to evaluate separately as each of these factors may interact to alter the marine environment. Arai (2001) demonstrated that scyphomedusae may benefit from eutrophication and suggested that the high abundance of *C. lamarckii* WND may be linked to eutrophication. The North Sea ecosystem may also have been modified through ‘fishing down the food web’ from long-lived, high trophic level, piscivorous bottom fish towards short-lived, low trophic level invertebrates and planktivorous pelagic fish (Hutchings 2000; Pauly et al. 2002).

Populations of *A. aurita* and *C. lamarckii* appear to be indicators of ecosystem variability, and interannual population fluctuations in abundance or distribution may be driven through climatic changes. As jellyfish have the potential to play an important role in ecosystem control, or proliferate following high fishing effort (Purcell and Arai 2001), further study, to elucidate mechanisms through which jellyfish respond to climatic changes and subsequent impacts on fisheries, is essential.

In summary, the inverse relationships found between the winter NAOI and the median abundance of medusae may imply that cooler, calmer conditions and possible changes in current influx (including a greater inflow of Norwegian water relative to Atlantic water) to the North Sea during the winter/spring period

of ephyra release and growth lead to greater abundances of *A. aurita* and *C. lamarckii* medusae in the regions EoS and WND in the summer months.

The present NAO high may exert a negative influence on *A. aurita* and *C. lamarckii* medusae, suppressing abundance. We speculate that a future reversal of the NAO phase may release the environmental inhibition on these jellyfish. North Sea fish stocks are presently in a perilous state. A boom in medusae may exacerbate the situation and hinder the recovery of fish stocks, even following the cessation of fishing.

## Chapter 3

### **Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries**

The work described here has been published as:

Lynam C.P., Hay S.J. and A.S. Brierley (2005). *Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries*. *Journal of the Marine Biological Association of the U.K.* 85: 435-450.

I estimate that I contributed 80% of the effort towards the paper, which can be broken down into the following five equally weighted areas: Data collection/preparation 15 %, the jellyfish data were gathered by SJH and others at Marlab and I prepared the jellyfish data from the raw paper files and I gathered climate and fisheries data from various sources; Inspiration 100 %; Analysis 95 %, where the remainder is attributable to suggestions from ASB; Conclusions 100 %; Publication 90 %, the paper was written by me but reviewed by ASB.

### **3. Jellyfish abundance and climatic variation: contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries.**

#### **3.1. Abstract**

The  $\ln(\text{median})$  abundances of *Aurelia aurita* and *Cyanea lamarckii*, in two of four North Sea regions studied: west of Northern Denmark and east of Scotland, have previously been linked to large-scale interannual climatic change, as quantified by the North Atlantic Oscillation Index (NAOI) (Chapter 2). North of Scotland, however, no link was found between the abundances of these species and the NAOI, while east of Shetland the median abundances of these species were often zero so regression analyses were not possible. A third species, *Cyanea capillata*, did not appear to be linked to NAOI fluctuations. Here, I seek to explore these relationships further in order to understand why the links between jellyfish abundance and a wide-ranging climatic index appear to be region- and species-specific. A further aim of my analyses is to understand why the outlier year (1983) appeared in the relationship between *A. aurita* abundance east of Scotland and the NAOI (Chapter 2).

I reanalyse the jellyfish raw abundance data and calculate maximum abundances in addition to checking the calculations of median abundances by Hay et al. (1990). I regress these newly calculated abundances against the winter (December to March) NAOI and also against the difference in March and February monthly NAOI values. I include two further indices that reveal the effect of atmospheric change of oceanographic factors influencing the North Sea: the Barents Sea-Ice Index (BSII), which measures the coverage of sea-ice in the Barents Sea, and the Gulf Stream North Wall (GSNW) that measures changes in the latitude of northern extent of the current. In the north-west and south-east North Sea *A. aurita* and *C. lamarckii* are shown to exhibit contrasting relationships to change in the NAOI and BSII: north of Scotland, where the North Sea borders the Atlantic, positive relationships were evident between the abundance of scyphomedusae (data from 1974 to 1986, except 1975) and the indices; whereas west of northern Denmark, a region much less affected by Atlantic inflow, negative relationships were found (data from 1973

to 1983, except 1974). Weaker negative relationships with the NAOI were also found in an intermediate region, east of Scotland, for the abundance of *A. aurita* and *C. capillata* medusae (1971 to 1982). East of Shetland, the abundance of jellyfish was not linked directly to the NAOI but, in contrast to all other regions, the abundances of *A. aurita* and *C. lamarckii* (1971 to 1986, not 1984) were found to be inversely related with changes in the GSNW, which itself was significantly positively correlated to the NAOI with a two year lag. On this evidence I suggest that, for jellyfish, there exist three regions of the North Sea with distinct environmental processes governing jellyfish abundance: one north of Scotland, another east of Shetland, and a more southerly group (i.e. east of Scotland and west of northern Denmark). Contrasting oceanographic conditions in these regions may lead to the differing trends in abundance. Impacts by jellyfish are likely to vary regionally and ecosystem management may benefit from considering this spatial variability.

### **3.2. Introduction**

The phase of the NAO (high/low) alters the prevailing wind field over northern Europe and influences atmospheric variables (i.e. wind speed and direction, air temperature, heat and moisture transport, and precipitation), which lead to changes in sea temperature, salinity, river run-off, vertical mixing, and oceanic circulation (Section 2.1). These factors, in turn, influence nutrient levels available for phytoplankton growth and zooplankton production (Drinkwater et al. 2003). The timescales by which oceanographic conditions respond to changes in the atmosphere vary. Surface temperatures and wind-driven currents change within days, whereas basin-scale ocean circulation may take many years to fully adjust to changes in atmospheric conditions (Reid et al. 1998). For example, it takes between two and three years for changes in the NAO to become evident in changes in the latitude of the Gulf Stream's 'North Wall' (GSNW) and in the coverage of sea ice in the Barents Sea. The Gulf Stream travels eastwards from the USA coast near 33°N 75°W, developing into the North Atlantic current at about 55°W, which drives Atlantic inflow into the North and Barents Seas. The high phase of the NAO: strengthens westerly and trade winds; favours more northerly paths of, and transport by, the Gulf Stream; and leads to a reduction in ice coverage in the Barents Sea (Drinkwater et al.

2003) (Figure 3.1). The NAOI and GSNW correlate strongly with zooplankton abundance in both the North Atlantic and North Sea (Drinkwater et al. 2003).

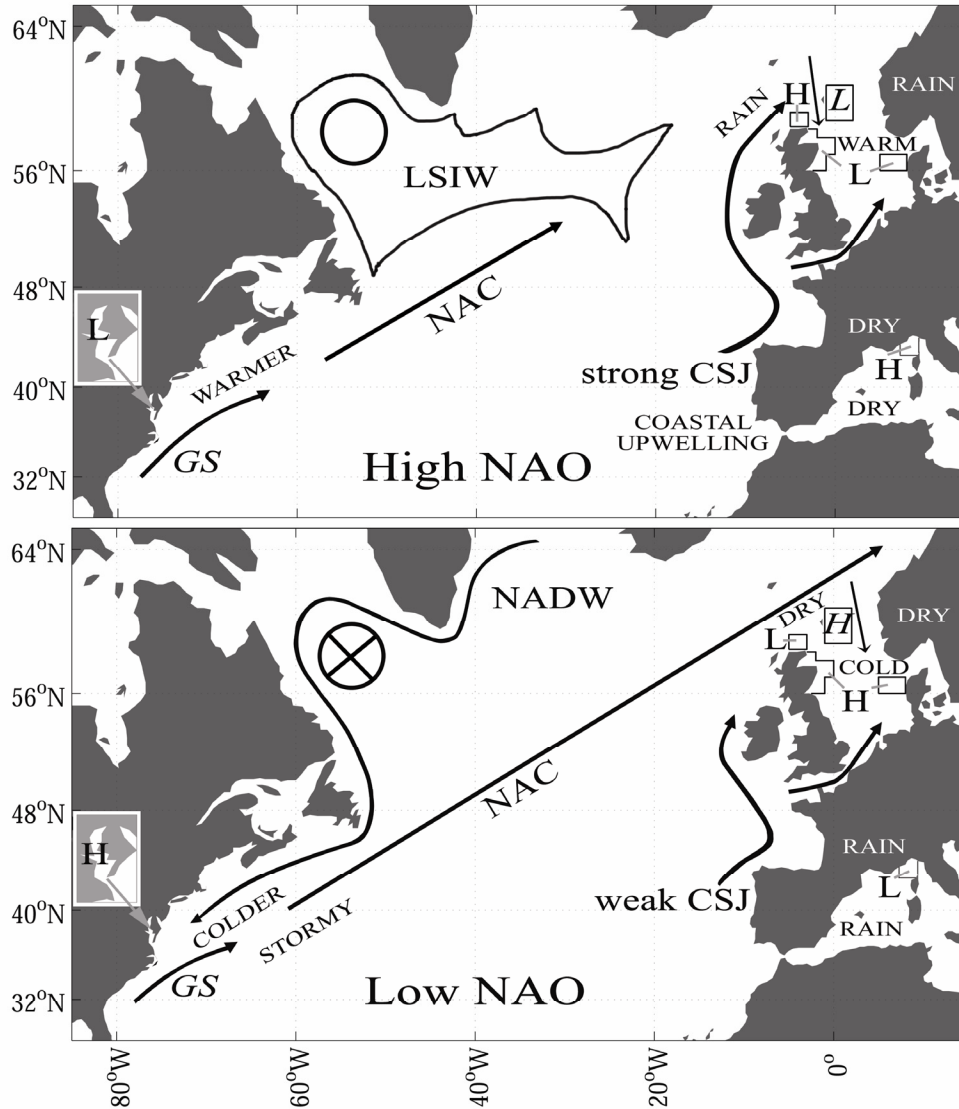


Figure 3.1 Schematic diagram of NAO-governed changes in the strength of Atlantic currents and the abundance of North Sea jellyfish, adapted from Reid et al. (1998). NAC, North Atlantic Current; GS, Gulf Stream; CSJ, Continental Shelf Jet; LSIW, Labrador Sea Intermediate Water; NADW, North Atlantic Deep Water. Note that the changes in CSJ, LSIW, and NADW may require a prolonged period of high/low NAO influence. H/L signifies a relatively high/low jellyfish abundance in the defined rectangular regions, and italics indicate a two-year lag to NAO changes. Small arrows showing the shifting location of NAO-driven inflow to the northern North Sea are adapted from Planque and Taylor (1998). Chesapeake Bay relationship from Purcell and Decker (2005) and Mediterranean relationship from Molinero et al. (2005).

### 3.3. Methods

Some errors were introduced to the jellyfish abundance data by the original data processing of Hay et al. (1990); medians of abundance were calculated initially by grid square ( $1^{\circ}$  latitude by  $0.5^{\circ}$  longitude) and those values were used to calculate the overall median abundance within the regions of interest (Figure 2.2, Section 2.3). It would have been more robust to take directly the median of all catches located within each region. In each region mistakes were also made in allocating catches to co-ordinates, particularly in 1982 and 1983 in the east of Scotland region. Therefore the data used here result from a reanalysis of the raw data. The reanalysis additionally enabled maximum values of abundance to be calculated in addition to the median values chosen by Hay et al. (1990). The maximum abundance of medusae is a measure of the peak of the jellyfish bloom, which serves as a good indicator of interannual variability in jellyfish abundance in the North Sea; the median is a useful additional measure, particularly for *C. capillata* which does not form dense aggregations (Purcell 2003). In addition, the use of the maximum abundance facilitated analyses for *A. aurita* and *C. lamarckii* in the low abundance regions, where in most years their median abundance was zero. The mean abundance is not a statistically acceptable measure of abundance due to the great patchiness in jellyfish aggregations and hence the highly skewed (non-normal and multinomial) range of densities. The distorted distributions were attributable to the patchiness of jellyfish populations and thus a high proportion of nil catches; in 1979, for example, 22% of 215 trawls did not contain any of the jellyfish species of interest, and *A. aurita*, *C. lamarckii* and *C. capillata* medusae were absent from 53%, 50% and 33% of trawls respectively.

Hay et al. (1990) identified four areas of the North Sea (Figure 2.2) that were representative of the major areas of jellyfish abundance, however the regions were not sampled uniformly. The regions were sampled as follows: east of Shetland (ESh) 1971 to 1986 not 1984 (14 years); north of Scotland (NoS) in 1974 and from 1976 to 1986 excluding 1984 (11 years); east of Scotland (EoS) from 1971 to 1983 (13 years) and the region west of northern Denmark (WND) was sampled in 1972 and from 1975 to 1983 (10 years). A fifth region east of Northumberland (EoN), sampled from 1971 to 1983 (13 years), is defined here

in order to gain insight into the advection of medusae by the Scottish coastal current (SCC, Figure 3.2). 85% of all *A. aurita* and 32% of *C. lamarckii* medusae were caught in the region East of Scotland (EoS); *C. lamarckii* was most abundant West of Northern Denmark (WND) (23% of medusae were caught here. Although this is 9% less than the number caught EoS the area WND is half the size). Peaks of *C. lamarckii* abundance WND coincided with those of *A. aurita*, but not with those of *C. capillata*; *C. capillata* was most abundant in the northern regions East of Shetland (ESh) (32% by medusae catch) and North of Scotland (NoS; 7% of catch). The majority of the remaining medusae were caught outside of the four regions reflecting a more widespread distribution of this species relative to the other two jellyfish species. *Aurelia aurita* and *C. lamarckii* were almost consistently present NoS and ESh (except in 1985), however these species were not abundant in either region ( $\leq 2\%$  of medusae of each species were caught in each area).



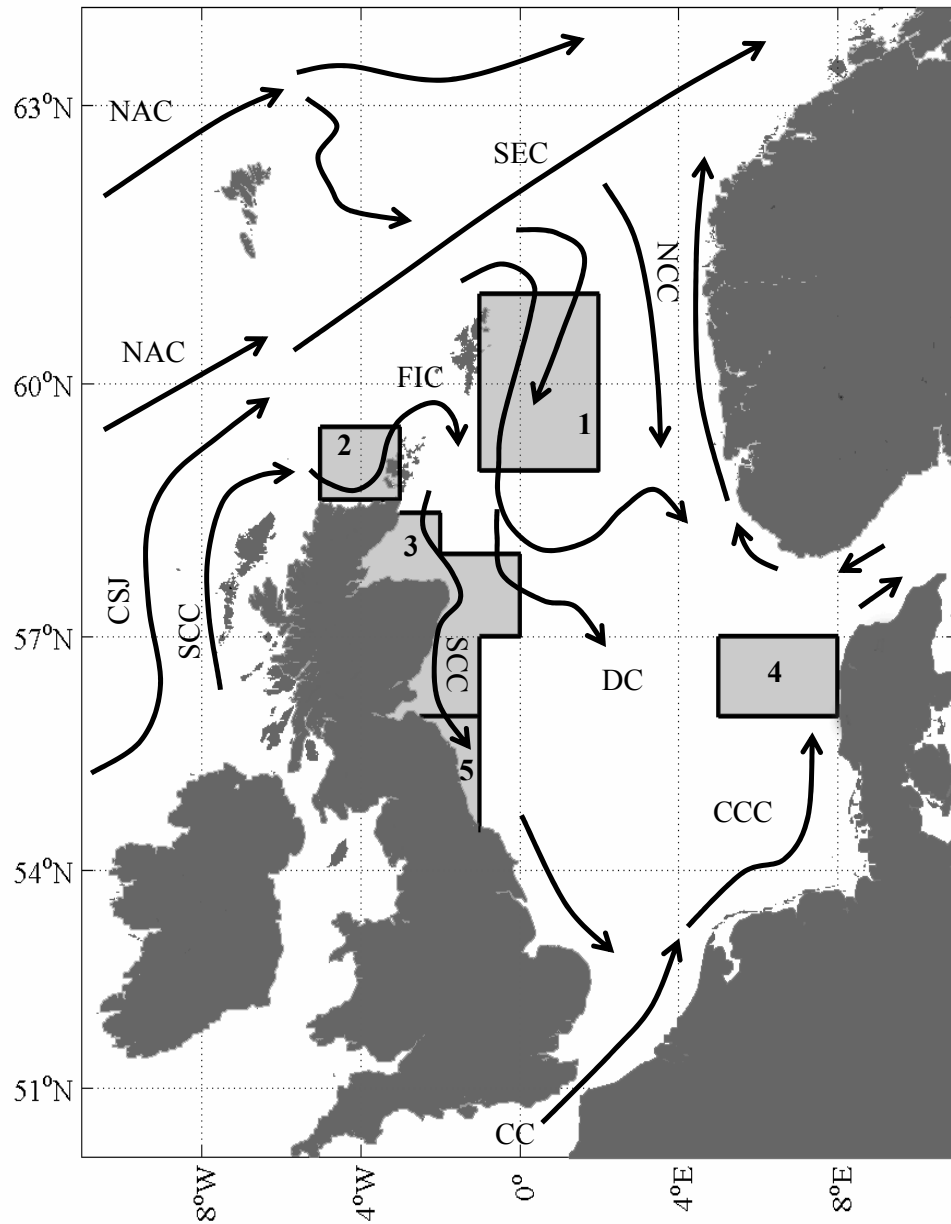


Figure 3.2 Map of survey area showing major currents, adapted from Holliday and Reid (2001), where region 1 is east of Shetland, 2 is north of Scotland, 3 is east of Scotland, 4 is west of northern Denmark, and region 5 is east of Northumberland. SEC, Shelf Edge Current; FIC, Fair Isle Current; DC, Dooley Current; SCC, Scottish Coastal Current; NCC, Norwegian Coastal Current; CCC, Continental Coastal Current; and CC, Channel Current.

To test for links between jellyfish abundance and environmental variables, I investigated data for each species in each area separately through regression analysis. The winter (December–March) NAOI was obtained from the National

Center for Atmospheric Research, Climate and Global Dynamics Division, Boulder, CO, USA, and monthly values were obtained from the University of East Anglia, Climatic Research Unit, Norwich, UK (Hurrell et al. 2003). The Gulf Stream North Wall (GSNW) and the Barents Sea–Ice Index (BSII) were also used in regression analyses; these indices incorporate the additional one– to two–year delayed impact of the NAO on the marine system, and together describe the strength and composition of inflowing water to the North Sea. Data for the annual mean of the 1st Principal Component of the GSNW (Taylor 1995) were obtained from the Plymouth Marine Laboratory, UK. The Barents Sea–Ice Index was supplied by the Institute of Marine Research, Bergen, Norway.

Interactions between medusae and commercial fish were also explored. The abundance of plaice (*Pleuronectes platessa*) in the Thames estuary has been negatively correlated with the NAOI (Attrill and Power 2002) and plaice recruitment in the southern North Sea is a useful indicator of changes in Atlantic inflow through the English Channel (Wegner et al. 2003). Given the link between plaice recruitment and inflow toward the west of Denmark region, correlations between jellyfish abundance WND and plaice recruitment were considered to ascertain whether or not similar advective processes may account for changes in jellyfish abundance there. Salmon landings in the central and northern North Sea were considered because the numbers of salmon caught have been linked to changes in northern hemisphere temperature and in zooplankton abundance, and jellyfish may play a part within this relationship (Purcell and Sturdevant 2001; Beaugrand and Reid 2003). Salmon landings for the central and northern North Sea were provided by ICES through *Fishstat Plus version 2.3 2000* (FAO Fisheries Department, Fishery Information, Data and Statistics Unit) and plaice recruitment data for ICES Subarea IV (North Sea) were from ICES (2003b).

Where necessary, medusa abundance data (median and maximum values) were natural logarithm transformed to normalize the variance of the distributions prior to further statistical analyses. Medusa abundance and the NAOI were also assessed for linear temporal trends, the significance of which was judged at the 0.05 level with a standard Student's *t*-test of the estimated slope parameter.

Linear trends were removed in order to compare interannual variability between time series. Linear regressions of abundance data ( $y$ ) against each climatic index ( $x$ ) were made, for each species in each area, to compute models of the form of equation 1 (Section 2.2). Regressions with fish recruitment and landings as the response variable ( $y$ ) were also made against medusa abundance ( $x$ ) (Equation 1) and similarly multivariate regressions (with two predictors:  $x_1$  total North Sea medusa abundance and  $x_2$  the NAOI) were made using the linear regression feature in SigmaPlot® 2001 for Windows. Parameter significances for all models were assessed using a Student's  $t$ -test at the 0.05 level to minimize corresponding Type II errors. The model assumptions (linearity, homogeneity of variance, normality, and independence of residuals) were tested and outliers were assessed as described in Section 2.2.

### 3.4. Results

Three linear trends with abundance increasing over time were detected in, and removed from, the median abundance data for: *Cyanea capillata* abundance data east of Shetland (ESh) ( $\ln(\text{median}) R^2 = 0.55, P < 0.01, N = 15$ ); west of northern Denmark (WND) (median  $R^2 = 0.36, P < 0.10, N = 10$ ); and for the combined abundance of all jellyfish species north of Scotland (NoS) ( $\ln(\text{median}) R^2 = 0.57, P < 0.10, N = 11$ ). In the area west of northern Denmark (WND), both the  $\ln(\text{maximum})$  and  $\ln(\text{median})$  abundance of *Aurelia aurita* and *Cyanea lamarckii* correlated significantly between species (Figure 3.3A,B). In the NoS region, a significant correlation was found between the median *C. lamarckii* and *C. capillata* medusa abundance (Figure 3.3C). The  $\ln(\text{median})$  *A. aurita* abundance correlated between the two regions east of Scotland (EoS) and WND, but only when the year 1983 was excluded did the regression satisfy the assumption of constant variances (Figure 3.3D).

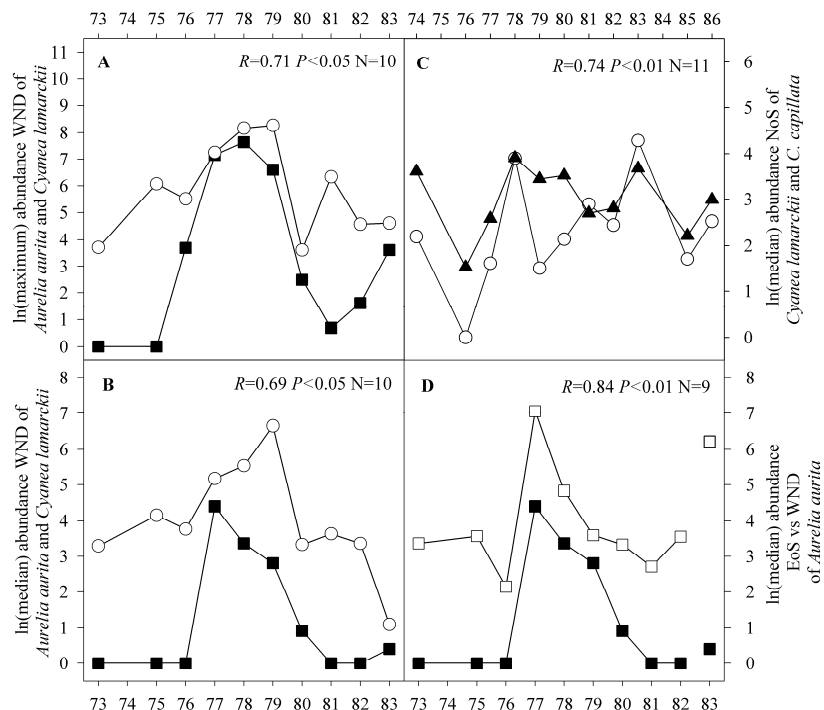


Figure 3.3 Interspecies correlations (showing Pearson correlation coefficients) for the abundance of *Aurelia aurita* and *Cyanea lamarckii* WND (A)  $\ln(\max)$  and (B)  $\ln(\text{median})$ ; (C)  $\ln(\text{median})$  *Cyanea lamarckii* and *Cyanea capillata* NoS. The inter-region relationship between *Aurelia aurita*  $\ln(\text{median})$  abundances EoS and WND is shown in (D). Note that the abundance of *Cyanea capillata* in C is  $3+\ln(\text{median})$  for ease of visual comparison.

#### *Jellyfish and the winter (December–March) North Atlantic Oscillation Index*

Significant regressions between jellyfish abundances and the winter NAOI were found in three of the five North Sea regions analysed (Figures 3.2 and 3.4); positive regressions were found NoS and negative regressions EoS and WND (Table 3.1). Although the median abundance of *A. aurita* EoS observed in 1983 was higher than predicted by the regression with the NAOI (outside of the 95% CI bounds, Figure 3.4D), the recalculated value was not as high as previously reported by Hay et al. (1990).

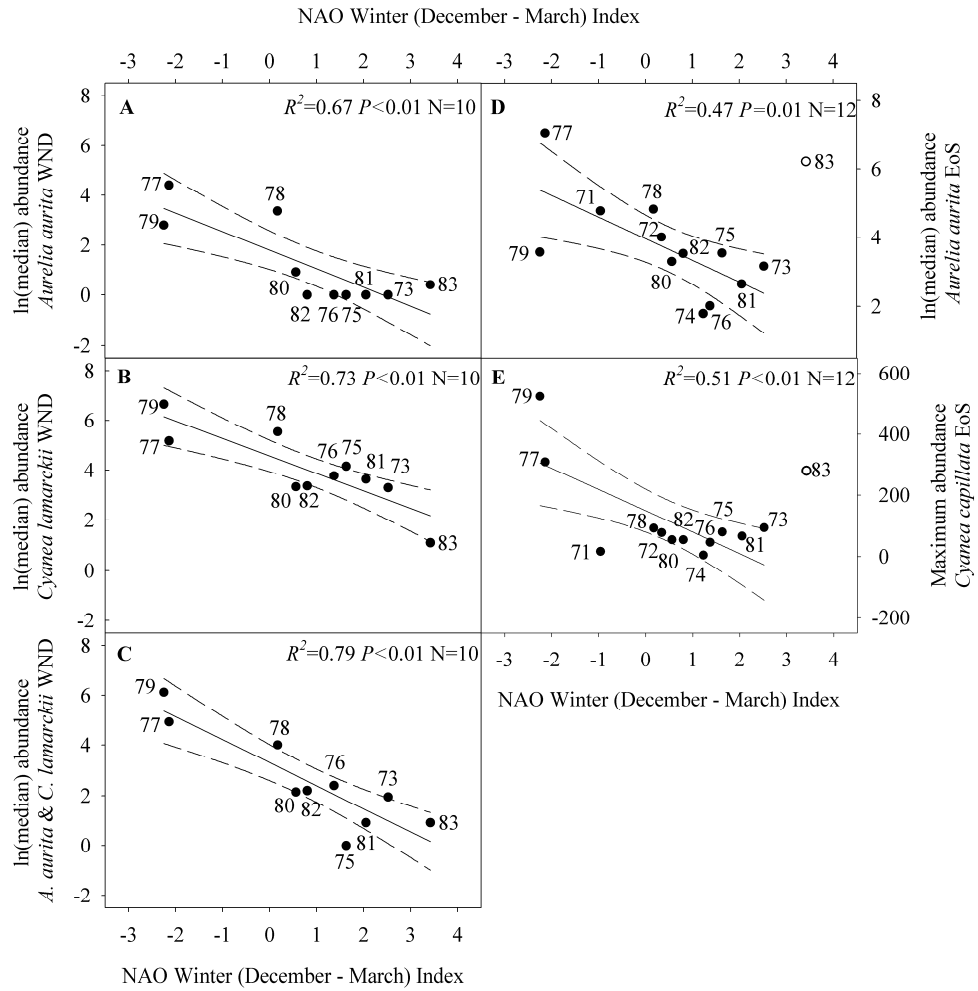


Figure 3.4 Regressions of median jellyfish abundance on the NAOI, left panels WND (A) *Aurelia aurita*,  $y = 1.80 - 0.75x$ ; (B) *Cyanea lamarckii*,  $y = 4.57 - 0.70x$ ; (C) for both species combined,  $y = 3.30 - 0.92x$ ; and right panels EoS (D) *Aurelia aurita*,  $y = 3.96 - 0.63x$ ; and (E) *Cyanea capillata*,  $y = 149 - 70x$ . All y-axis are ln(median) except E which is maximum abundance.

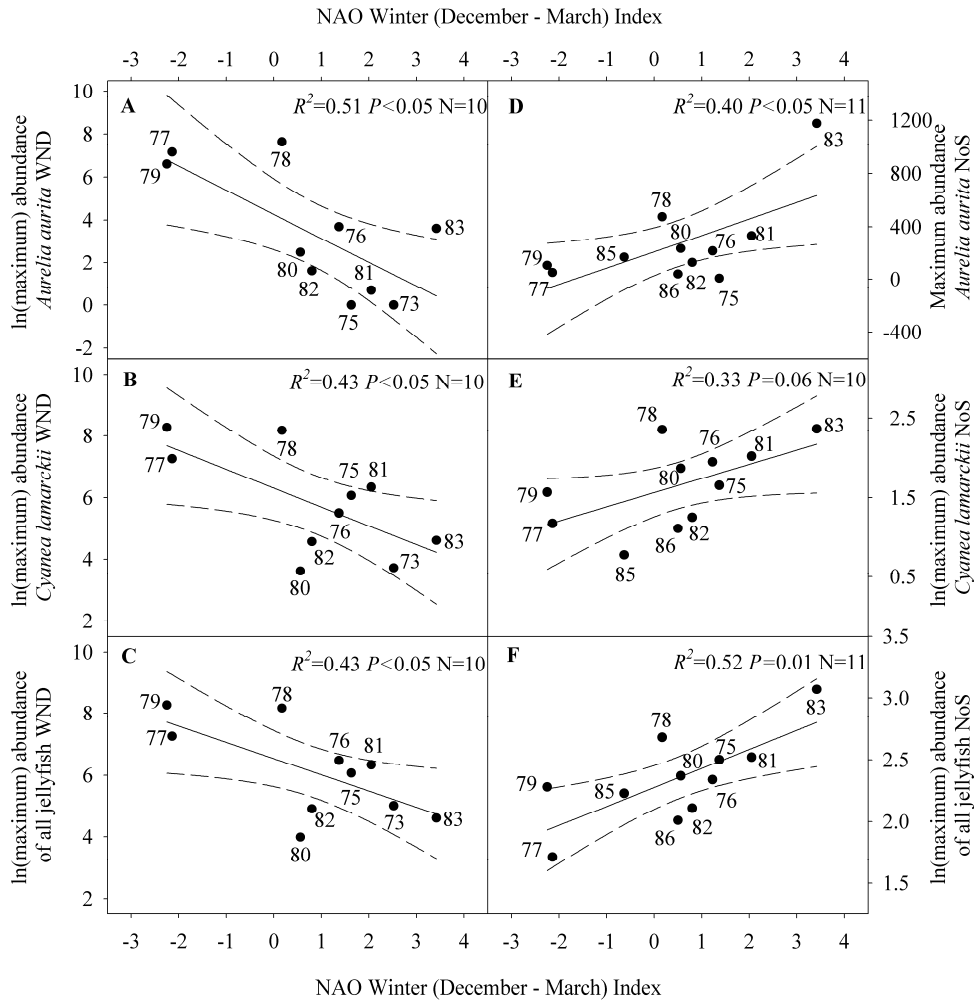


Figure 3.5 Regressions of maximum jellyfish abundance on the NAOI, left panels WND (A) *Aurelia aurita*,  $y = 4.26 - 1.12x$ ; (B) *Cyanea lamarckii*,  $y = 6.31 - 0.61x$ ; (C) all species combined,  $y = 6.54 - 0.52x$ ; and right panels NoS (D) *Aurelia aurita*,  $y = 209 + 124x$ ; (E) *Cyanea lamarckii*,  $y = 1.56 + 0.18x$ ; (F) all species combined,  $y = 2.28 + 0.15x$ . All y-axis are ln(maximum) except D which is maximum abundance.

| Region | N  | Sign, $R^2$ , and significance for relationships between<br>ln(median) medusa abundance and the NAOI |                             |                             |   |
|--------|----|--|-----------------------------|-----------------------------|---|
|        |    | <i>Aurelia<br/>aurita</i>  | <i>Cyanea<br/>lamarckii</i> | <i>Cyanea<br/>capillata</i> | <i>A. aurita</i> &<br><i>C. lamarckii</i><br>combined |
| WND    | 10 | - 0.67 ***   | - 0.73 ***                  | n.s.                        | - 0.79 ****   |
| EoS    | 12 | - 0.47 <sup>a</sup> **   | n.s.                        | n.s.                        | n.s.  |
| NoS    | 11 | n.s.   | n.s.                        | n.s.                        | n.s.  |

| Region | N  | Sign, $R^2$ , and significance for relationships between<br>ln(maximum) medusa abundance and the NAOI |                             |                             |                         |
|--------|----|---|-----------------------------|-----------------------------|-------------------------|
|        |    | <i>Aurelia<br/>aurita</i>   | <i>Cyanea<br/>lamarckii</i> | <i>Cyanea<br/>capillata</i> | All species<br>combined |
| WND    | 10 | - 0.51 **   | - 0.43 **                   | n.s.                        | - 0.43 ** <sup>b</sup>  |
| EoS    | 12 | n.s.  | n.s.                        | - 0.51 <sup>a c</sup> ***   | n.s.                    |
| NoS    | 11 | + 0.40 <sup>c</sup> **  | + 0.33 *                    | n.s.                        | + 0.52 **               |

Table 3.1 Significant linear regressions of maximum and median medusa abundances with the NAOI for three regions of the North Sea for *Aurelia aurita*, *Cyanea lamarckii*, and *Cyanea capillata* species of jellyfish. N, number of observations; +/- indicates a positive or negative relationship between the variables; \*\*\*\*  $P < 0.001$ ; \*\*\*  $P < 0.01$ ; \*\*  $P < 0.05$ ; \*  $P < 0.10$ ; n.s.,  $P > 0.10$ . Notes: <sup>a</sup>, one year (1983) was excluded; <sup>b</sup>, The regression WND is dominated by the regular high abundance of *C. lamarckii* and thus has an identical proportion of variability explained by the regression with *C. lamarckii* alone. The non-significant regression EoS merely replicates the *A. aurita* regression as *A. aurita* was most abundant EoS each year; <sup>c</sup>, No ln transformation was necessary for the measure of abundance to fulfil the test for constant variance and was therefore not made.

### *Jellyfish and the monthly North Atlantic Oscillation Index*

The complex phenomenon that is the NAO is often reduced to a dimensionless index, and it is assumed that if two years have the same NAOI value then similar climatic influences will be exerted on the environment. However, NAO cycles are rarely the same and monthly variation may result in subtly varying interactions with the marine environment. To explore this variation, the monthly NAOI values were grouped by phase for extremely low (1977 and 1979) and high (1973, 1975 and 1981) years and for 1983 (Figure 3.6A–C). In years of low NAOI, when jellyfish were most abundant east of Scotland and west of

northern Denmark, the winter (December to March) NAOI showed an opposite monthly pattern to the years of high NAO when jellyfish were abundant north of Scotland (Figure 3.6A,B). I named the cycles Type I and II respectively. The NAO monthly cycle in the outlier year 1983 was expected to follow Type II, as the overall phase was high, and in December and January the cycle appeared to be an extreme form of Type II. However, in February and March the cycle had Type I properties (Figure 3.6C). I then created a difference index (March minus February) and used this in regressions of abundance in each area. Significant regressions were found for *A. aurita* medusae east of Scotland (EoS) (Figure 3.6D) and east of Northumberland (EoN) (Figure 3.6E–F). All regressions included all available years of the time series and were significant with the unusual year 1983 included.

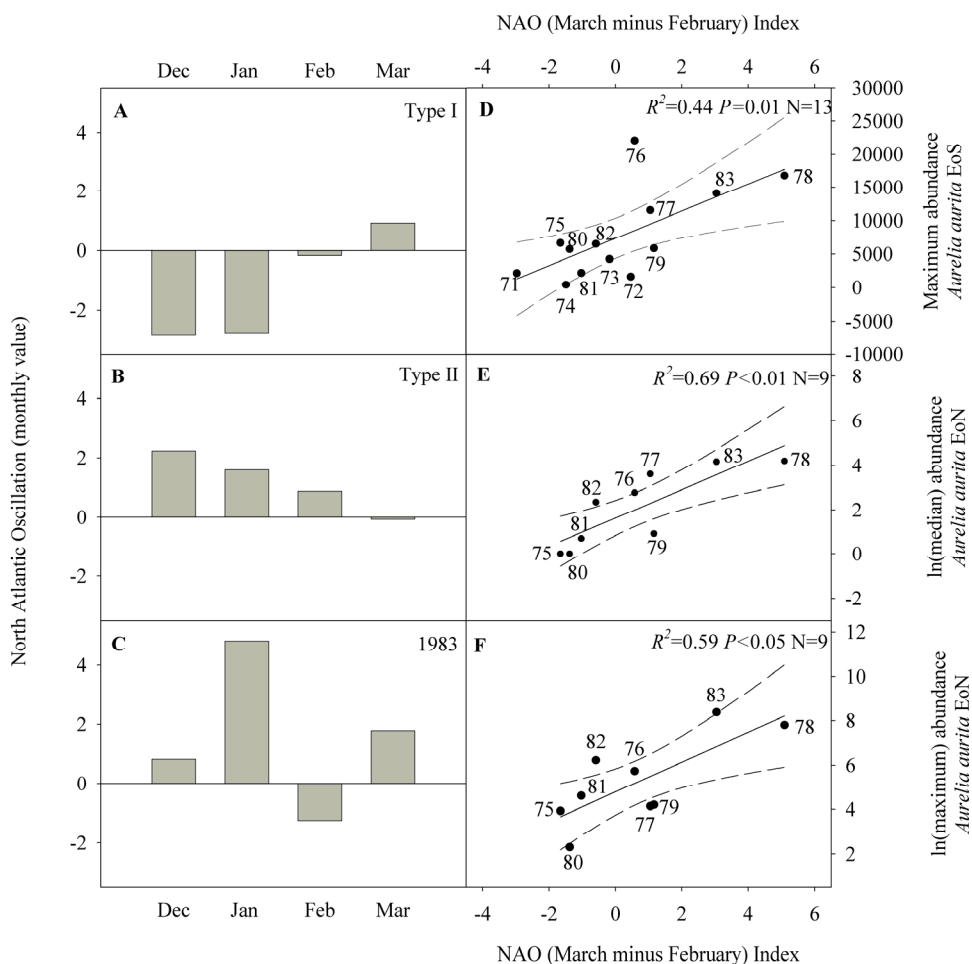


Figure 3.6 Caption on following page



↑Figure 3.6 Monthly patterns in NAO winter index, (A) is Type I for the low NAO years 1977 and 1979; (B) is Type II for 1973, 1975 and 1981; and (C) is the NAO for 1983, where Type I/II corresponds to high/low median abundance of jellyfish EoS and WND and the outlier year appears as a combination of both types. (D–F) Type I response to the NAO evident in regressions of *Aurelia aurita* abundance in two regions: east of Scotland (D, maximum *A. aurita* abundance including all years,  $y = 7372 + 2037x$ ) and east of Northumberland (E  $\ln(\text{median})$ ,  $y = 1.63 + 0.64x$ , and F  $\ln(\text{maximum})$  *A. aurita* abundance,  $y = 4.79 + 0.67x$ ) to the NAO (March minus February) Index.

*Jellyfish abundance, the Gulf Stream North Wall and the Barents Sea–Ice Index*

A significant linear trend was removed from the GSNW index for the period 1971 to 1986 ( $R^2 = 0.39$ ,  $P < 0.01$ ,  $N = 16$ ) so that the interannual variability in this time series could be compared robustly to that in the jellyfish abundance data and NAOI. The detrended GSNW and the Barents Sea–Ice Index (BSII) were found to lag changes in the NAO by 2 years (once a linear trend was also removed from the NAOI 1969 to 1984 data, Figure 3.7A). Negative regressions were found for the  $\ln(\text{maximum})$  abundance of medusae (*A. aurita* and *C. lamarckii*) east of Shetland (ESh) against both the BSII and the detrended GSNW (Figure 3.7B,C,E). The BSII was also positively related with both median *A. aurita* abundance north of Scotland and  $\ln(\text{median})$  abundance of *C. lamarckii* west of Denmark (Figure 3.7D,F).

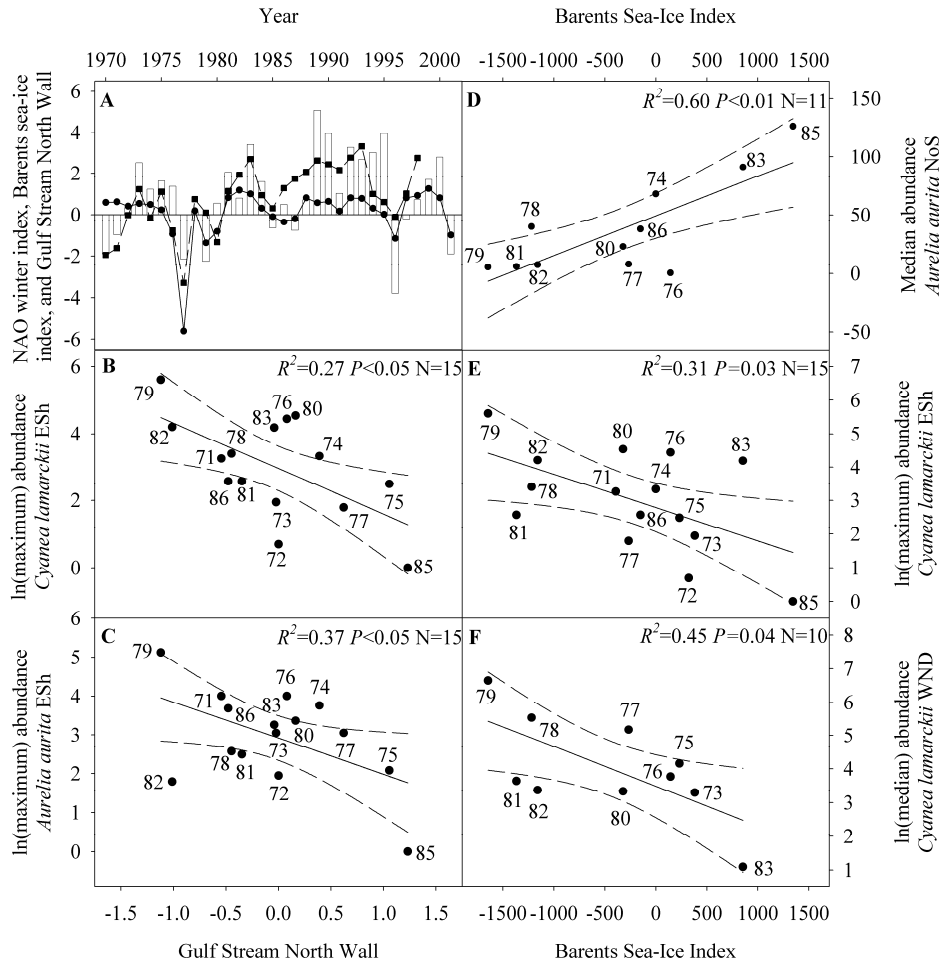


Figure 3.7 (A), The NAO winter index (bars) for 1970–2001 with the (detrended) Gulf Stream North Wall (GSNW squares and dashed line, correlation with NAO 1970–1998  $R^2 = 0.37$ ,  $P < 0.01$ ,  $N = 29$  and 1971–1986  $R^2 = 0.46$ ,  $P < 0.01$ ,  $N = 16$ ) and the Barents Sea–Ice Index (BSII, circles and line, correlation with NAO 1970–2001  $R^2 = 0.23$ ,  $P < 0.01$ ,  $N = 32$  and 1971–1986  $R^2 = 0.34$ ,  $P = 0.02$ ,  $N = 16$ ) both lagged by two years relative to the NAO. When positive, the NAO has a warming effect on the North Sea and two years later the Gulf Stream follows a more northerly path and the Barents Sea has reduced ice coverage. (B–C) are regressions of ln(maximum) jellyfish abundance east of Shetland against the GSNW, B: *Cyanea lamarckii*,  $y = 2.96 - 1.36x$ , C: *Aurelia aurita*,  $y = 2.91 - 0.93x$ . (D–F) are regressions of ln(maximum) jellyfish regional abundance against the BSII, D: *Aurelia aurita* north of Scotland,  $y = 49.3 + 0.04x$ ; E: *Cyanea lamarckii* east of Shetland,  $y = 2.79 - 0.001x$ , and F: *Cyanea lamarckii* west of northern Denmark,  $y = 3.49 - 0.001x$ .

*Cyanea capillata* and the recruitment of plaice (*Pleuronectes platessa*)

Recruitment of plaice to age-1 was not found to be correlated significantly with long-term changes in the spawning stock biomass (SSB) nor for landings in the period 1960–2000. Linear temporal trends over the period 1970–1986 (when jellyfish data are available) were evident in recruitment data of plaice ( $R^2 = 0.48$ ,  $P < 0.01$ ,  $N = 17$ ) and also in the landings data ( $R^2 = 0.65$ ,  $P < 0.01$ ,  $N = 17$ ). Once detrended, the recruitment data for 1973–1983 (no recruitment data for 1974) correlated with the median abundance of *C. capillata* WND (Figure 3.8A).

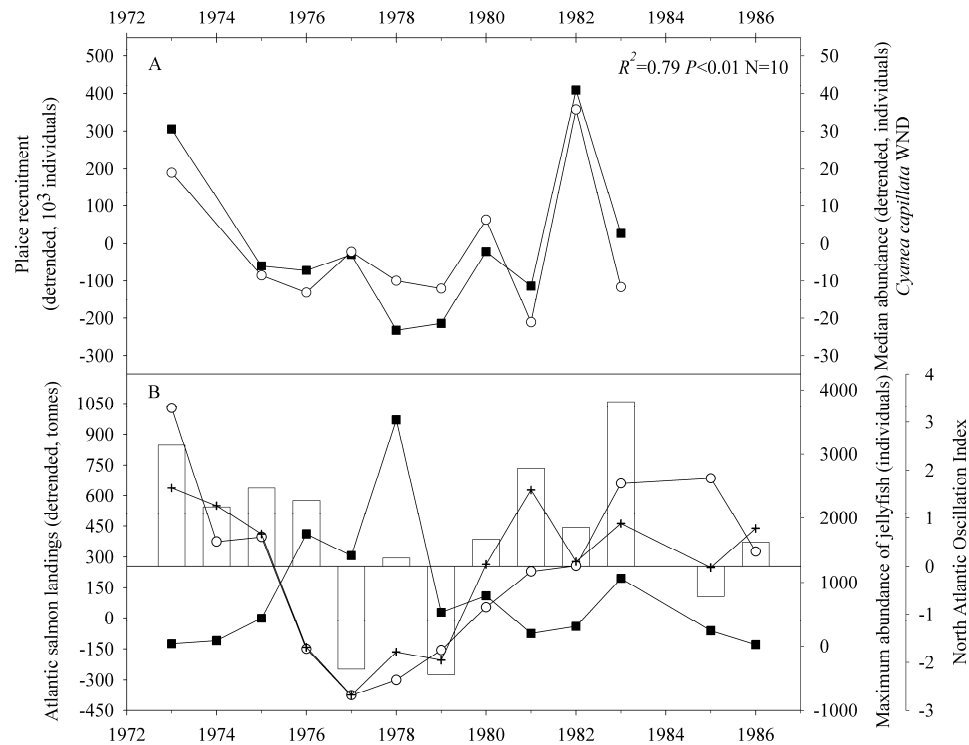


Figure 3.8 (A) Correlation between plaice recruitment (open circles and solid line) in the southern North Sea and *Cyanea capillata* abundance west of northern Denmark (squares and solid line). (B) Time series of salmon (*Salmo salar*) landings in the central and northern North Sea (open circles and solid line), the maximum abundance of *Cyanea lamarckii* medusae (squares and solid line) and the NAO (bars) showing the modelled salmon landings (crosshairs and solid line; correlation with detrended landings:  $R^2 = 0.68$ ,  $P < 0.01$ ,  $N = 10$ ,  $y = 321 - 0.23x_1 - 134x_2$ , where  $x_1$  is the maximum abundance of *Cyanea lamarckii* and  $x_2$  is the NAO. Pearson correlation coefficients between salmon landings and: the NAOI  $R = 0.62$ ,  $P = 0.02$ ,  $N = 13$ ; the maximum abundance of *C. lamarckii*  $R = 0.63$ ,  $P = 0.02$ ,  $N = 13$ .

*Atlantic salmon landings (Salmo salar) and jellyfish abundance*

In the central and northern North Sea (ICES areas IVa and b), between 1971 and 1986, the landings of salmon, once detrended (linear negative trend;  $R^2 = 0.52$ ,  $P < 0.01$ ,  $N = 13$ ), were positively correlated with the NAOI and negatively with the maximum abundance of *C. lamarckii* in the North Sea (Figure 3.8B). 68% of the variability in salmon landings was explained by multivariate regression against both the NAOI and the maximum abundance of *C. lamarckii* (Figure 3.8B). Although the maximum abundance of all jellyfish, or of *Aurelia aurita* only, did not significantly correlate with salmon landings when modelled as the sole explanatory variable, both measures of abundance did significantly correlate when the NAOI was included as an additional explanatory variable ( $R^2 = 0.69$  and  $P = 0.003$  for both models).

### 3.5. Discussion

Relationships between the NAO and abundance of various marine organisms have previously been shown. Attrill and Power (2002) demonstrated the significance of the NAO as a principal controlling influence on commercially important marine fish in the Thames estuary. Numerous NAO related factors could influence fish and jellyfish abundance. In the North Sea, the NAOI is positively correlated with the SST (Fromentin and Planque 1996; Edwards et al. 2001), the west component of wind stress (Fromentin and Planque 1996), annual mean phytoplankton colour (Edwards et al. 2001), changes in the copepod community structure (Beaugrand et al. 2002b), and the distribution and abundance of the copepod *Calanus helgolandicus* (Fromentin and Planque 1996). The NAOI is negatively correlated with the distribution and abundance of the copepod *C. finmarchicus* (Fromentin and Planque 1996). Therefore, it is not surprising that the NAOI correlates with the regional abundance of medusae in the North Sea. Evidence for a NAO-driven influence on jellyfish abundance also exists for Chesapeake Bay, where a low NAOI also results in a high abundance of *Chrysaora quinquecirrha* (Scyphozoa) (Purcell and Decker 2005), and the Ligurian Sea, where a high NAOI may be beneficial for a gelatinous zooplankton assemblage (including the scyphozoan *Pelagia noctiluca*) (Molinero et al. 2005).

Variations in SST depend partly on heat exchange with the atmosphere (Kushnir 1999), and in the North Sea this is governed largely by the NAO

(Becker and Pauly 1996; Fromentin and Planque 1996; Marshall et al. 2001). However, advective transports from the Atlantic will also cause some of the variability in SST, particularly at the entrances to the North Sea (Becker and Pauly 1996; Turrell et al. 1996). Becker and Pauly (1996) found that the NAOI is significantly spatially correlated with SST anomalies in the North Sea, with high correlation in the central North Sea and in the area covering the WND region, i.e. where regressions with jellyfish abundance were found to be most explanatory. The lowest correlations between the NAO and SST were found where Atlantic waters enter the North Sea (Becker and Pauly 1996), including the region ESh and by implication NoS, where regressions of jellyfish abundance on the NAO were least explanatory and non-significant.

Although advection of Atlantic water is relatively weak during the survey period (June to August), it is strong during December to February and may play a role in the dispersion of ephyrae away from the northern regions into the central North Sea (Turrell et al. 1996). Planque and Taylor (1998) report on modelling work that shows significant negative correlation between inflow of Atlantic water to the North Sea during winter and the NAO, which may imply that jellyfish ephyrae released NoS and ESh are swept into the North Sea by wind-driven currents. Little is known about the natural distribution of jellyfish scyphistomae in the North Sea; however, the almost cosmopolitan *A. aurita* may settle preferentially in shallower waters than either of the *Cyanea* species (Hay et al. 1990). Advection from the Baltic Sea, where jellyfish are often abundant, might also explain some of the variation in jellyfish abundance WND.

The NAO was found to explain 58% (Fromentin and Planque 1996) of *C. finmarchicus* abundance in the North East Atlantic and North Sea between 1958 and 1995. Winter inflow from the North Atlantic to the North Sea has been significantly ( $P < 0.01$ ) correlated with the NAOI and thus, the likely advection of overwintering *C. finmarchicus* into the North Sea from the Faeroe–Shetland Channel may partially explain the relationship between *C. finmarchicus* abundance in the North Sea and the NAOI (Planque and Taylor 1998).

Fromentin and Planque (1996) have suggested that the NAO may affect the timing and abundance of the spring phytoplankton bloom through its effect on wind induced mixing of the North Sea: a high NAO (positive NAOI) generates

a strong mixing of surface waters during winter and spring, which may delay the spring phytoplankton bloom, while a low NAO (negative NAOI) may allow earlier stratification of the surface layer, resulting in an earlier initiation of the spring bloom. This mechanism could also affect the release of ephyrae, which occurs early in the year, and subsequent development rates: Båmstedt et al. (2001) indicated that phytoplankton might be a significant food item in the early development of ephyrae. Given the above links between the NAOI and the North Sea ecosystem, I modify the conceptual model presented in Chapter 2 (Figure 2.5) to incorporate these new findings (Figure 3.9).

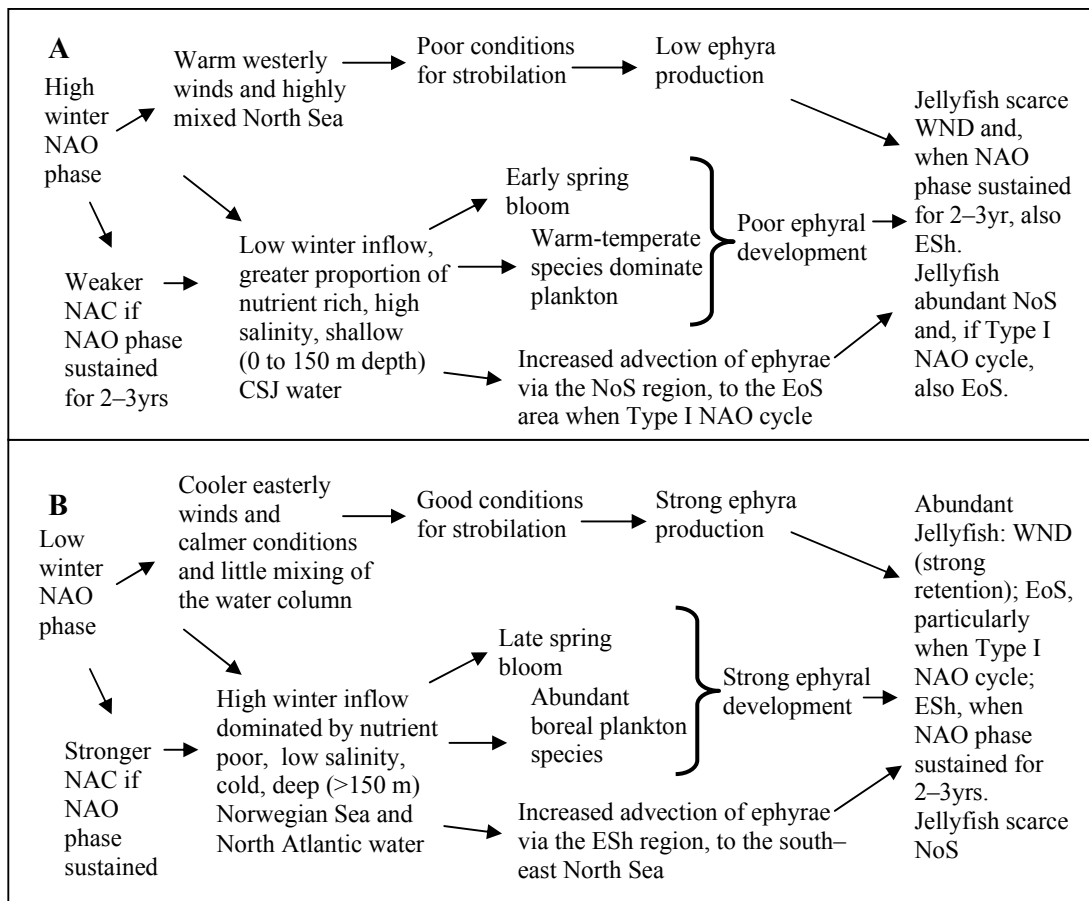


Figure 3.9 Conceptual model of possible links between the North Atlantic Oscillation (NAO) phase (high → positive index, low → negative index) and the region abundance of jellyfish in the North Sea. Regions are: North of Scotland (NoS); East of Scotland (EoS); west of northern Denmark (WND); and east of Shetland (ESh).

*Jellyfish and the NAO*

This analysis has shown that jellyfish abundance throughout the North Sea is linked to the climate as quantified by the North Atlantic Oscillation Index (NAOI). Furthermore, the investigation of maximum abundance of medusae has revealed a population of jellyfish north of Scotland (NoS) that shows an opposite response to the NAO-driven environmental change relative to jellyfish populations in the regions east of Scotland (EoS) and west of northern Denmark (WND). The spatial variability shown in the relationship between jellyfish abundance and the NAOI does not falsify my proposition that the climate is a primary factor influencing jellyfish abundance, but rather it supports it. The pattern of spatial variability is consistent with the pattern found in the strength of correlations between the NAOI and sea surface temperature (SST) (Figure 3.10). Salinity in the shallow, south-eastern North Sea is affected greatly by NAO-related precipitation. Whereas in the deeper, colder waters of the northern North Sea (NoS and ESh) salinity is influenced primarily by oceanic inflow. The region WND includes an amphidromic point, indicating zero tidal movement, which may serve to aggregate medusae. I suggest that, of the five regions studied (Figure 3.2), the region WND is the most isolated from external oceanic influences, which reduces the likelihood of species migrations and enhances locally the relationship between abundance and climate.

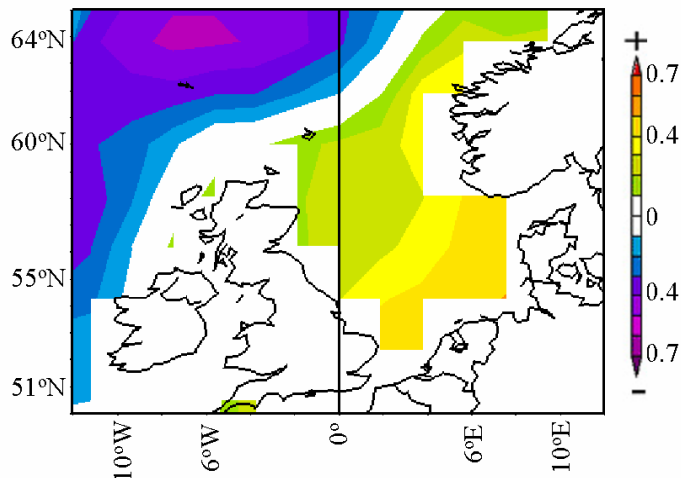


Figure 3.10 Geographic pattern of correlations between the NAO winter index (December to March) and SST (March to June) in the North Sea for the period 1948–2003. Produced using NCAR/NCEP Reanalysis Project [www.cdc.noaa.gov](http://www.cdc.noaa.gov) (Kalnay et al. 1996).

*Regional Patterns**East of Shetland: the North Atlantic Current influence on jellyfish abundance*

The abundance of medusae ESh was negatively related to both the Gulf Stream North Wall (GSNW) and the Barents Sea–Ice Index (BSII) (Figure 3.7). Wintertime Atlantic inflow ESh is also significantly negatively correlated with the NAOI (Planque and Taylor 1998). So, it appears that longer-term changes (of the order of two years) in the composition and/or flow rate of the North Atlantic Current may exert a stronger influence on jellyfish abundance ESh than do concomitant changes in the NAOI. Together the relationships imply that it is the negative phase of the NAOI that is favourable to jellyfish abundance ESh, as it is EoS and WND, but in this high flow region the integrating effect of the ocean on the atmospheric variability appears to delay the impact on jellyfish abundance.

*North of Scotland: the contrasting response of jellyfish to the NAO and the influence of the North Atlantic Current and the Continental Shelf Jet (CSJ)*

The mixed advective region NoS is located on a boundary of the North Sea and Atlantic Ocean. We can see from a NAOI–SST correlative map (Figure 3.10) that the region NoS occupies the intermediate area between positive and negative correlations between the NAOI and SST (in agreement with Planque and Taylor 1998). In contrast to the inflow in the region ESh the inflow NoS by the Fair Isle current during the winter is significantly positively correlated with the NAO (Planque and Taylor 1998). Interestingly, the temperature and the current flow measured in the Svinvøy section (that runs northwest from 62°N on the Norwegian coast to 64°40'N) of the Faeroe–Shetland Channel is also positively correlated with the NAOI (Mork and Blindheim 2000; Orvik et al. 2001). Positive relationships between medusae abundance and both the NAOI and the BSII (high abundance in years of low ice coverage) were found (Figures 3.6D–F and 3.7D), indicating that the environmental conditions NoS are different from elsewhere in the North Sea and/or that changes in the NAO are manifest in differing environmental effects.



*Interacting oceanographic influences*

The high NAO conditions in the 1990s have been associated with a weak North Atlantic Current, a strong Continental Shelf Jet (Reid et al. 1998) and a strong inflow via the Fair Isle Current through the region NoS (Planque and Taylor 1998) (Figure 3.2). Assuming this relationship held during the jellyfish survey period (1971–1986), the high medusa abundances seen NoS under high NAO conditions, and WND/EoS under low NAO conditions, imply that a strong Continental Shelf Jet and weak North Atlantic Current resulted in increased advection to the NoS region of oceanic water, whereas the reverse resulted in elevated advection to more southerly areas of the North Sea through a greater inflow ESh. Modelling has shown that during the first three months of the year the NAOI is related to overall Atlantic inflow to the northern North Sea (including inflow from both the North Atlantic Current and the Continental Shelf Jet); for water between 0 and 150 m deep the NAO is positively correlated with inflow, while for deeper water (150–500 m, that largely derives from the Norwegian trench) the NAOI is negatively correlated with inflow (Reid et al. 2003). The shallow waters dominate the inflow through the shelf edge region NoS, while the major entrance for deep water to the northern North Sea is through the ESh region and from there the current is directed toward the WND region. So the mechanism that explains the opposite relationship between jellyfish abundance and the NAOI prevailing NoS relative to WND could be a wind-driven strengthening of shallow or deep water inflow to the northern North Sea.

*1983, the transport of medusae NoS/ESh to EoS/EoN, and the NAO monthly pattern*

The year 1983 was a statistical outlier in the regression of *A. aurita* abundances between the regions EoS and WND (Figure 3.3D). In the relationship between *A. aurita* abundance and the NAOI EoS, 1983 was not a significant outlier (Bonferroni corrected  $P > 0.10$ ); however, 1983 was still the most influential year (Cook's distance 0.6 for 1983; all others  $< 0.2$ ). The inclusion/exclusion of this year results in a non-significant/significant regression of  $\ln(\text{median } A.$

*aurita* abundance EoS, and also of maximum *C. capillata* abundance EoS, against the NAOI (Figure 3.4D,E). 1983 was clearly an unusual year.

Although the interannual variability in abundance of *A. aurita* in the regions EoS and WND was largely in phase, a separate Atlantic influence may drive dynamics EoS by advecting medusae, nutrients, and/or prey into the region from more northern areas (Figures 3.4D and 3.6) (Frid and Huliselan 1996). In 1983, a late summer inflow of a large body of Atlantic water was deemed to have forced the migration of herring from their northern spawning grounds (near the Orkneys and west of the Shetland Isles) to Aberdeen Bank in the Buchan region EoS, from where they had been absent for the previous 16 years (Corten 1999b). However, herring larvae were found in each of the years 1971–1986 in the Buchan region EoS and their abundance positively correlated with that of *A. aurita* ( $R = 0.66$ ,  $P < 0.05$ ,  $N = 10$ ), suggesting that both herring larvae and medusae are advected into the region (Section 5.4.2). Inspection of the spatial distribution of the median abundance of medusae revealed that only during 1983 were medusae of both *A. aurita* and *C. capillata* abundant in the Fair Isle Current (between the three regions EoS, NoS, and ESh), indicating that this may be the principal source of Atlantic water inflow (Figure 3.2 and Chapter 4). The Fair Isle Current flows south into the Scottish Coastal Current towards the Northumberland coast and also into the Dooley Current that sweeps into the central North Sea, i.e. the two areas where medusae were also unusually abundant in 1983.

Two copepod species, *Candacia armata* and *Metridia lucens*, which are both Atlantic water indicators, were also found in high abundance during 1983 off the coast of Northumberland, in the Continuous Plankton Recorder data (Evans and Edwards 1993). Analysis here of CPR data (obtained from D. Stevens of SAHFOS) for the east of Scotland region, found that 75% and 79% of the total CPR catch between 1971 and 1986 of *C. armata* and *M. lucens* respectively was found in 1983. Corten (1999a) created an index of the combined abundance of *C. armata* and *M. lucens* and found that between 1965 and 1982 the index was lower than its mean for the period 1948 to 1996, but in 1983 the index rose to a value higher than the mean for the first time in 19 years. The low period of the *Candacia/Metridia* index corresponded to a

declining period of the abundance of mackerel (*Scomber scombrus*, an Atlantic fish species) in the north–western North Sea, and a period of increased abundance of sprat (*Sprattus sprattus*, a neritic species), indicating that inflow during this time was relatively low (Corten 1999a). Therefore, the direct air–sea influence of the NAO may have been dominant prior to 1983. Beaugrand et al. (2002b) defined biogeographic groups of Calanoid copepods and found that the number of southern–shelf–edge species and of psuedo–oceanic temperate species increased, north and east of Scotland after 1983, suggesting that they had been brought into the North Sea from the Atlantic via the Continental Shelf Jet.

1983 was also an unusually warm year: a high temperature anomaly (greater than any value between 1977 and 1988) was found at the Norwegian coastal station, Utsira (Furnes 1992), and in the Svinvøy section of the Faeroe–Shetland Channel (Mork and Blindheim 2000). Mork and Blindheim (2000) showed that in the summer of 1983 the warm offshore (200 to 350 km) waters of the Svinvøy section, dominated by the Shelf Edge Current that develops from the North Atlantic Current (Figure 3.2), were restricted to the surface (<150 m deep). In contrast, during the low NAO year of 1987 warm waters extended much more deeply (between 200 and 500 m deep). This difference in the association of deep and shallow water temperature with the NAO mirrors the changing influence of the NAO on inflow to the North Sea (Reid et al. 2003). Reduced sea–ice cover in the Barents Sea in 1983 indicates that warm, saline waters (i.e. Atlantic) penetrated both the North and Barents Seas. As 1983 was the fourth consecutive high NAO year we would expect that this inflowing water was due to a strong CSJ and that this, combined with the switch in the NAO monthly cycle to Type I, elevated the SCC so that nutrients, prey and/or medusae were advected EoS (Figure 3.2). This may explain the outlier year (1983) found in the winter NAOI–*A. aurita* regression EoS.

The highly positive or negative values of the NAOI between December and February largely determine whether or not the overall winter (December–March) NAOI is positive or negative. Therefore I hypothesize that the NAO in these months determines the principal impact on the environment of the North Sea, and that the subsequent switching of the cycle in February and March could

result in a distinct, secondary influence that is felt most strongly along the British north–eastern coast. The mechanism linking the December and February NAOI to the North Sea is most likely through: the direct warming/cooling of the sea surface during the winter by warm/cool air brought in by westerly/easterly winds; the modification of nutrient inflows to the North Sea by wind–driven strengthening or weakening of the Continental Shelf Jet and the North Atlantic Current relative to each other; wind–induced mixing of the water column; and advection of zooplankton prey species as indicated by changes in the distributions of *Calanus finmarchicus* and *C. helgolandicus*. In the regions EoS and EoN, the difference between the March and February NAOI monthly values is also predictive of jellyfish abundance. All regressions between *A. aurita* abundance EoS and EoN against the NAO (March – February) difference index were positive, therefore when the March NAOI value is much greater than the February NAOI value high abundances are expected both EoS and EoN. This implies that a Type I NAO cycle, particularly during February and March, is favourable to medusae in both areas, which agrees with the negative regressions against the winter NAOI found EoS and WND since negative NAOI years generally had a Type I cycle. Between January and April, *A. aurita* ephyrae are being liberated from the benthic scyphistomae and dispersed by advection, therefore wind–driven currents governed by the NAO may be particularly important during this period.

It appears that the NAO winter index can be considered in two ways in terms of its effect on jellyfish abundance. Firstly, the overall phase (high/positive or low/negative) of the cycle and, secondly, the monthly evolution and phase switch between February and March. The overall phase is the dominant driving force on most of the North Sea; however, a weaker secondary force, influencing the prevailing conditions along the north–eastern coast of Britain, may also exist. During the summer, the north Atlantic pressure dipole becomes much weaker and the immediate effect of the NAO on North Sea conditions (e.g. temperature and inflow) becomes non–significant. However, the earlier winter/spring influence has a lasting impact that continues to be evident in the summer months. The final phase of the cycle in March, which is often opposite to the overall phase, may exert a significant secondary

force on wind-driven currents (such as the SCC, Figure 3.2) and on the resulting marine environment during the summer. The combination of the two forces, the primary (overall phase of the December–March index) and secondary (February to March switch), appears to explain the spatial variability between the jellyfish abundance–NAOI relationships. West of northern Denmark, where the direct air–sea effects (such as wind-induced mixing and warming) are the primary driving factors, the overall phase of the NAOI is strongly related with the abundance of medusae. In the intermediate region east of Scotland, the primary influence of the NAOI is related significantly with the abundance of medusae if the extreme year 1983 is excluded. This year appears to be influenced by a late inflow of Atlantic water and the secondary March–February NAO index may account for this. The waters north of Scotland (NoS) appear to be in the ‘Atlantic regime’, in contrast to the ‘North Sea regime’ prevailing west of northern Denmark (WND); and, as a result, the abundance of jellyfish NoS shows a response to the primary influence of the NAOI and also to the BSII, that is opposite to the response of jellyfish abundance WND to these factors. The region east of Shetland is in the area of major oceanic inflow to the North Sea and, as such, jellyfish abundance here is related not with the direct (primary or secondary) influence of the NAO but with the delayed response of the Gulf Stream and the BSII, indicating that the North Atlantic current is the dominant influence in this region.

*Similar spatial variability in the response of crustacean and gelatinous zooplankton to environmental change.*

Beare et al. (2002) reported a north–west/south–east divide in the response of zooplankton abundance to salinity, temperature, and stratification changes in the North Sea. Our finding of contrasting responses by jellyfish to the NAOI are consistent with their analysis. For the north–western North Sea, Beare et al. (2002) found salinity to be correlated positively with abundance of *Calanus finmarchicus* (a northern boreal species) and negatively with an index of abundance of temperate Atlantic taxa (*Centropages typicus*, *Calanus helgolandicus* and *Candacia armata*); the opposite was found in the south–east. Beare et al. (2002) suggested that the temperate Atlantic taxa were most likely

brought into the northern North Sea via the CSJ inflow (NoS) that feeds the Fair Isle Current, in agreement with Beaugrand (2002) (Figure 3.2). In contrast, Beare et al. (2002) argued that *Calanus finmarchicus* is brought into the North Sea via the North Atlantic Current (flowing ESh). The oscillation between high abundance of *Calanus finmarchicus* and of *C. helgolandicus* in the North Sea has been shown to be correlated with fluctuations in the NAOI (Planque and Taylor 1998). The advection of *C. finmarchicus* into the North Sea from its overwintering area in the deep Shetland canal mirrors that of the change in distribution of jellyfish abundance in the North Sea. Years of high NAOI result in a more northern distribution and low NAOI years a more southern distribution of jellyfish and *C. finmarchicus*.

#### *Pelagic–benthic community coupling*

Scyphozoan jellyfish have both benthic (scyphistomae) and pelagic (medusae) stages. Changes in the abundance of medusae in the North Sea might be due to an impact by hydroclimatic factors on the benthic or the pelagic stage, or on both. Strobilation of the scyphistomae (i.e. the development of ephyrae) is triggered environmentally, usually following a rapid drop in temperature (Russell 1970; Brewer and Feingold 1991; Omori et al. 1995; Lucas 2001). Lucas (2001) suggested that “*the time-period between the initiation of strobilation and actual release of ephyrae probably depends on the winter minimum temperature and food availability affecting the strobilation process*” and Omori et al. (1995) proposed that the “*environmental conditions during the polyp stage may be the underlying causes of mass occurrences*” of *A. aurita*. I have emphasized the effect of climate on the distribution of medusae, but changes in prey levels and other environmental effects could also lead to the observed changes in the abundance of medusae, possibly through increased strobilation (Purcell 2005). The warm sea temperature in 1983 may also have contributed to the extremely high medusa abundance, since high temperatures can increase the rate of strobilation and ephyra production (Purcell et al. 1999; Ma and Purcell 2005).

A shift in the community composition of the plankton between 1979 and 1980 (identified using CPR data for 1973 to 1988) in the eastern North Sea

(CPR area C1, which includes the region WND) but not the western North Sea was reported by Austen et al. (1991). A shift delayed by one year in the benthos in the Skagerrak and off the coast of Northumberland was also reported, indicating that the pelagic and benthic communities in the eastern, but not the western, North Sea, are linked (Austen et al. 1991). The time lag of the benthic shift was attributed to the slow reproductive rates of the benthic species relative to the plankton. Austen et al. (1991) noted that the plankton east of Northumberland is influenced strongly by Atlantic inflow, and they suggested that this might explain the difference in the strength of the pelagic–benthic coupling there. Similarly, I have suggested that the rate and composition of Atlantic inflow to the North Sea may explain the observed deviations of *Aurelia aurita* abundance from the NAO relationship east of Scotland and Northumberland. If the benthic communities are indeed linked, then I may hypothesize that the NAO–related changes in the North Sea alter strobilation (during January–April) of the scyphistomae, both EoS and WND, and that the response WND is greatest due to the minimized effects of Atlantic water on the pelagic stage there.

The contrasting response of jellyfish abundance NoS to the NAOI may also be explained by the response of benthic scyphistomae. Dippner and Kroncke (2003) report a positive relationship between the NAOI and macrozoobenthos abundance and biomass in the southern North Sea in Spring between 1978 and 1999. Tunberg and Nelson (1998) found significant ( $P < 0.05$ ) positive and negative correlations between the NAOI and macrobenthic community biomass along the Swedish west coast. Correlations were negative inshore and at a deep (300 m) station but positive at two mid–depth (50 and 100 m) stations. Therefore the location and depth of scyphistomae may be important in determining the response of jellyfish production to environmental changes associated with the NAO.

#### *Plaice age–1 recruitment and Cyanea capillata abundance*

The positive correlation between the abundance of jellyfish WND and the recruitment success of plaice indicates that much of the interannual variation in

both species is driven by similar changes in the hydroclimatic environment. WND, however, neither measure correlates with the NAOI. The abundance of plaice in the Thames estuary has been shown to be negatively correlated with the NAOI (Attrill and Power 2002). Wind-induced currents and the intrusion of Atlantic water into the North Sea via the English Channel have been suggested to advect plaice eggs and larvae towards their nursery grounds along the Dutch, German, and Danish coasts (Wegner et al. 2003). At times, *C. capillata* is also highly abundant WND and may be influenced by similar advective processes.

Although the positive correlation between plaice recruitment and *C. capillata* abundance indicates that there is no significant predatory impact on the fish population by jellyfish, this does not mean that *C. capillata* do not inflict some mortality on plaice eggs and larvae. *Aurelia aurita* have been recorded consuming newly hatched plaice at a hatchery in Port Erin (Russell 1970), and plaice larvae are highly susceptible to predation by these medusae (Bailey and Batty 1984). The larger *C. capillata* medusae, with greater surface area than *A. aurita* and many more and longer tentacles, may be a more successful predator on plaice than *A. aurita*. Plaice spawn from mid-December to early March in the southern and central North Sea, and the larvae may spend up to three months in surface waters before reaching the near-shore nursery areas (Wegner et al. 2003). *Cyanea capillata* ephyrae may appear from February onwards, small medusae are present in April and May, while larger medusae are commonly found between June and October; very large animals may even overwinter. Even small *C. capillata* may consume fish eggs and larvae (Purcell and Arai 2001) and these jellyfish may prey on those plaice eggs and larvae that are spawned toward the end of the season both in the area WND and also on those that are swept in the circulation currents from their spawning grounds further south.

#### *Salmon landings and jellyfish abundance*

The inverse relationships found here between *Cyanea lamarckii* abundance and salmon landings are unlikely to indicate a direct negative impact by these relatively small medusae on adult fish. However, pink salmon (*Oncorhynchus gorbuscha*) and *C. capillata* in Prince William Sound, Alaska, have been shown



to be potentially direct competitors, particularly for larvacean prey (Purcell and Sturdevant 2001). Salmon landings were significantly regressed against the maximum abundance of all jellyfish species when the NAOI was included as an additional explanatory variable; this result may suggest that either there is a climatically mediated relationship between jellyfish and salmon or that salmon landings are linked to environmental changes as indicated by changes in the abundance of jellyfish and the NAOI. A high abundance of jellyfish in the North Sea, or a negative NAOI, may indicate poor local conditions for feeding by salmon, resulting in an early/strong migration northwards to feeding grounds in the Norwegian and Greenland Seas and thus lower landings.

Jellyfish are highly abundant during the summer, particularly in coastal areas of the North Sea, so it is likely that salmon post-smolts may come into close proximity with jellyfish aggregations as soon as they emerge from the rivers. Dense aggregations of jellyfish (including *A. aurita* and *Cyanea* spp.) have been particularly damaging to farmed salmon. When small medusae and nematocysts shed from larger animals have passed into the cages/nets they have caused severe lesions in, and the death of, thousands of farmed salmon (Båmstedt et al. 1998). In the wild, fish may actively avoid jellyfish (Xian et al. 2005) so dense and widespread aggregations of medusae in the North Sea may encourage a northerly migration. Therefore the low salmon landings, when jellyfish abundances are high, might be due in part to active avoidance of the jellyfish or of food-impooverished areas. Alternatively, jellyfish abundance may be high due to an absence of salmon. Catches of Atlantic salmon in the North Sea have been found to be negatively related to northern hemisphere temperatures in the years 1966 to 2000 (Beaugrand and Reid 2003). Therefore it is probable that both salmon landings and the abundance of *C. lamarckii* have changed similarly with the environment.

### **3.6. Summary**

Gelatinous zooplankters are important predators of zooplankton, including fish eggs and larvae (Purcell 1997; Purcell and Arai 2001). Many gelatinous zooplankton populations have shown increases in biomass (Table 1.5) as they exploit rapidly opening environmental niches (Alldredge 1983, cited in Purcell and Arai 2001), whether these niches are presented through anthropogenic

disturbance (Arai 2001; Brodeur et al. 2002; Pérez-Ruzafa et al. 2002) or climatic change (Brodeur et al. 1999; Dawson et al. 2001). Due to their voracious predatory feeding (Frandsen and Riisgård 1997), which may exert top-down control (Schneider and Behrends 1998), jellyfish are important members of the zooplankton and are capable of altering the composition of the zooplankton community and inhibiting fisheries recovery (Purcell and Arai 2001).

A few geographic regions have shown reductions in gelatinous zooplankton abundance and diversity (Benovic et al. 1987; Buecher and Gibbons 2000; Mills 2001), thus not all changes are necessarily favourable to these adaptable animals, and reliable surveying of populations is required in order to gain a fuller understanding of how populations are changing and of the impact that jellyfish exert on the marine ecosystem. As jellyfish are difficult to sample quantitatively using conventional netting techniques, acoustic methods that could be used quantitatively and rapidly over wide areas should continue to be developed. Further study is required to explore the aforementioned and other possible effects of jellyfish on North Sea fisheries. Ecosystem based analyses of the marine environment should be conducted in order to examine the regulatory role of medusae on zooplankton abundance and fish recruitment, and the regional impact of jellyfish ought to be considered in ecosystem management schemes.

## **Chapter 4**

### **The distribution of medusae in the North Sea in relation to hydroclimatic variability and zooplankton community change**

The work described here is in review:

Lynam C.P., Beare D. J., Hay S.J. and A.S. Brierley. The distribution of medusae in the North Sea in relation to hydroclimatic variability and zooplankton community change. *Journal of Marine Systems*

I estimate that I contributed 85% of the effort towards this paper, which can be broken down into the following five equally weighted areas: Data collection/preparation 70 %, I gathered environmental data from ICES and plankton data from SAHFOS, I had already prepared the jellyfish data from the raw paper files; Inspiration 90 %; Analysis 80 %, where the remainder is attributable to modelling suggestions from DJB and SJH; Conclusions 100 %; Publication 85 %, the paper was written by me but reviewed by ASB.

#### **4. The distribution of medusae in the North Sea in relation to hydroclimatic variability and zooplankton community change.**

##### **4.1. Abstract**

The abundance of jellyfish (*Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata*) in the North Sea during 1971–1986 has previously been linked to fluctuations in the winter North Atlantic Oscillation index and changes in the northerly extent of the Gulf Stream (Chapter 2, Lynam et al. 2004; 2005a). Here, the mechanisms by which long-term hydroclimatic changes may be linked to changes in jellyfish abundance are explored. To identify whether or not there is change in the distributions of these species of jellyfish as a result of hydroclimatic variability, the probability of capture of each species of jellyfish, fish larvae, copepods and euphausiids was mapped through modelling by General Additive Models (GAMs). Hydrographic data (surface and bottom temperature and salinity) were similarly mapped to compare environmental and biological trends. Copepod species were classified into groups that are considered indicative of both community change and variability in the composition of oceanic inflow to the North Sea. Contrasting region-specific mechanisms were identified through which hydroclimatic changes may influence jellyfish abundance and distribution: west of Denmark, where oceanic influences are relatively minor, it appears that a low NAO may indicate an increased retention of medusae, leading to high medusa abundance there during the summer; east of Shetland, high jellyfish abundance may result from a strong inflow of Norwegian Sea/Arctic water, as indicated by a high probability of capture of *Calanus finmarchicus* there during spring and summer; north of Scotland, a sustained positive NAO may increase the advection of nutrients by the Continental Shelf Jet, stimulating a phytoplankton bloom, resulting in a high abundance of warm-temperate species during the spring and subsequently good conditions for jellyfish development. Negative correlations between jellyfish and larval fish probability of capture, and between jellyfish probability of capture and larval fish abundance, are found around the Scottish eastern, and Danish north-western, coasts, which may indicate detrimental impacts by jellyfish on larval survival.

## 4.2. Introduction

Jellyfish (Scyphozoa) are an important, yet often overlooked, component of the North Sea ecosystem. Medusae are carnivorous and consume crustacean zooplankton (the major prey for many fish) and ichthyoplankton in such great numbers that jellyfish may impact detrimentally on the recruitment of commercial fisheries (Purcell and Arai 2001; Purcell 2003). Interannual variability in the abundance of jellyfish in the North Sea has been linked to variability in the climate, as encompassed by changes in the North Atlantic Oscillation Index (NAOI) and the northerly extent of Gulf Stream, and by changes in the distribution of sea ice in the Barents Sea (Chapters 2 and 3, Lynam et al. 2004; 2005a). The NAOI has similarly been linked to changes in the abundance of jellyfish in Chesapeake Bay, and hydroclimatic fluctuations are believed to drive the periodic occurrence of *Pelagia noctiluca* in the Mediterranean (Purcell 2005; Purcell and Decker 2005). Jellyfish thus seem sensitive indicators of hydroclimatic variation. Hydroclimatic variability has the potential to alter relationships within and between trophic levels through changes in the marine environment (i.e. on temperature, salinity and wind-driven currents) and subsequent shifts in zooplankton community composition (Reid et al. 2003; Beaugrand 2004; Purcell 2005). Jellyfish may ‘bloom’ rapidly to a position of dominance within the food web and thus jellyfish may play an important role in community reorganisation following environmental change (Pérez-Ruzafa et al. 2002; Sommer et al. 2002; Stibor et al. 2004).

The wide-reaching influence of the North Atlantic Oscillation Index (NAOI, Sections 2.1 and 3.1) is demonstrated by a lagged change (2–3 year delay) in the northerly extent of the Gulf Stream (positive NAOI → more northerly path of the Gulf Stream) and in the sea-ice coverage of the Barents Sea (positive NAOI → reduced ice coverage). Atmospheric variability may influence sea temperature and salinity, phytoplankton production and zooplankton abundance (Drinkwater et al. 2003). I proposed in Chapter 2 that NAOI-driven fluctuations in the environment might impact upon the production, development or dispersal of medusae in the North Sea. In Chapter 3, I showed that the influence of the NAOI on the abundance of jellyfish in the North Sea was region-specific (i.e. a positive relationship was shown between

the abundance of jellyfish north of Scotland, whereas a negative relationship was found west of northern Denmark, Figure 3.5) and was likely to be modified by local hydrographic influences (Lynam et al. 2005a). Here I seek to integrate these findings and examine the relative importance of temperature, salinity, advection, phytoplankton production, and zooplankton abundance to the distribution of jellyfish in the North Sea. Generalised Additive Models (GAMs) are used to map the spatial distributions of Continuous Plankton Recorder (CPR) plankton and the prevailing hydrographic conditions (salinity and temperature) in the North Sea. Similarities in temporal change by ICES grid square ( $1^{\circ}$  latitude by  $0.5^{\circ}$  longitude), and in pre-selected regions identified from previous study by Hay et al. (1990), were found through linear correlations between the probability of capture of jellyfish species and zooplankton groups, or between jellyfish and environmental variables. As jellyfish are important predators on zooplankton and may impact on the survival of herring larvae (Möller 1984; Purcell 2003), I also consider the possible impact of jellyfish on those fish larvae (predominantly Clupeids, Coombes 1980) sampled by the CPR during the herring spawning period.

### 4.3. Methods

#### 4.3.1. Data collection

North Sea phytoplankton colour data and zooplankton abundance data for the period 1971 to 1987 were obtained from the Sir Alister Hardy Foundation For Ocean Science (SAHFOS) Continuous Plankton Recorder (CPR) dataset (Hays and Lindley 1994; Warner and Hays 1994; Batten et al. 2003). Data for fish larvae, euphausiid spp. and the following copepod species were analysed: *Acartia* spp.; *Calanus finmarchicus*; *Calanus helgolandicus*; total *Calanus* spp.; *Candacia armata*; *Centropages hamatus*; *Centropages typicus*; total euphausiid spp.; *Metridia lucens* and *Temora longicornis*. Copepod species were classified into the following four groups, which characterise the origin of oceanic inflow into the North Sea: Atlantic/sub-Arctic (*Calanus finmarchicus*), warm-temperate (*C. helgolandicus*, *Candacia armata* and *Centropages typicus*), cold-temperate (*Acartia* spp. and *M. lucens*), and neritic/residents (*T. longicornis*, and *C. hamatus*) (Beare et al. 2002; Beaugrand et al. 2002a). Total *Calanus* and

euphausiid spp. were considered to indicate the availability of prey for fish larvae (dominantly planktivorous Clupeids during June-September, Coombes 1980).

Surface and bottom salinity and temperature data, where the surface data corresponds to the top 5 m and the bottom data to within 20 m of the seabed, or 50 m if the depth was >100 m, were supplied by ICES. The North Atlantic Oscillation Index (NAOI) data was obtained from the National Center for Atmospheric Research, Climate and Global Dynamics Division, Boulder, CO, USA. The standard winter (December - March) NAOI of the normalized sea level pressure (SLP) difference between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (Ottosen et al. 2001; Hurrell et al. 2003) was used in order to simplify analyses of the influence of climatic fluctuations. Gulf Stream data were obtained from the Plymouth Marine Laboratory, UK; the annual mean of the 1st Principal Component was chosen because this minimises variability due to the meandering of the stream (Taylor 1995). The Barents Sea–Ice Index was supplied by the Institute of Marine Research, Bergen, Norway.

For the period 1971 to 1986 (not 1984), medusa presence/absence was determined in 1° latitude by 0.5° longitude grid squares of the North Sea from the raw data collected during the ICES International 0–group Gadoid Surveys of the North Sea (Section 2.2, Hay et al. 1990). The jellyfish catch data were geographically patchy, and modelled using General Additive Models (GAMs) to produce continuous distribution maps of the probability of capture of medusae (see *Modelling*, Section 4.2.2). The smoothed jellyfish data were compared to the similarly–modelled distributions of plankton, and to maps of surface and bottom temperature and salinity data. For each grid square, linear correlations were computed between pairwise combinations of the distribution maps, e.g. the probability of capture of *Aurelia aurita* and surface salinity. The significance value of each correlation (i.e. at each grid cell) was calculated and corrected using the expected false discovery rate, so that spurious correlations were rendered insignificant (Benjamini and Hochberg 1995). Correlative maps were produced, showing the correlation coefficients for those grid squares where the significance value once corrected ( $p_{\text{cor}}$ ) was < 0.05. Time series were further examined at the regional level for areas where jellyfish were most abundant (i.e.

mean values were computed for the regions: East of Shetland; East of Scotland; North of Scotland; and West of Denmark, Figure 4.2) in order to evaluate the importance of the correlations found between the maps.

### 4.3.2. Modelling

In this section, I use the term **prevalence** to signify the **probability of capture** of each species or group of species within each grid square of the North Sea.

#### 4.3.2.1. Gelatinous and crustacean zooplankton

Zooplankton abundance data were transformed into binary variables (one per set) indicating presence/absence. All computation was conducted in *R Version* 1.8.1 (2003). The probability of capture of each species within a grid square was estimated with the following logistic model (Collett 1991):

$$\ln(P_{i,j,t1,t2} / (1 - P_{i,j,t1,t2})) = \text{smooth}(i,j,t1,t2) + \varepsilon \quad (1)$$

where  $P_{i,j,t1,t2}$  is the estimated probability of recording a species or group at locations  $i, j$ , at year  $t1$  and in month  $t2$ , and the binomial error term  $\varepsilon$  has mean zero. Locations  $i$  and  $j$  represent the Lambert conical distance-preserving transformation of latitude and longitude. Year and month are absolute times. For jellyfish, however, complete monthly data were not available since sampling was only conducted throughout the North Sea during June and July (additional sampling in August occurred in 1971 and 1972 only). Therefore, the monthly variable ( $t2$ ) was excluded from the jellyfish model and the probability of occurrence of jellyfish ( $P_{i,j,t1}$ ) was calculated from the latitude, longitude and year variables using combined June and July data.

The size of the smoothing parameter in equation 1 relates to the amount, or geographic coverage and temporal span, of data used in the averaging process. A small smoothing parameter produces an irregular output, while a large smoothing parameter produces a less variable output. The smoothing parameters were selected automatically using penalised thin plate regression splines, by the *mgcv* algorithm in *R*, through minimisation of the *UnBiased Risk Estimator (UBRE)* (Wood 2004) so that a balance between over- and under-fitted models was found. The *UBRE* can be considered as an approximation to the *Akaike information criterion (AIC)* score. Residual analyses, chi-square tests, and



visual inspection of the fitted and interpolated values were also used to assess adequacy of fit (Cleveland 1993; Beare and McKenzie 1999; Beare et al. 2002).

#### 4.3.2.2. Temperature, salinity, phytoplankton and fish larvae

The surface and bottom temperature and salinity distributions, abundance of fish larvae and the phytoplankton colour index were modelled using the following general additive model:

$$X_{i,j,t1,t2} = \text{smooth}(i,j,t1,t2) + e \quad (2)$$

where the response variable  $X$  was the estimated temperature, salinity, phytoplankton colour, or zooplankton abundance. The error term,  $e$ , had constant unit variance and zero mean; the other variables are as for equation 1.

The fitted parameters of the models (equations 1 and 2) were used to interpolate over a spatio-temporal grid of the North Sea (Figures 4.1 and 4.2). Latitude was resolved at one-degree intervals from 54°N–61°N, and longitude at half-degree intervals from 4°W–9°E. The winter (December–March) North Atlantic Oscillation Index (NAOI), Barents Sea-Ice Index (BSII), and the Gulf Stream North Wall (GSNW) data were also mapped onto the North Sea grid to enable correlative analyses by grid square; these yearly data were considered to be spatially invariable within years.

### 4.4. Results

#### 4.4.1. Gelatinous zooplankton distribution

A combined map of the prevalence (probability of capture) of each species shows that during the entire survey period jellyfish were found most commonly near to the Danish and Scottish coasts and were least likely to be found in the central North Sea (Figure 4.1). The temporal change from 1971–1986 (not 1984) in the distribution of the jellyfish *Aurelia aurita*, *Cyanea lamarckii*, and *Cyanea capillata* is shown in Figure 4.2. Each species became more prevalent (higher probability of capture) around the Scottish coast, and the distribution of *C. capillata* in particular increased dramatically to become widespread throughout the North Sea, in the early 1980s. The distribution of *A. aurita* was much more variable than that of either *Cyanea* spp; although the overall probability of catching *A. aurita* increased during the survey period, decreases

were found in the eastern North Sea during 1976–1979 and east of Scotland during 1980–1981.

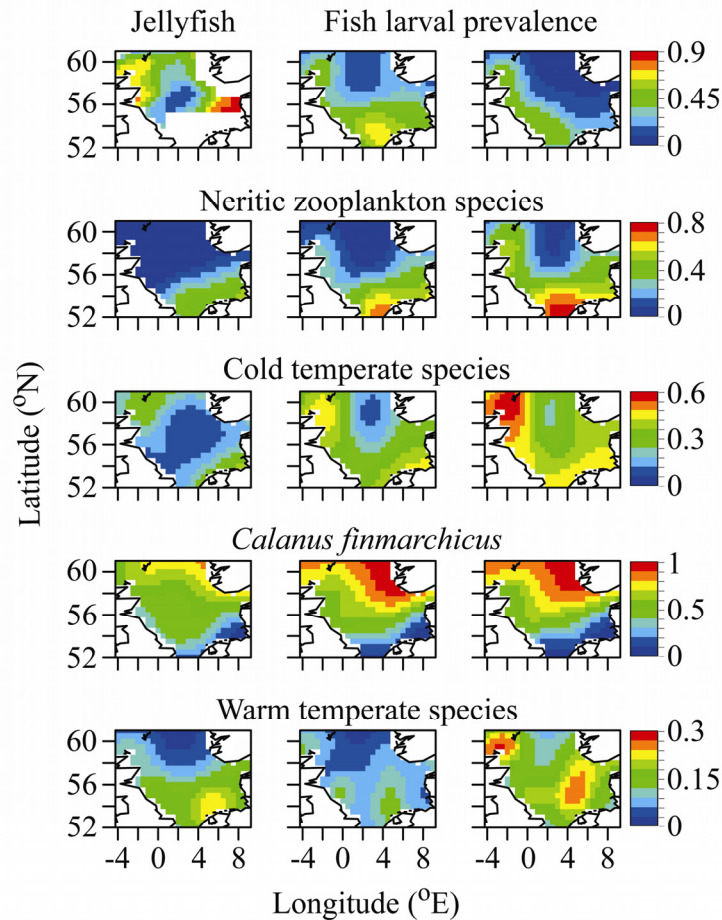


Figure 4.1 The probability of occurrence of zooplankton in the North Sea for all years combined (1971–1986) for the following species groupings: jellyfish (*Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata*) during summer (01 June to 31 July, nb. no 1984 data) (top left); fish larvae during summer (top centre) and autumn (01 August to 30 September) (top right); neritic species (second row), cold-temperate species (third row), *Calanus finmarchicus* (fourth row) and warm-temperate species (fifth row) during winter (01 December to 28 February, left), spring (01 March to 31 May, centre) and summer (right). Note: fish larvae data is dominated by clupeids during summer and autumn only.

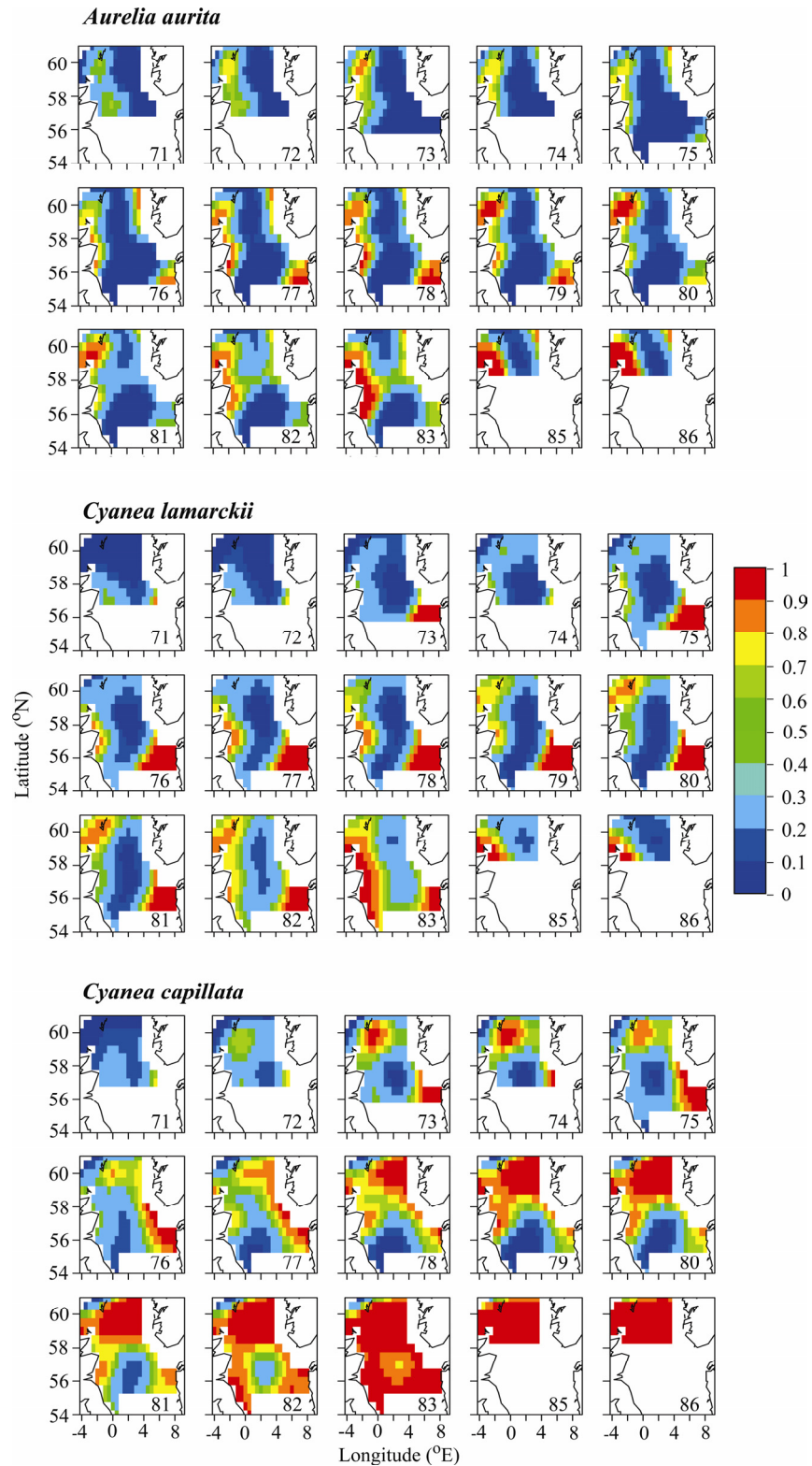


Figure 4.2 Probability of occurrence of *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* in the North Sea during summer (1 June to 31 July). Year labels are shown on each map in the format 19xx.

## 4.4.2. Correlations with jellyfish prevalence

### 4.4.2.1. Temperature

Over the entire survey period (1971–1986), the sea surface temperature (SST) showed a strong gradient across the North Sea from an average of 17°C during the summer (June–July) in the south–east to 11°C in the north–west (Figure 4.3). The sea bottom temperature (SBT) map during the summer showed a similar gradient with warm temperatures (up to 17°C) in the shallow coastal areas and coldest temperatures (down to 5°C) in the north–east, which is the dominant area for deep inflow of Atlantic Ocean and Norwegian Sea waters. Significant ( $P_{cor} < 0.05$ ) negative correlations with SST during spring (March–May) and summer (June–July) were found for each species' probability of capture north of Scotland during the summer (Figure 4.4 and Table 4.1). Cold SST east of Scotland during spring was significantly linked to the high prevalence of *Cyanea capillata* and *Aurelia aurita* there during summer. High mean prevalences of *C. capillata* and *A. aurita* also appear to be linked to the SST west of Denmark: for *C. capillata* the correlation appears positive during winter and spring; for *A. aurita* the correlation appears negative during spring and summer (Table 4.1).

The sea bottom temperature (SBT) correlated with *C. capillata* prevalence similarly to the correlation with SST (Figure 4.4). For all species, the SBT correlations appear strongest during the spring. All species show an additional negative correlation with summer SBT in the western North Sea, east of Northumberland. The correlation north of Scotland with SBT is much weaker than the link to SST. For *A. aurita*, the negative correlations with SST west of Denmark were also shown in the SBT correlation (Table 4.1); however, the link to SBT appears to be earlier than that to SST (Figure 4.4). The correlative map for *C. lamarckii* against SBT is the most different to that shown with SST. A negative correlation east of Scotland with SBT is significant during the spring. While in the far north both positive (in the north–west) and negative (north–east) correlations were found for spring and summer SBT with *C. lamarckii* probability of capture (Figure 4.4).

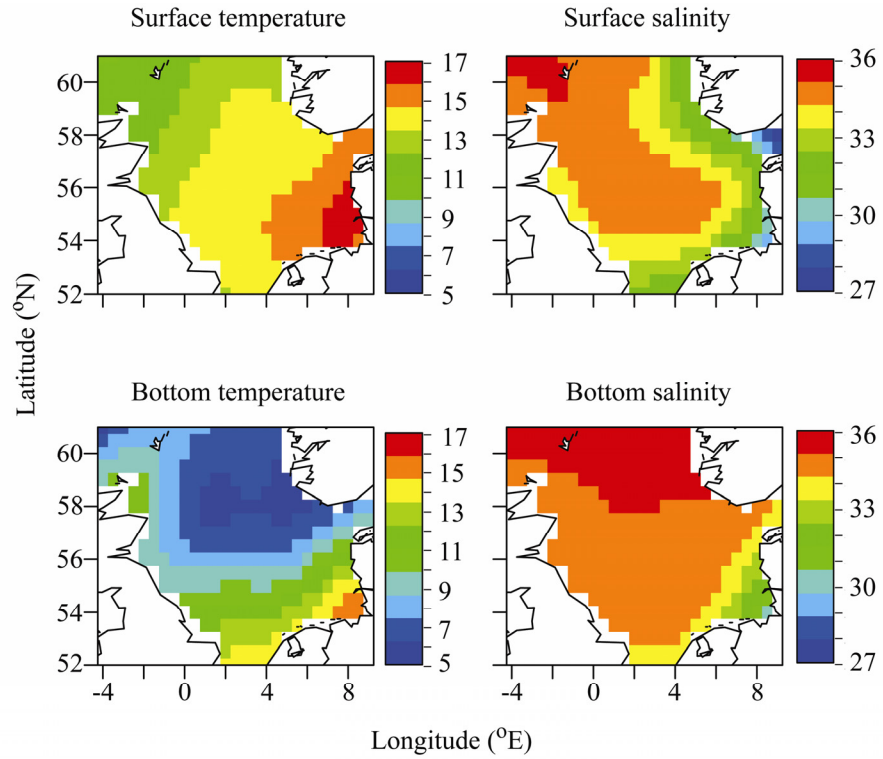


Figure 4.3 Maps of surface and bottom temperature and salinity in the North Sea during the summer (1 June to 31 July) for all years combined (1971–1986).

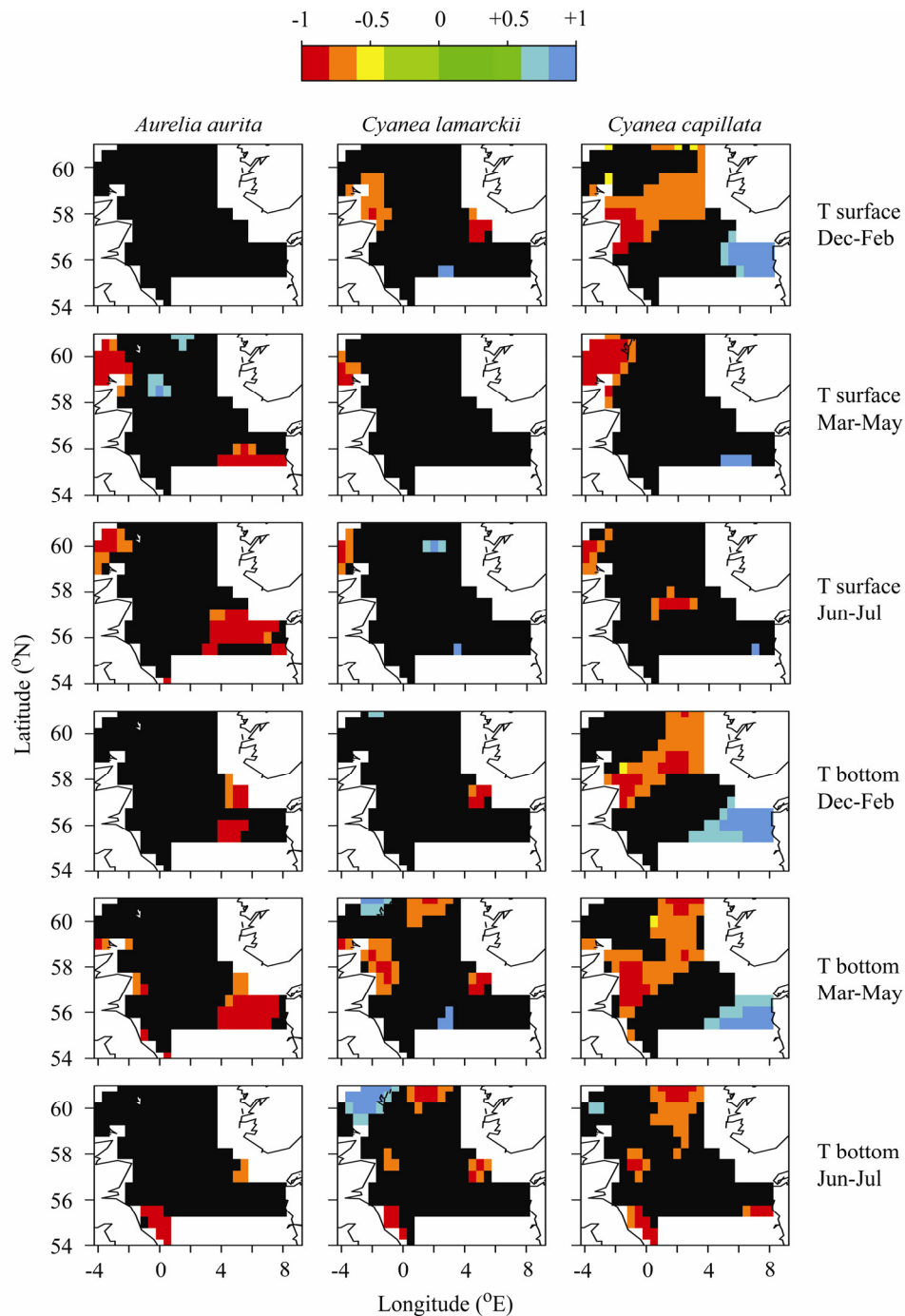


Figure 4.4 Maps showing significant correlations between the probability of occurrence of *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* and surface temperature during December–February, March–May, June–July and with bottom temperature during December–February, March–May, June–July. Data covers the period 1971 to 1986 (not 1984, below 56° latitude only 1971 to 1973). The coloured areas show those grid squares where the correlation is significant ( $P_{cor} < 0.05$ ), black areas show non-significant correlation and white areas indicate no data.

| Region                   | Jellyfish summer prevalence | Model period | Temperature surface |          |                        | Temperature bottom |          |                        | Salinity surface |          |                        | Salinity bottom |          |                        |     |
|--------------------------|-----------------------------|--------------|---------------------|----------|------------------------|--------------------|----------|------------------------|------------------|----------|------------------------|-----------------|----------|------------------------|-----|
|                          |                             |              | <i>r</i>            | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>           | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>         | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>        | <i>p</i> | <i>p<sub>cor</sub></i> |     |
| East of Shetland         | <i>Aurelia aurita</i>       | winter       |                     |          |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
|                          |                             | spring       |                     |          |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
|                          |                             | summer       |                     |          |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
|                          | <i>Cyanea lamarckii</i>     | winter       |                     |          |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
|                          |                             | spring       | -0.58               | *        |                        | -0.53              | *        |                        |                  |          |                        |                 | -0.91    | ***                    | *** |
|                          |                             | summer       |                     |          |                        | -0.61              | *        | *                      |                  |          |                        |                 |          |                        |     |
| <i>Cyanea capillata</i>  | winter                      | -0.59        | *                   | *        | -0.52                  | *                  |          |                        |                  |          |                        | -0.74           | **       | **                     |     |
|                          | spring                      | -0.60        | *                   | *        |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
|                          | summer                      |              |                     |          | -0.56                  | *                  |          |                        |                  |          |                        | -0.52           | *        |                        |     |
| East of Scotland         | <i>Aurelia aurita</i>       | winter       | -0.59               | *        |                        | -0.72              | **       | *                      |                  |          |                        |                 | -0.87    | ***                    | *** |
|                          |                             | spring       | -0.65               | *        | *                      |                    |          |                        |                  |          |                        |                 | -0.63    | *                      |     |
|                          |                             | summer       |                     |          |                        |                    |          |                        |                  |          |                        |                 | -0.81    | ***                    | **  |
|                          | <i>Cyanea lamarckii</i>     | winter       |                     |          |                        | -0.62              | *        | *                      |                  |          |                        |                 | -0.72    | **                     | **  |
|                          |                             | spring       |                     |          |                        |                    |          |                        |                  |          |                        |                 | -0.64    | *                      | *   |
|                          |                             | summer       |                     |          |                        |                    |          |                        |                  |          |                        |                 | -0.60    | *                      |     |
| <i>Cyanea capillata</i>  | winter                      | -0.81        | **                  | **       | -0.64                  | *                  | *        |                        |                  |          |                        | -0.91           | ***      | ***                    |     |
|                          | spring                      | -0.77        | **                  | **       | -0.91                  | ***                | ***      |                        |                  |          |                        | -0.72           | **       | *                      |     |
|                          | summer                      |              |                     |          |                        |                    |          |                        |                  |          |                        | -0.95           | ***      | ***                    |     |
| West of northern Denmark | <i>Aurelia aurita</i>       | winter       | -0.69               | *        |                        | -0.80              | **       | *                      |                  |          |                        |                 | -0.63    | *                      |     |
|                          |                             | spring       | -0.87               | **       | **                     | -0.90              | ***      | **                     |                  |          |                        |                 | -0.91    | ***                    | *** |
|                          |                             | summer       | -0.86               | **       | **                     | -0.80              | **       | *                      |                  |          |                        |                 | -0.63    | *                      |     |
|                          | <i>Cyanea lamarckii</i>     | winter       |                     |          |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
|                          |                             | spring       |                     |          |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
|                          |                             | summer       |                     |          |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
| <i>Cyanea capillata</i>  | winter                      | 0.92         | ***                 | **       | 0.95                   | ***                | **       |                        |                  |          |                        |                 |          |                        |     |
|                          | spring                      | 0.80         | **                  | *        | 0.90                   | ***                | **       |                        |                  |          |                        |                 |          |                        |     |
|                          | summer                      | 0.69         | *                   |          |                        |                    |          |                        |                  |          |                        |                 |          |                        |     |
| North of Scotland        | <i>Aurelia aurita</i>       | winter       |                     |          |                        | -0.62              | *        | *                      |                  |          |                        |                 |          |                        |     |
|                          |                             | spring       | -0.90               | ***      | ***                    | -0.73              | **       | *                      |                  |          |                        |                 |          |                        |     |
|                          |                             | summer       | -0.68               | **       | *                      | -0.73              | **       | *                      |                  |          |                        |                 | -0.91    | ***                    | *** |
|                          | <i>Cyanea lamarckii</i>     | winter       |                     |          |                        | -0.63              | *        | *                      |                  |          |                        |                 |          |                        |     |
|                          |                             | spring       | -0.89               | ***      | ***                    | -0.80              | ***      | **                     |                  |          |                        |                 |          |                        |     |
|                          |                             | summer       | -0.75               | **       | **                     | -0.52              | *        |                        |                  |          |                        |                 | -0.89    | ***                    | *** |
| <i>Cyanea capillata</i>  | winter                      |              |                     |          | -0.68                  | **                 | *        |                        |                  |          |                        |                 |          |                        |     |
|                          | spring                      | -0.89        | ***                 | ***      | -0.71                  | **                 | *        |                        |                  |          |                        |                 |          |                        |     |
|                          | summer                      | -0.77        | ***                 | **       | -0.59                  | *                  | *        |                        |                  |          |                        | -0.88           | ***      | ***                    |     |

Table 4.1 Linear correlation coefficient (*r*), correlation significance (*p*) and the significance level once corrected for multiple tests (*p<sub>cor</sub>*) for correlations between the probability of capture (prevalence) of jellyfish during the summer by region with hydrographic variables during winter (1 December to 28 February), spring (1 March to 31 May) and summer (1 June to 31 July). \* <0.05, \*\* <0.01, \*\*\* <0.001

#### 4.4.2.2. Salinity

The correlative maps of surface and bottom salinity against jellyfish prevalence (Figure 4.5) suggest that low salinity during spring and summer is most indicative of high jellyfish prevalence during the summer. However, the winter bottom salinity levels east of Scotland may also influence jellyfish prevalence there (Table 4.1), and in particular *C. capillata* prevalence (Figure 4.5). Whether or not jellyfish are found in the central and north–eastern North Sea is largely determined by the salinity of surface water there during the spring and summer. The prevalence of jellyfish north of Scotland was significantly ( $P_{cor} < 0.05$ ) negatively correlated with the bottom salinity during the spring and summer and also with the surface salinity during the summer (Table 4.1).



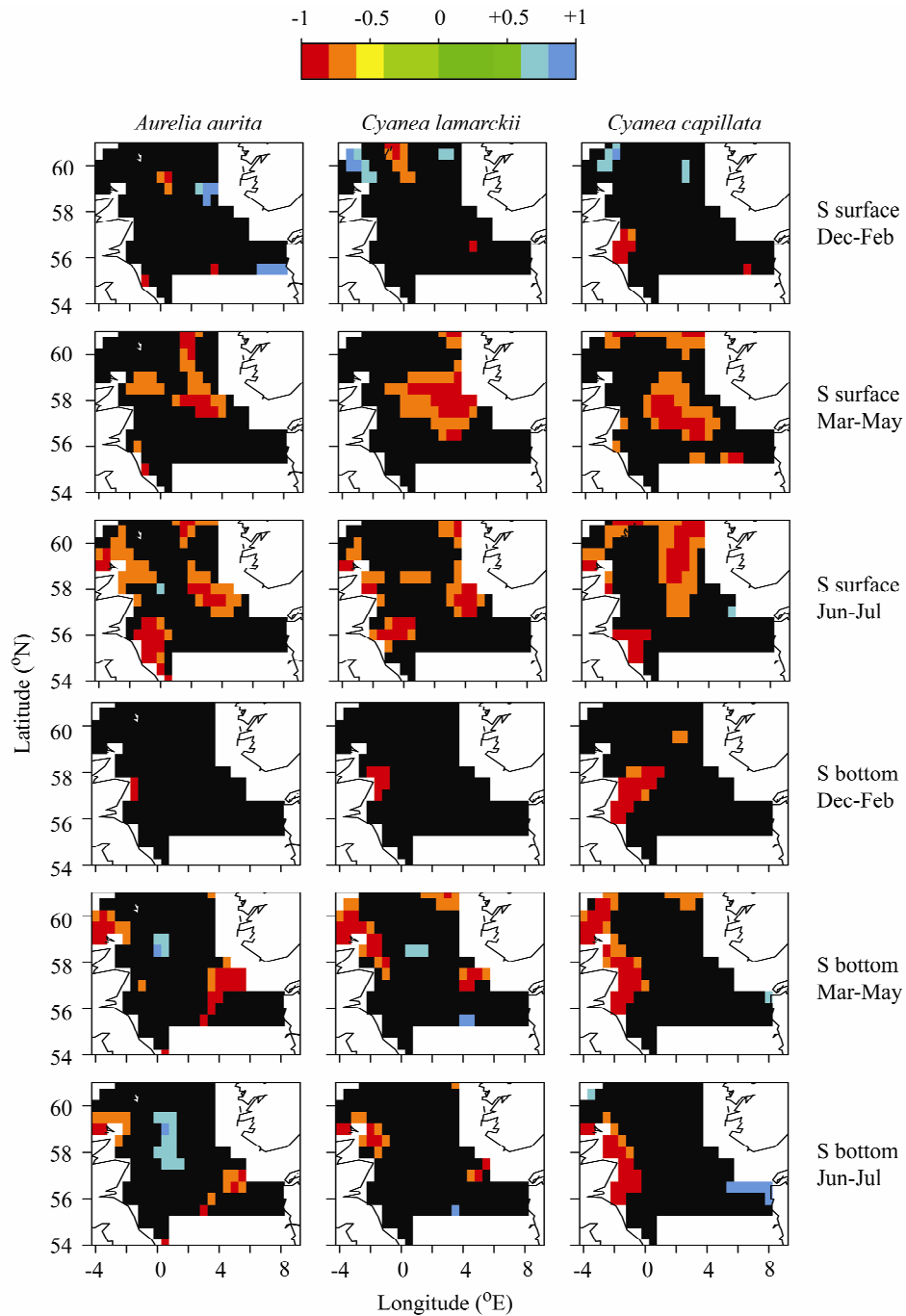


Figure 4.5 Maps showing significant correlations between the probability of occurrence of *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* and surface salinity during December–February, March–May, June–July and with bottom salinity during December–February, March–May, June–July. Data covers the period 1971 to 1986 (not 1984, below 56° latitude only 1971 to 1973). The coloured areas show those grid squares where the correlation is significant ( $P_{cor} < 0.05$ ), black areas show non-significant correlation and white areas indicate no data.

#### 4.4.2.3. Phytoplankton

Significant ( $P_{cor} < 0.05$ ) positive correlations were found between the prevalence of medusae in the north–western North Sea during the summer and phytoplankton colour during the spring. For *C. capillata* this link persisted into the summer; while in the south–western North Sea (east of Northumberland) the prevalence of each species was negatively correlated with phytoplankton colour (Figure 4.6). In the north of Scotland region, the mean probability of capture of each species correlated positively and significantly with the mean phytoplankton colour during spring ( $0.90 \geq R > 0.80$ ,  $P_{cor} \leq 0.001$ ,  $N = 15$ ). During the summer, the mean probability of capture of *A. aurita* west of Denmark negatively correlated in the region ( $R = -0.96$   $P_{cor} < 0.05$   $N = 10$ ), while east of Scotland a positive correlation with *C. capillata* was significant prior to  $p$ -value correction ( $R = 0.73$   $P_{cor} < 0.05$   $N = 13$ ).

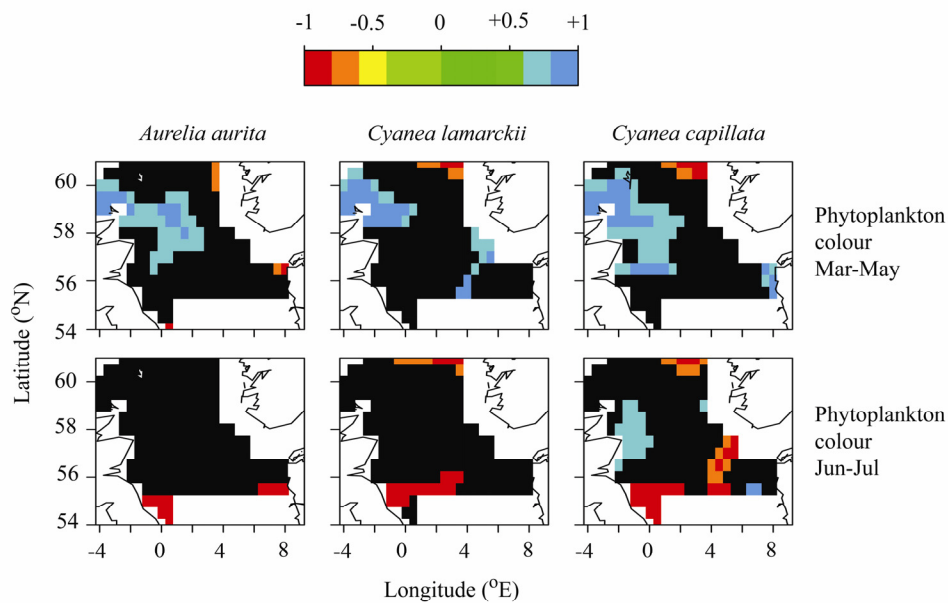


Figure 4.6 Correlative maps showing significant correlations between *Aurelia aurita*, *Cyanea lamarckii*, *Cyanea capillata* and phytoplankton colour during March–May and June–July. Data covers the period 1971 to 1986 (not 1984, below 56° latitude only 1971 to 1973). The coloured areas show those grid squares where the correlation is significant ( $P_{cor} < 0.05$ ), black areas show non-significant correlation and white areas indicate no data.

#### 4.4.2.4. Copepods

The correlative maps with the zooplankton groups show that the prevalence of each jellyfish species during the summer in the northern North Sea is linked to the prevalence of the temperate species there (Figures 4.7–4.9): in the north-east, each jellyfish species prevalence is significantly correlated with the warm-temperate species prevalence there in the winter; along the Scottish coasts jellyfish prevalence is linked to the prevalence of both warm- and cold-temperate copepod species, and of *Calanus finmarchicus* prevalence, particularly during the spring and summer. The exceptions to this pattern are the negative correlations between prevalence of *C. lamarckii* and neritic species during the spring and summer in the north-eastern North Sea, and during the winter in the area between the Orkney and Shetland Isles (Figure 4.8). The prevalence of jellyfish in the south-western North Sea also appears to be linked to that of neritic species there during the summer. In the south-eastern North Sea, the prevalence of *Aurelia aurita* appears to be linked to that of warm-temperate species in each period and cold-temperate species during the spring, while during the summer *Cyanea lamarckii* prevalence is linked to neritic species and *Cyanea capillata* is linked to *Calanus finmarchicus* prevalence.

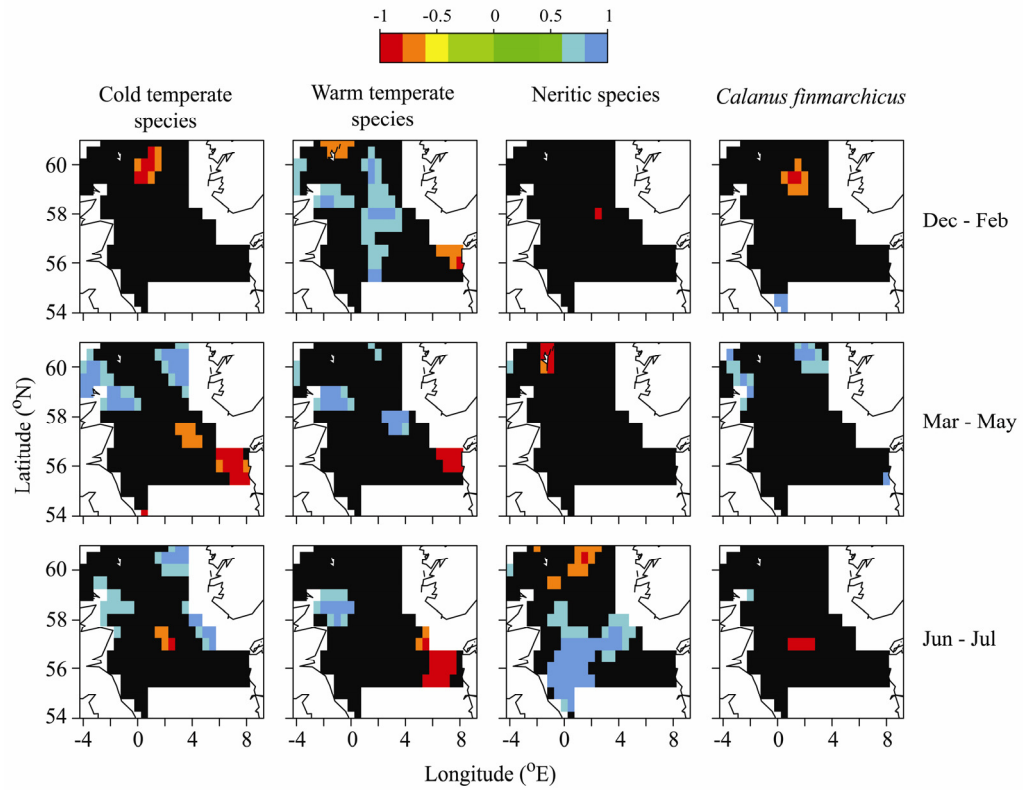


Figure 4.7 Correlative maps showing significant correlations between *Aurelia aurita* prevalence and cold-temperate zooplankton species, warm-temperate species, neritic species and *Calanus finmarchicus* during December–February and March–May and June–July.

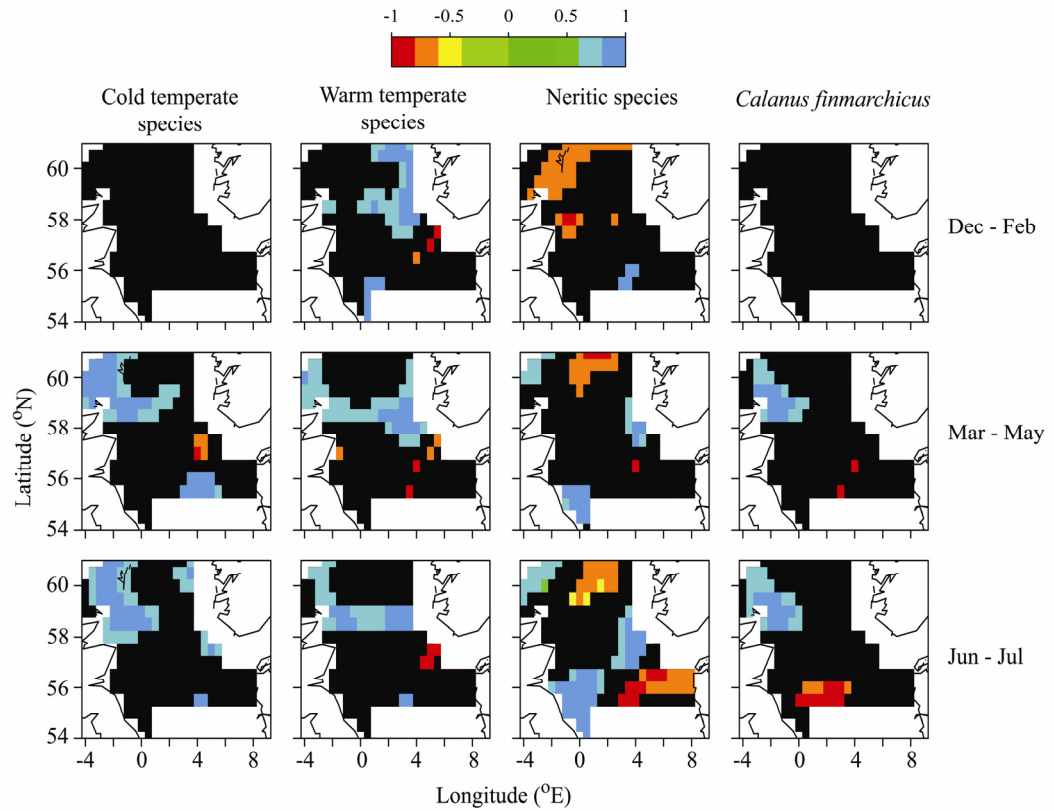


Figure 4.8 Correlative maps showing significant correlations between *Cyanea lamarckii* prevalence and cold-temperate zooplankton species, warm-temperate species, neritic species and *Calanus finmarchicus* during December-February, March-May, and June-July.

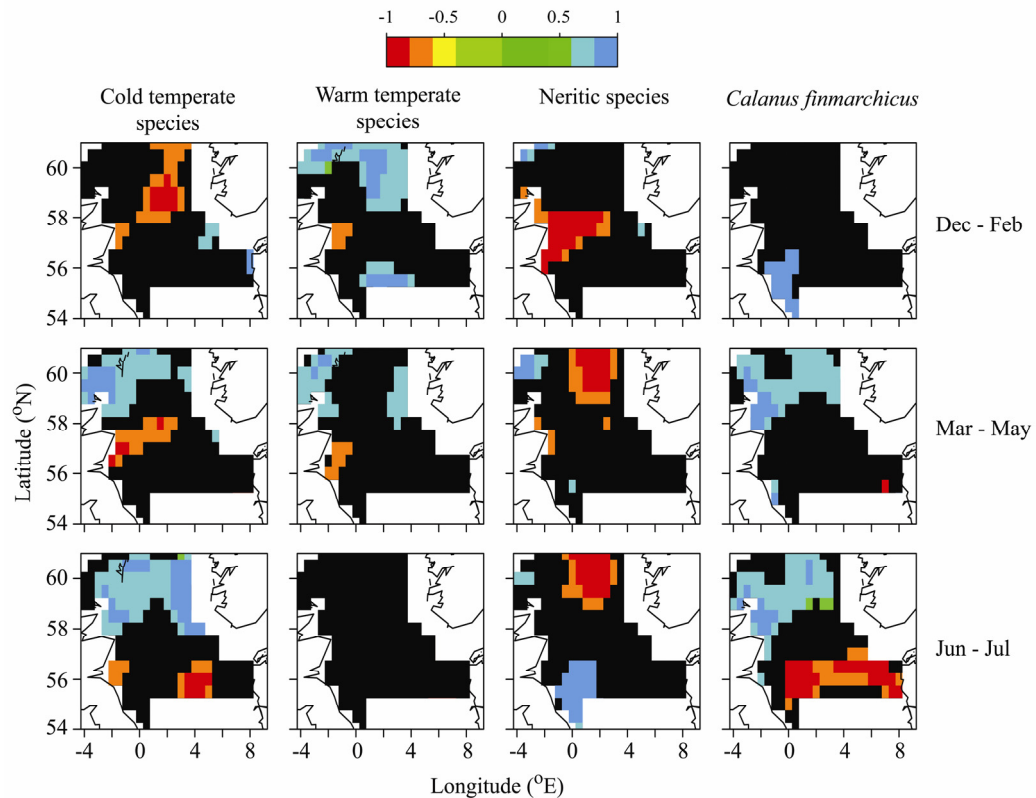


Figure 4.9 Correlative maps showing significant correlations between *Cyanea capillata* prevalence and cold-temperate zooplankton species, warm-temperate species, neritic species and *Calanus finmarchicus* during December-February, March-May, and June-July.

The significant ( $P_{cor} < 0.05$ ) regional correlations suggest that the mean jellyfish prevalence during the summer in the inflow area east of Shetland is linked to each zooplankton group, except warm-temperate species: *A. aurita* was negatively correlated with the prevalence of cold-temperate species during the winter; *C. lamarckii* was negatively correlated with neritic species during spring and summer; *C. capillata* was positively correlated with the prevalence of *C. finmarchicus* during the spring and summer and cold-temperate species during the summer; *C. capillata* was also negatively correlated with the neritic index during the summer (Table 4.2). In contrast, the mean prevalence of each species of jellyfish in the north of Scotland area is positively correlated with warm-species prevalence during the spring. Little significant correlation was found

east of Scotland; however, the prevalence of *Cyanea capillata* was linked negatively to the neritic and temperate indices there during the winter and spring. In the west of Denmark region, the mean prevalence of *C. capillata* correlated negatively with *C. finmarchicus* prevalence during the winter and summer ( $P_{cor} < 0.05$ , Table 4.2); in addition, the mean prevalence of warm-temperate species during the winter and summer correlated negatively with the summertime prevalence of *A. aurita* and positively with that of *C. capillata*.

| Region                   | Jellyfish summer prevalence | Model period | <i>Calanus finmarchicus</i> |          |                        | Neritic species |          |                        | Cold temperate |          |                        | Warm temperate |          |                        |
|--------------------------|-----------------------------|--------------|-----------------------------|----------|------------------------|-----------------|----------|------------------------|----------------|----------|------------------------|----------------|----------|------------------------|
|                          |                             |              | <i>r</i>                    | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>        | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>       | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>       | <i>p</i> | <i>p<sub>cor</sub></i> |
| East of Shetland         | <i>Aurelia aurita</i>       | winter       |                             |          |                        |                 |          |                        | -0.77          | ***      | *                      |                |          |                        |
|                          |                             | spring       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                             | summer       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | <i>Cyanea lamarckii</i>     | winter       |                             |          |                        |                 |          |                        |                |          |                        | -0.52          | *        |                        |
|                          |                             | spring       |                             |          |                        | -0.74           | **       | *                      |                |          |                        |                |          |                        |
|                          |                             | summer       | 0.66                        | **       |                        | -0.73           | **       | *                      | 0.59           | *        |                        |                |          |                        |
| <i>Cyanea capillata</i>  | winter                      |              |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | summer                      | 0.74         | **                          | *        | -0.64                  | *               |          | 0.61                   | *              |          |                        |                |          |                        |
| East of Scotland         | <i>Aurelia aurita</i>       | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                             | spring       |                             |          |                        | -0.57           | *        |                        |                |          |                        |                |          |                        |
|                          |                             | summer       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | <i>Cyanea lamarckii</i>     | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                             | spring       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                             | summer       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
| <i>Cyanea capillata</i>  | winter                      |              |                             |          | -0.72                  | **              | *        | -0.76                  | **             | *        | -0.60                  | *              |          |                        |
|                          | spring                      |              |                             |          | -0.79                  | **              | *        | -0.80                  | **             | *        | -0.77                  | **             |          |                        |
|                          | summer                      | 0.64         | *                           |          |                        |                 |          | -0.68                  | *              |          |                        |                |          |                        |
| West of northern Denmark | <i>Aurelia aurita</i>       | winter       |                             |          |                        |                 |          |                        |                |          |                        | -0.80          | **       |                        |
|                          |                             | spring       |                             |          |                        |                 |          |                        |                |          |                        | -0.73          | *        |                        |
|                          |                             | summer       |                             |          |                        |                 |          |                        |                |          |                        | -0.95          | ***      |                        |
|                          | <i>Cyanea lamarckii</i>     | winter       | 0.70                        | *        |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                             | spring       | 0.75                        | *        |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                             | summer       |                             |          |                        | -0.70           | *        |                        |                |          |                        |                |          |                        |
| <i>Cyanea capillata</i>  | winter                      | -0.79        | **                          |          |                        |                 |          |                        |                |          | 0.80                   | **             |          |                        |
|                          | spring                      |              |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | summer                      | -0.95        | *                           | **       |                        |                 |          |                        |                |          | 0.69                   | *              |          |                        |
| North of Scotland        | <i>Aurelia aurita</i>       | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                             | spring       |                             |          |                        |                 |          |                        | 0.61           | *        |                        | 0.67           | **       |                        |
|                          |                             | summer       |                             |          |                        |                 |          |                        |                |          |                        |                | *        |                        |
|                          | <i>Cyanea lamarckii</i>     | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                             | spring       |                             |          |                        |                 |          |                        |                |          |                        | 0.72           | **       |                        |
|                          |                             | summer       |                             |          |                        |                 |          |                        |                |          |                        |                | *        |                        |
| <i>Cyanea capillata</i>  | winter                      |              |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | spring                      |              |                             |          |                        |                 |          |                        |                |          | 0.66                   | **             |          |                        |
|                          | summer                      | 0.61         | *                           |          |                        |                 |          |                        |                |          |                        | *              |          |                        |

Table 4.2 Linear correlation coefficient (*r*), correlation significance (*p*) and the significance level once corrected for multiple tests (*p<sub>cor</sub>*) for correlations between the prevalence of jellyfish during the summer by region with the prevalence of zooplankton groups during winter (1 December to 28 February), spring (1 March to 31 May) and summer (1 June to 31 July). \* <0.05, \*\* <0.01, \*\*\* <0.001





Table 4.3 As Table 4.2, but here showing correlations between the annual hydroclimatic indices (NAOI, GSNW, BSII) and hydrographic variables (temperature and salinity).

#### 4.4.3.2. Copepods

Although no significant correlation ( $P_{cor} < 0.05$ ) was found between the probability of capture (prevalence) of copepods in the North Sea during 1971–1986 and the North Atlantic Oscillation Index (NAOI), many significant positive correlations ( $P_{cor} < 0.05$ ) were found between the oceanic species groupings (*Calanus finmarchicus*, cold- and warm-temperate species) and with the Gulf Stream North Wall (GSNW) and the Barents Sea Ice Index (BSII) (Table 4.4). The prevalence of neritic copepod species (*Temora longicornis*, and *Centropages hamatus*), that are residents of the North Sea, was not linked to hydroclimatic changes. East of Shetland, the prevalence of both temperate groups and of *Calanus finmarchicus* during spring and summer was positively correlated with the GSNW; the warm-temperate group also positively correlated with the BSII during winter and summer. A single negative correlation was found between the prevalence of *Calanus finmarchicus* north of Scotland in the summer and the BSII. The only significant (and positive) correlation west of Denmark was that between wintertime warm-temperate species (*Calanus helgolandicus*, *Candacia armata* and *Centropages typicus*) and the BSII. North of Scotland, the summertime prevalence of warm-temperate species was also positively correlated with the BSII. East of Scotland, the summertime prevalence of cold-temperate species (*Acartia* spp. and *Metridia lucens*), and that of warm-temperate species during all periods, correlated positively with the BSII.

| Region                   | Annual climate index       | Model period | <i>Calanus finmarchicus</i> |          |                        | Neritic species |          |                        | Cold temperate |          |                        | Warm temperate |          |                        |
|--------------------------|----------------------------|--------------|-----------------------------|----------|------------------------|-----------------|----------|------------------------|----------------|----------|------------------------|----------------|----------|------------------------|
|                          |                            |              | <i>r</i>                    | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>        | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>       | <i>p</i> | <i>p<sub>cor</sub></i> | <i>r</i>       | <i>p</i> | <i>p<sub>cor</sub></i> |
| East of Shetland         | North Atlantic Oscillation | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | Gulf Stream North Wall     | winter       |                             |          |                        |                 |          |                        |                |          |                        | 0.57           | *        |                        |
|                          |                            | spring       | 0.71                        | **       | *                      |                 |          |                        | 0.79           | ***      | **                     | 0.69           | **       | *                      |
|                          |                            | summer       | 0.67                        | **       |                        |                 |          |                        | 0.77           | ***      | **                     | 0.67           | **       | *                      |
|                          | Barents Sea Ice Index      | winter       |                             |          |                        |                 |          |                        |                |          |                        | 0.60           | *        | *                      |
|                          |                            | spring       |                             |          |                        | 0.56            | *        |                        | 0.65           | **       |                        | 0.59           | *        |                        |
| summer                   |                            |              |                             |          | 0.51                   | *               |          |                        |                |          | 0.75                   | ***            | *        |                        |
| East of Scotland         | North Atlantic Oscillation | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | Gulf Stream North Wall     | winter       |                             |          | 0.61                   | *               |          |                        |                |          |                        |                |          |                        |
|                          |                            | spring       |                             |          | 0.54                   | *               |          |                        |                |          |                        |                |          |                        |
|                          |                            | summer       |                             |          | 0.66                   | *               |          |                        |                |          |                        |                |          |                        |
|                          | Barents Sea Ice Index      | winter       |                             |          |                        |                 |          |                        | 0.56           | *        |                        | 0.72           | **       | *                      |
|                          |                            | spring       |                             |          |                        |                 |          |                        | 0.60           | *        |                        | 0.62           | **       | *                      |
| summer                   |                            |              |                             |          | 0.68                   | *               |          | 0.75                   | **             | *        | 0.73                   | ***            | *        |                        |
| West of northern Denmark | North Atlantic Oscillation | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | Gulf Stream North Wall     | winter       |                             |          |                        | 0.65            | **       |                        | 0.64           | **       |                        | 0.52           | *        |                        |
|                          |                            | spring       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                            | summer       |                             |          |                        | 0.61            | *        |                        | 0.55           | *        |                        |                |          |                        |
|                          | Barents Sea Ice Index      | winter       |                             |          |                        |                 |          |                        |                |          |                        | 0.65           | **       | *                      |
|                          |                            | spring       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
| summer                   |                            | -0.55        | *                           |          |                        |                 |          |                        |                |          |                        |                |          |                        |
| North of Scotland        | North Atlantic Oscillation | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | Gulf Stream North Wall     | winter       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                            | spring       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          |                            | summer       |                             |          |                        |                 |          |                        |                |          |                        |                |          |                        |
|                          | Barents Sea Ice Index      | winter       |                             |          |                        |                 |          |                        |                |          |                        | 0.58           | *        |                        |
|                          |                            | spring       |                             |          |                        |                 |          |                        |                |          |                        | 0.55           | *        |                        |
| summer                   |                            | -0.77        | ***                         |          | 0.57                   | *               |          |                        |                |          | 0.62                   | *              | *        |                        |

Table 4.4 As Table 4.2, but here showing for correlations between annual hydroclimatic indices (NAO, GSNW, BSII) with the prevalence of zooplankton groups: *Calanus finmarchicus*; Neritic species *Temora longicornis*, and *Centropages hamatus*; cold temperate species *Acartia* spp. and *Metridia lucens*; and warm temperate species *Calanus helgolandicus*, *Candacia armata* and *Centropages typicus*.

#### 4.4.3.3. Larval fish

No significant correlations ( $P_{cor} < 0.05$ ) were found between the abundances of fish larvae and any hydroclimatic index (NAOI, GSNW, BSII) in any region. However, one significant correlation was found between the BSII and the probability of capture of fish larvae east of Scotland during autumn ( $R = 0.78$   $P_{cor} < 0.01$   $N = 16$ ).

#### 4.4.4. Correlations between fish larvae and zooplankton

Significant negative correlations were found with larval fish prevalence for: *A. aurita* prevalence east of Shetland during summer (June–July) and autumn (August–September) and west of Denmark during autumn; *C. capillata* west of Denmark during autumn ( $p_{cor} \leq 0.001$ , Figure 4.10). When the abundance of fish larvae was correlated against the prevalence of jellyfish, the area of negative correlation was much greater: both *Cyanea* spp. were negatively correlated with fish abundance in the north–eastern North Sea during summer and autumn, *C. capillata* was negatively correlated with larval abundance east of Scotland during autumn, while *A. aurita* was negatively correlated in the central North Sea during summer.

East of Shetland, there were no significant correlations between larval fish prevalence or abundance with prevalences of either euphausiids or *Calanus* spp.. The lack of correlation was evident in both periods (summer and autumn), and also with the fish measures lagged by one season (autumn fish prevalence/abundance vs summer prevalence of euphausiids or *Calanus* spp.). However, significant trends were evident between larval fish prevalence and abundance with *Calanus* spp. and euphausiid spp. in each of the other regions. Correlations with *Calanus* spp. were positive ( $R > 0.58$ ,  $P_{cor} < 0.02$ ): during the summer, east and north of Scotland; during the autumn, east of Scotland (prevalence only) and west of Denmark (abundance only). Negative correlations with euphausiid spp. were significant north of Scotland during both the summer and autumn (abundance only) ( $R > -0.54$ ,  $P_{cor} < 0.03$ ). A lagged positive correlation between fish larval abundance during the autumn and euphausiid spp. in the summertime was found in the region west of Denmark ( $R = 0.63$   $P_{cor} < 0.01$ ) (Figure 4.11).

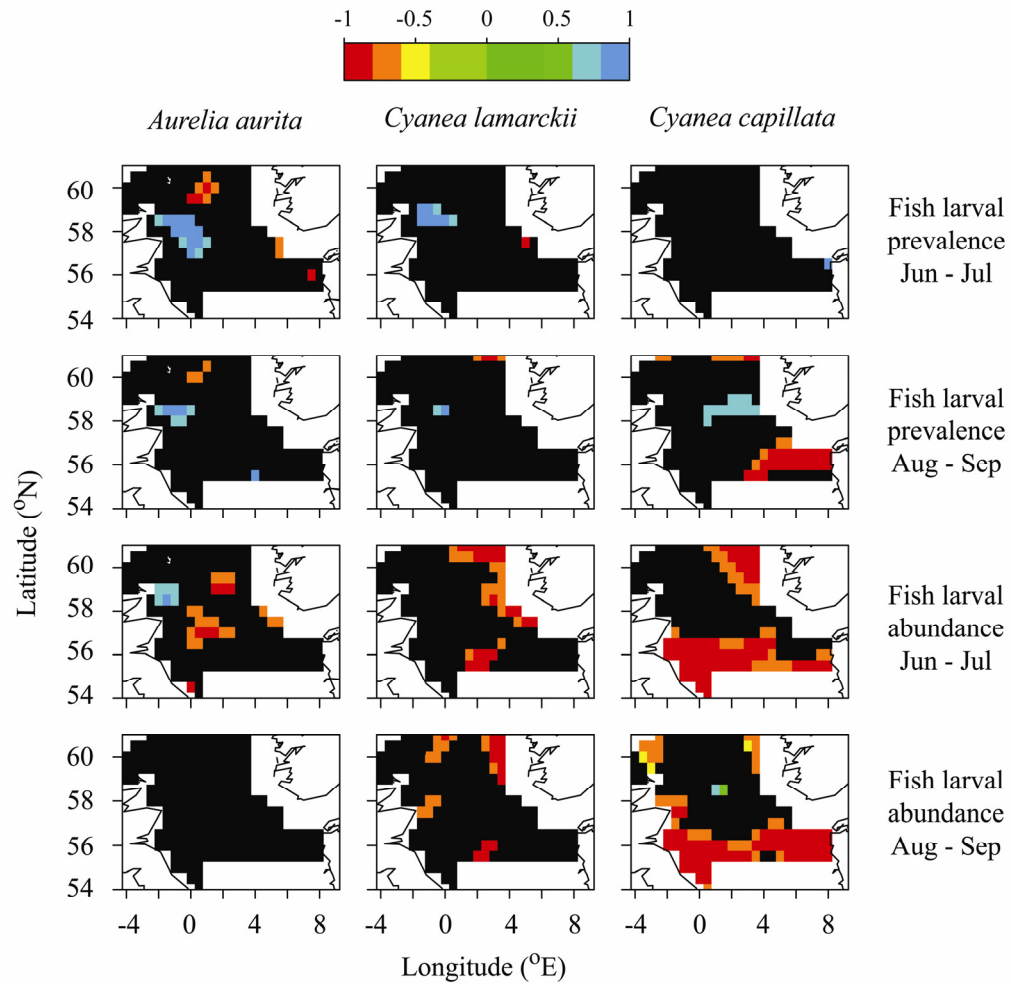


Figure 4.10 Correlative maps showing significant correlations between *Aurelia aurita*, *Cyanea lamarckii*, *Cyanea capillata* and fish larvae prevalence during June–July, and August–September, and with fish larval abundance during June–July and August–September. Data covers the period 1971 to 1986 (not 1984, below 56° latitude only 1971 to 1973). The coloured areas show those grid squares where the correlation is significant ( $P_{cor} < 0.05$ ), black areas show non-significant correlation and white areas indicate no data.

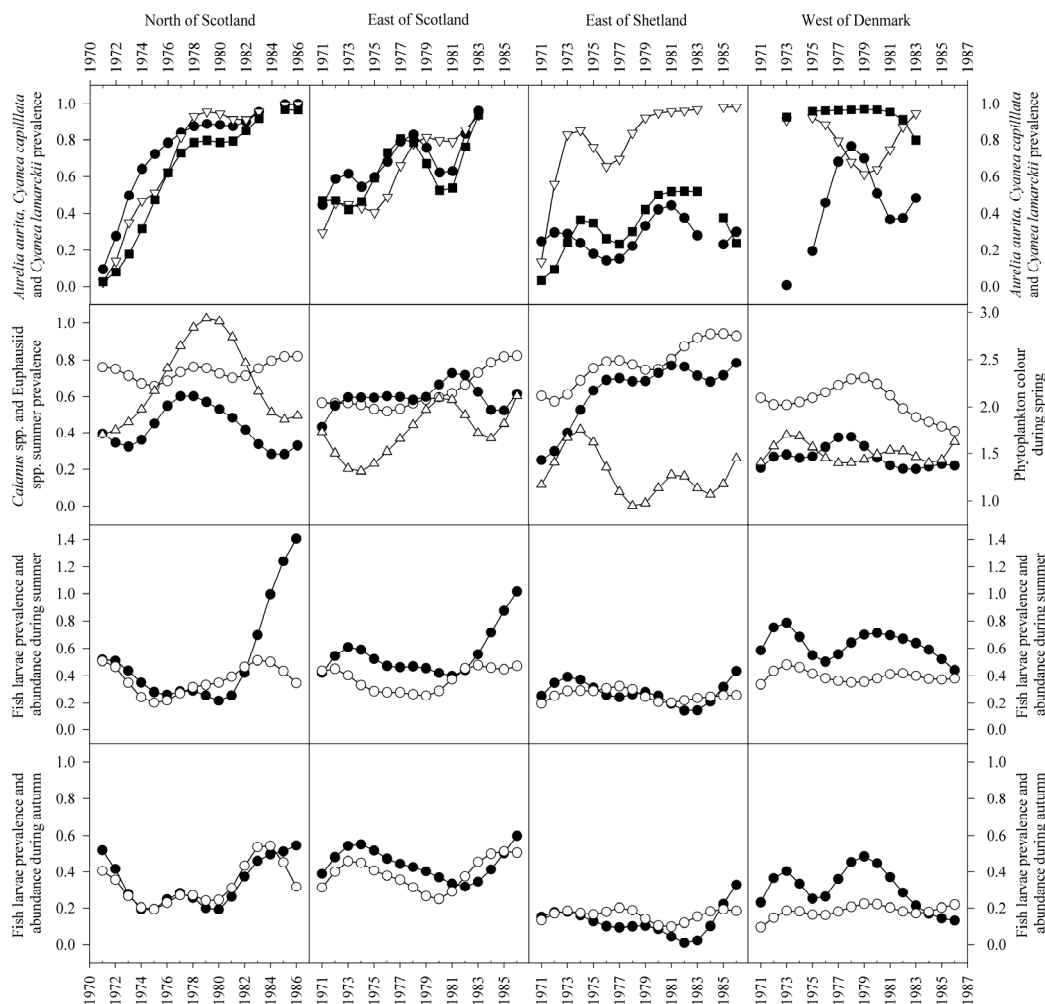


Figure 4.11 Time-series by region, showing prevalence of *Aurelia aurita* (solid circles), *Cyanea capillata* (open downward triangles) and *C. lamarckii* (solid squares) during summer (June–July) (top row), *Calanus* spp. prevalence (open circles) and euphausiid spp. prevalence (solid circles) and the spring phytoplankton colour index (open upward triangles) during summer (second row). Larval fish prevalence (open circles) and abundance (solid circles) during summer (middle row), and Larval fish prevalence (open circles) and abundance (solid circles) during autumn (August–September) (bottom row).

## 4.5. Discussion

### 4.5.1. Jellyfish production in the North Sea

The three jellyfishes studied all develop ephyrae (small medusoids) from scyphistomae (benthic polyps) through the process of strobilation (segmentation) during the winter (December–February). The ephyrae are released during the spring (March–May) and by summer (June–July) most have

developed to form the adult medusae (although the *C. capillata* cycle may be delayed by about a month relative to the other two species, (Russell 1970)). Strobilation is triggered by a combination of factors, including temperature and salinity changes during the winter, and requires the consumption of sufficient prey by the scyphistomae (Russell 1970). It has been shown that warm temperatures increase the rate of strobilation and number of ephyrae produced (Ma and Purcell 2005; Purcell 2005). Therefore warm sea–bottom temperatures during the winter should increase the production of jellyfish, while warm water–column temperatures during the spring should increase the rate of ephyral development. However, jellyfish are also dispersed through advection, and this may mask local temperature effects.

In the region west of northern Denmark, which has been suggested to be the region least affected by advection (Chapter 3, Lynam et al. 2005a), there is a positive correlation between the prevalence of *C. capillata* and bottom temperature, suggesting that if scyphistomae are located then they may be responding to the warmer conditions. *Cyanea lamarckii* are often the most abundant jellyfish west of northern Denmark and were found in the majority of catches there every year ( $p_r(\text{capture}) > 0.9$  for 1973–1982 and  $p_r(\text{capture}) = 0.8$  in 1983), suggesting that regardless of long–term changes in winter temperature this may be a favourable area for their scyphistomae.

#### 4.5.2. Advection of zooplankton and jellyfish

The negative correlations north and east of Scotland between jellyfish prevalence and temperature (Table 4.1) may indicate that low temperatures there occur concomitantly with favourable conditions for strobilation, such as prey levels, but do not directly impact on strobilation. When considered in conjunction with the negative correlations between salinity and jellyfish summer prevalence (Figure 4.4) and with the positive correlation between jellyfish summer prevalence and spring phytoplankton colour (Figure 4.7), these relationships suggest that the inflow of cold, saline, nutrient rich oceanic water may result in the advection of zooplankton and jellyfish to Scottish coastal waters and also provide good conditions for a ‘bloom’ of medusae.

Relationships between jellyfish and the copepod groups suggest that a predominance of *Calanus finmarchicus* east of Shetland during summer is concomitant with high prevalence of *Cyanea capillata*. By region, the following

correlations are significant ( $P_{cor} < 0.05$ ): mean prevalence of cold–temperate species during winter and summertime *A. aurita* prevalence; mean summertime prevalence of *Calanus finmarchicus* and *Cyanea capillata* (Table 4.2), which suggests that if there is a link here it may be due to advection of medusae and/or prey into the region. Temperate species and both *A. aurita* and *C. lamarckii* are usually rare east of Shetland, therefore the link between *Calanus finmarchicus* and *Cyanea capillata* is likely to be more influential over the total change in medusae abundance (Hay et al. 1990).

The prevalence of each jellyfish species during summer was similarly linked to the distribution of each copepod group during spring and summer (Figures 4.8 – 4.10). A high prevalence of immigrant copepod species (particularly cold temperate) during spring in the northern (particularly north–western) North Sea may be concomitant with advection of ephyrae to the area, or may result in high jellyfish prevalence through increased prey to the developing ephyrae. The effect of advection on ephyral dispersal might also be shown in the correlations between spring and summer salinity and jellyfish summertime prevalence, since jellyfish are prevalent in the central North Sea when salinity is low (Figure 4.6).

In the south–western North Sea, a high prevalence of neritic species during the summer is concomitant with high jellyfish prevalence, suggesting that high prey levels here may favour ‘bloom’ conditions. In contrast, high jellyfish prevalence in the south–eastern North Sea during the summer appears to coincide with low zooplankton prevalence, possibly because in this shallow region, where jellyfish are usually abundant, the zooplankton stock may be depleted rapidly.

#### 4.5.3. Larval fish

The negative relationships with *C. capillata*, along the British coastline, and with *A. aurita*, east of Shetland, might support a possible impact upon larval fish by these medusae (Figure 4.10). It appears that the prevalence and abundance of fish larvae at spawning grounds, other than that east of Shetland, varies concomitantly with *Calanus* spp. prevalence (Figure 4.11).

#### 4.6. Links between hydroclimatic fluctuations and jellyfish abundance

The aim of this study was to evaluate the relative importance of the various mechanisms proposed in Chapters 2 and 3 to link NAO fluctuations to regional jellyfish abundance in the North Sea. I suggested that the relationship between NAO fluctuations and jellyfish abundance varies regionally because of local conditions, therefore each region must be considered individually (Lynam et al. 2005). Based on this study the following mechanisms appear probable for the three regions:

##### *North of Scotland*

NAOI positive → strong CSJ → high inflow of nutrients → phytoplankton bloom → high prevalence of warm temperature species → good conditions for jellyfish development → high jellyfish (each species) prevalence and abundance during summer

##### *West of Denmark*

NAOI negative → lower prevalence of immigrant temperate zooplankton species and greater retention of medusae → abundant *Aurelia aurita* and *Cyanea lamarckii*

##### *East of Shetland*

Prolonged period of positive NAOI → positive GSNW → greater inflow of water in surface layer (<150 m deep) → high prevalence of *C. finmarchicus* and temperate species during spring and summer (in CPR surface samples) → high prevalence of *Cyanea capillata* during summer

No clear link was evident east of Scotland, possibly because jellyfish are nearly always prevalent here irrespective of the environmental conditions. This region was considered in Chapter 3 to show a response to NAO fluctuations that was intermediate between the relationships displayed west of Denmark and north of Scotland. In the north of the region, the prevalence of jellyfish appears to be linked to phytoplankton and temperate zooplankton species abundance, similarly to jellyfish prevalence north of Scotland, but in the remaining area no clear relationship is shown. The prevalence of *C. capillata* does appear to be



linked to that of *Calanus finmarchicus* during the summer, which may suggest that this species is advected from the northern North Sea into the region (Figure 4.10). South of the east of Scotland region, *A. aurita* and *C. lamarckii* prevalence is positively correlated with the prevalence of neritic species.

The overall probability of capture of all species of jellyfish in the North Sea increased throughout the period 1971–1986. However, variability in the regional distribution and abundance of jellyfish in the North Sea appears to be driven by hydroclimatic change and therefore the possible predatory impact of these medusae on North Sea zooplankton may rise and fall between years. Considering the potential of medusae to impact on the ecosystem, extensive sampling of these jellyfish species should be conducted in order to monitor long-term population change and more research made into the possible interactions between jellyfish and other organisms.

## Chapter 5

### **Evidence for an impact by medusae on North Sea herring (*Clupea harengus*) 0–group recruitment**

The work described here has been published as:

Lynam C.P., Heath M.R., Hay S.J. and A.S. Brierley. *Evidence for impacts by jellyfish on North Sea herring recruitment*. Marine Ecology Progress Series. 298: 157–167.

I estimate that I contributed 70% of the effort towards the paper, which can be broken down into the following five equally weighted areas: Data collection/preparation 20 %, the jellyfish data were gathered by SJH and others at Marlab and I prepared the data from the raw paper files and gathered fisheries data from ICES; Inspiration 90 %; Analysis 80 %, where the remainder is attributable to suggestions from MRH and ASB; Conclusions 80 % with suggestions from MRH /ASB; Publication 80 %, the paper was written by me but reviewed by ASB/MRH/SJH.

## 5. Evidence for an impact by medusae on North Sea herring (*Clupea harengus*) 0–group recruitment.

### 5.1. Abstract

Jellyfish (Scyphozoa) prey on and consume many of the same food items as do larvae of herring (*Clupea harengus*), and could therefore have a detrimental impact on larval survival. A reduction in the spawning stock biomass of herring may release jellyfish from competition for prey with herring and exacerbate any impact by jellyfish on survival of the remaining herring. Both jellyfish abundance and the spawning success of herring fluctuate from year to year and increase under similar environmental conditions. The abundance of medusae (1 to 47 cm diameter, sampled Jun-Aug during 1971-1986) at herring spawning areas in the North Sea was correlated positively with the abundance of recently hatched herring larvae (<1 cm, sampled 1-15 Sep during 1971-1986); this concurrence heightens the potential for competition. A significant negative relationship ( $P < 0.05$ ) between the survival of herring to Age-0 (approximately 12 months) and the abundance of *Aurelia aurita* implies that jellyfish might adversely impact the North Sea herring population. Furthermore, regression analyses suggested that climate variability may mediate the possible impact by *A. aurita* on herring residual survival and 0–group recruitment through changes in the North Atlantic Oscillation index and the abundance of *C. capillata* ( $R^2 > 0.60$ ,  $P < 0.05$ ). Management of North Sea herring may benefit from the inclusion of predation and competition effects of medusae in forecasting models of herring recruitment.

### 5.2. Introduction

Jellyfish abundance is increasing in many marine ecosystems (Section 1.12) (Mills 2001; Xian et al. 2005) and, being significant consumers of zooplankton, including ichthyoplankton, jellyfish might have an increasingly adverse affect on fish populations (Section 1.9) (Schneider and Behrends 1998; Purcell and Arai 2001; Sommer et al. 2002). *Aurelia aurita* have had devastating impacts on larvae of Atlantic herring (*Clupea harengus*) in a Baltic Sea fjörd (Möller 1984) and *Aequorea victoria* is a major cause of mortality of Pacific herring larvae (*Clupea pallasii*) in Kulleet Bay, British Columbia (Purcell and Grover 1990). Möller (1984) reported that even a small *A. aurita* ephyra (6 mm diameter) was

able to catch Atlantic herring larvae, and found 68 larvae in the stomach of a single medusa only 42 mm in diameter. Competition for food between medusae and adult fish has also been shown, with dietary similarities of 73% and 50% respectively for Pacific herring and medusae of *Aurelia labiata* and *Cyanea capillata* (Purcell and Sturdevant 2001).

In the North Sea, the abundance of the jellyfish *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* fluctuated substantially between 1971 and 1986 (Chapters 2 and 3) (Hay et al. 1990). At a regional level, part of the interannual variability has been linked to changes in the climate as quantified by the winter (December to March) North Atlantic Oscillation Index (NAOI). The abundance of medusae was generally high west of Denmark and east of Scotland when the NAOI was low (Chapter 2). Similarly, a low NAO phase has been associated with beneficial conditions for Bohuslän herring in the Skagerrak (Alheit and Hagen 1997). Conversely, a high NAO appears to result in better conditions for jellyfish north of Scotland, in an area subject to a greater oceanic influence (Chapter 3), and for spring-spawning herring in the English Channel (Alheit and Hagen 1997). So, not only the abundance of medusae and herring but also their distribution appears to be linked to climatic variation.

The distributions of jellyfish and herring in the North Sea overlap spatially and partially temporally (Chapter 4 and Figures 4.1 and 4.2), so the possibility exists that jellyfish impact upon herring recruitment either directly or indirectly. Furthermore, when environmental conditions favour high jellyfish abundance the possible impact by jellyfish on herring may increase. This study describes correlative associations and coupled trends that suggest possible links between herring and jellyfish and the climate. There is a growing acceptance that fisheries management needs to progress from single species models to a more holistic ecosystem approach (Pikitch et al. 2004; Cury et al. 2005). This study could be a contribution to that goal.

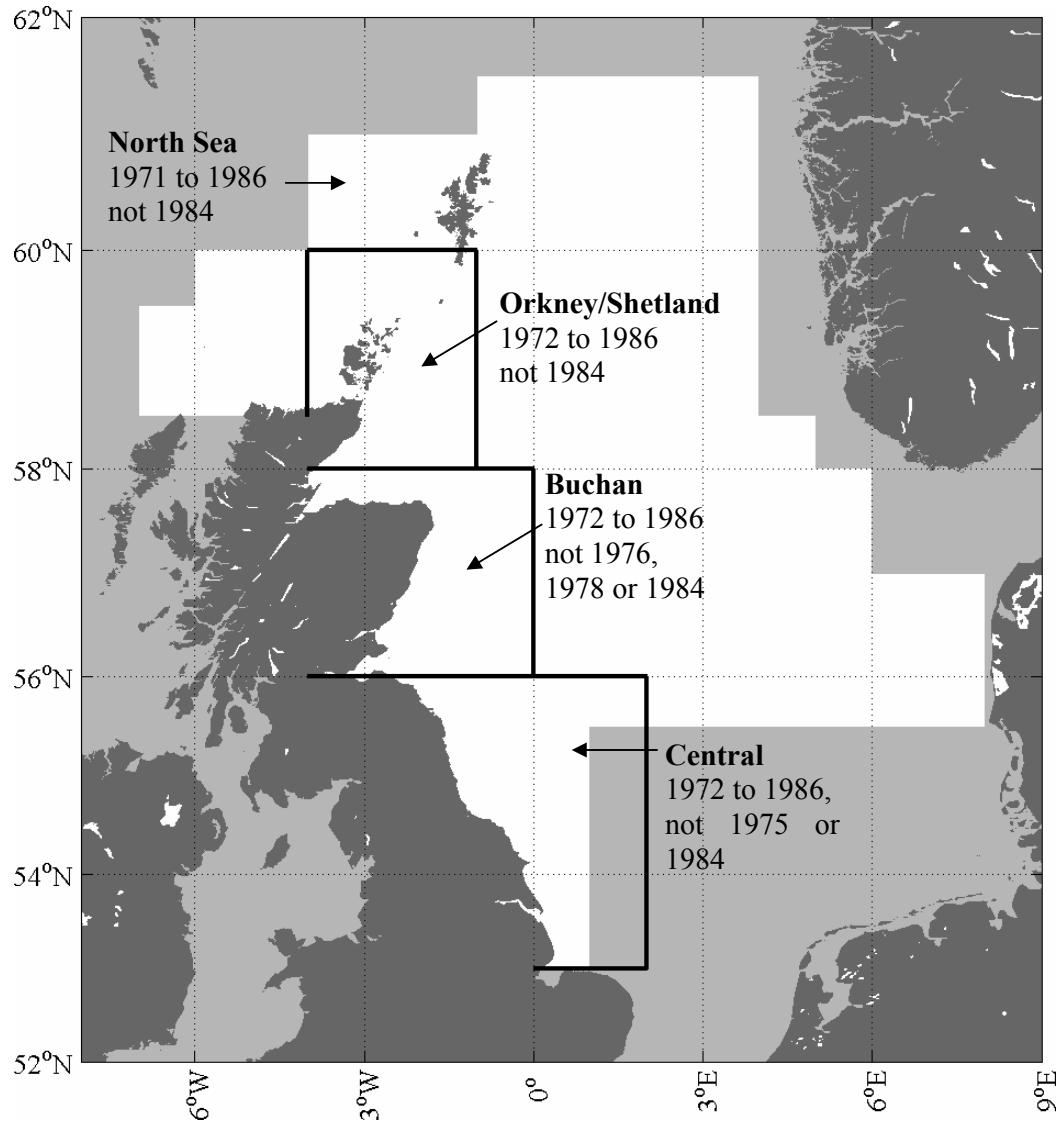


Figure 5.1 Map of the North Sea showing the regions where herring larvae (boxes) and medusae (white area) were sampled over more than one year. Dates give years in which data were available for correlations. Dotted grid shows 3 by 2 degree squares.

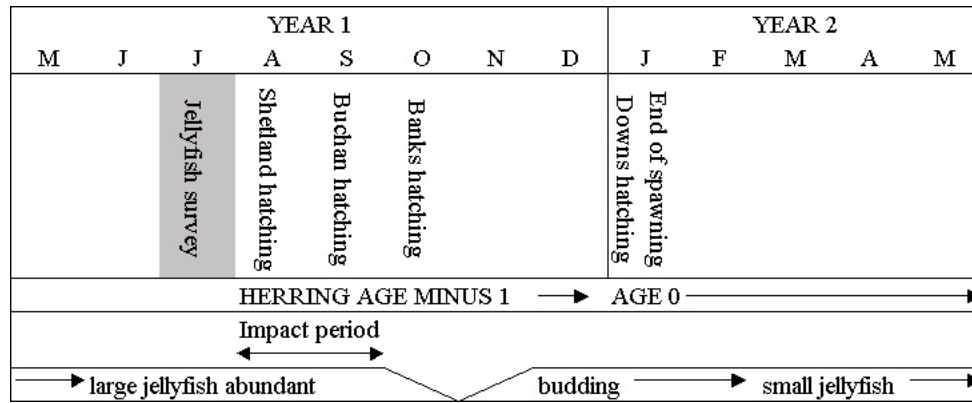


Figure 5.2 Timeline showing North Sea herring spawning periods, approximate periods of occurrence of jellyfish and possible impact zone.

**5.3. Methods**

*Jellyfish abundance*

Medusa abundance data were collected over 15 years (1971 to 1986, excluding 1984) during the routine summer International Council for the Exploration of the Sea (ICES) International 0–group Gadoid Surveys of the North Sea (Hay et al. 1990). Jellyfish were a bycatch of these surveys. Full survey methods are given in Hay et al. (1990) and in Section 2.3. Only regions of the North Sea that were sampled in more than one year were included in analyses here (Figure 5.1), and all abundance values were recalculated from the raw data collected by Hay et al. (1990) (Section 3.2). Jellyfish medusae were sampled throughout the Buchan and Orkney/Shetland areas; however, in the Central region data are missing east of the spawning bank between 53 and 55.5 °N and from 1 to 2 °E.

*Herring larval abundance*

I used the herring Larval Abundance Index (LAI reported by Rohlf and Gröger 2003) to provide the mean number of larvae per ICES rectangle in the Buchan, Central, and Orkney/Shetland areas (Heath 1993). This index arises from the ICES international herring larvae surveys, which caught herring larvae <10 mm long using a Gulf III ‘standard sampler’ (260 µm nylon mesh and a 20 cm mouth aperture). These standard surveys operated a double oblique haul from the surface to within 5 m of the seabed and back, with a vertical ascent rate of approximately 5 m per min. The volume of water filtered by the net was measured with a calibrated flowmeter mounted in the centre of the mouth

opening of the nose cone. Herring larvae, aged between 10 and 15 days, were caught between 1-15 September from 1972 to 1987, and these larvae were most likely spawned in mid-August (Heath 1993) when medusae are abundant (Russell 1970). For the Orkney/Shetland area the time-series is complete throughout the jellyfish survey period, but the years 1976 and 1978 are missing from the Buchan region and 1975 is missing from the Central North Sea time-series.

#### *Herring 0-group recruitment and stock biomass data*

Recruitment and spawning stock biomass data for autumn-spawning herring are published by ICES for the North Sea, Eastern English Channel, Skagerrak and Kattegat combined (ICES 2003c, 2004). Herring are assigned to the 0-group if they have no winter growth rings in their otoliths; larvae do not gain a ring in their first winter so that herring hatched in the autumn, say, of 1970 would metamorphose in spring/summer 1971 and would be referred to as 0-group throughout the year until they recruit to the 1-group on 1 January 1972 (Heath et al. 1997). Although the recruitment value is an estimate of 0-group recruitment for 1 January in the year following the autumn hatching, the year class refers to the year of hatching. The Multiplicative Larval Abundance Index (MLAI) is used for tuning the spawning stock biomass value in the ICES Integrated-Catch-at-Age (ICA) model, and therefore the regional LAIs are used indirectly in the recruitment estimate process. However, due to the great influence of the adult catch data and the convergence features of the ICA model, the ICA is relatively insensitive to the MLAI (H. Sparholt, pers. comm. 2004). The regional LAIs can therefore be considered independently of 0-group recruitment.

#### *Ricker modelling of herring survival to Age-0*

I used a Ricker model (Equation 3) to account for any variation in herring recruitment due to long-term population change. This model predicts recruitment from the spawning stock biomass (SSB, tonnes):

$$R_{Ricker} = (a \cdot SSB) \cdot \exp(-b \cdot SSB) \quad (3)$$

where  $R_{Ricker}$  = recruits (millions) to 0-group (Figure 5.2) for year class  $y$ . The constants  $a = 1.16 \times 10^{-1}$  and  $b = 8.53 \times 10^{-7}$  were fitted by non-linear least-

squares estimation using the Gauss-Newton algorithm in *R Version 1.8.1* (R Development Core Team 2003).

The relative survival index ( $S$ ) of herring to approximately Age-0 can be calculated from the difference between the natural logarithms of the SSB and 0-group recruitment level ( $R$ ):

$$S = \ln(R) - \ln(SSB) \quad (4)$$

where the units of survival are the logged number of recruits per tonne of spawning stock. Substitution of either the observed or Ricker-modelled estimate of recruitment for  $R$  in equation 4 provides a measure of the observed or expected larval survival respectively. The difference between the observed and the expected survival, the residual survival, is a dimensionless measure of external impacts on larval survival:

$$\begin{aligned} S_{residual} &= S_{observed} - S_{expected} \\ S_{residual} &= \ln(R_{observed}) - \ln(R_{expected}) \\ S_{residual} &= \ln(R_{observed} / R_{expected}) \end{aligned} \quad (5)$$

### *Climate*

The winter (December - March) North Atlantic Oscillation Index (NAOI) of the normalized sea level pressure difference between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland was obtained from the National Center for Atmospheric Research, Climate and Global Dynamics Division, Boulder, CO, USA (Hurrell et al. 2003).

## **Analysis of jellyfish, NAOI, and herring relationships**

### *Long-term trends*

In data with non-zero temporal trends, Pearson correlations were made to assess the similarity in the raw data. Correlations were conducted in SigmaPlot®2001 for Windows and correlation significance, normality and homogeneity of variances, were assessed at the 0.05 level using a Student's t-test.

### *Interannual variability*

Prior to use in statistical analysis of interannual variability, medusa abundance, herring residual survival and recruitment, the LAI and NAOI were assessed for linear and polynomial temporal trends, by taking least squares fits against time, and corrected where necessary. The significance of temporal trends was judged



at the 0.05 level with a standard Student's  $t$ -test of the estimated slope parameter.

Multiple linear regressions of medusa abundance and the NAOI against either survival, recruitment, or LAI were made to compute models of the form:

$$y_t = \beta_0 + \beta_1.x_{1t} + \beta_2.x_{2t} + \beta_3.x_{3t} + \beta_4.x_{2t}.x_{3t} + e_t \quad (6)$$

where  $y_t$  was the residual survival, recruitment, or LAI for year class  $t$ ,  $x_{1t}$  is the abundance of medusae in year  $t$ ,  $x_{2t}$  and  $x_{3t}$  are either the NAOI or the abundance of another jellyfish species or set to zero,  $x_{2t}.x_{3t}$  is the interaction term,  $e_t$  is an error term with unit variance and zero mean,  $\beta_0$  was the intercept, and  $\beta_1$   $\beta_2$   $\beta_3$  and  $\beta_4$  are the slope parameters estimated using linear regression. Natural logarithm transforms were used where necessary to normalise the distribution of residuals from linear correlations and regressions. Parameter significance for all models was assessed at the 0.05 level using a Student's  $t$ -test. The model assumptions (linearity, homogeneity of variance, normality, and independence of residuals) were tested following procedures outlined in Krzanowski (1998). Correlations between variables, linear regressions without interactions, and tests for normality and homogeneity of variances were conducted in *SigmaPlot*® 2001 for Windows. Regressions with interactions were calculated and assessed in *R* (2003) using the *Shapiro-Wilk* normality test, the *Breusch-Godfrey* test for serial correlation, and plots of residuals against order and model values to test independence and variance homogeneity respectively. The significance level for each test was chosen to minimize corresponding Type II error (Krzanowski 1998).

## 5.4. Results

### 5.4.1. Long-term trends

#### *Temporal trends*

Significant positive linear temporal trends ( $P < 0.05$ ) were found in North Sea herring recruitment (observed data), spawning stock biomass and residual survival in the North Sea as a whole. Positive trends were also found in the Orkney/Shetland region in the abundance of herring larvae, and  $\ln(\text{median})$  abundance of *Cyanea capillata*. Significant quadratic trends (decreasing then increasing) were also found in herring total stock biomass and in *C. capillata*  $\ln(\text{maximum})$  abundance in the North Sea. In contrast, a significant negative

trend was found in the Ricker-modelled survival of herring. All temporal trends were removed from the data in order to investigate relationships in interannual variability.

*Herring larval abundance and jellyfish abundance in herring spawning areas*

In the Orkney/Shetland region only, a long-term trend was found in the herring larval abundance index (LAI). This data correlated positively ( $P < 0.01$   $N = 14$ ) with *C. capillata* raw abundance data there ( $\ln(\text{median})$   $R = 0.78$  and median abundance  $R = 0.83$ ).

*Herring stock biomass and jellyfish abundance in the North Sea*

The raw herring spawning stock biomass (SSB) correlated negatively with the abundance of *Aurelia aurita* ( $\ln(\text{maximum})$   $R = -0.75$   $P < 0.01$   $N = 15$  and maximum  $R = -0.47$   $P = 0.08$   $N = 15$ , Figure 5.3). Although the herring SSB did not significantly correlate with the maximum abundance of *Cyanea capillata*, significant positive correlations were found using  $\ln(\text{median})$  abundance ( $R = 0.67$   $P < 0.01$   $N = 15$ ) and median abundance ( $R = 0.86$   $P < 0.01$   $N = 15$ ). The maximum abundance of *A. aurita* did not correlate with the median abundances of *C. capillata*. The negative relationships between herring SSB and *A. aurita* abundance suggest that herring compete for prey with *A. aurita*. Herring SSB was also significantly positively correlated with the recruitment of herring ( $R = 0.89$   $P < 0.01$   $N = 16$ , Figure 5.3), so much of the long-term variability in herring recruitment is due to changing adult abundance; this must be accounted for when exploring the effect of medusae and fish on herring survival. The long-term change (between 1971 and 1986) in recruitment due to SSB variability was successfully captured by the Ricker model (Equation 3); the Pearson correlation coefficient between observed and modelled recruitment was  $R = 0.89$  ( $P < 0.01$   $N = 16$ ). The Ricker-modelled survival of herring, i.e. the survival expected on the basis of SSB and modelled recruitment, correlated positively with the  $\ln(\text{maximum})$  abundance of *A. aurita* throughout the North Sea ( $R = 0.75$   $P < 0.01$   $N = 15$ ) suggesting that *A. aurita* were abundant in years when high larval survival should have been attained. However, to explore whether or not *A. aurita* might have had an impact on the

survival of herring the interannual variability in the residual survival (observed minus modelled) of herring has to be examined.

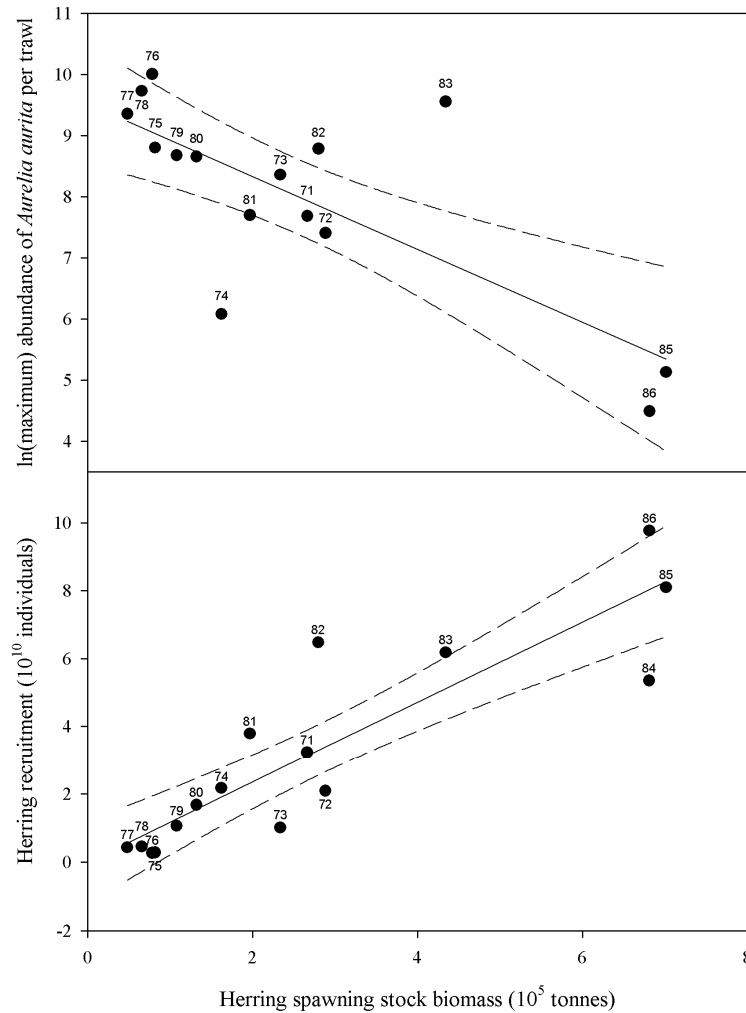


Figure 5.3 Herring and *Aurelia aurita* in the North Sea: Correlations between the raw herring SSB and recruitment ( $R = 0.89 P < 0.01$ , bottom) and between SSB and the ln(maximum) abundance of *Aurelia aurita* ( $R = 0.75 P < 0.01$ , top).

**5.4.2. Interannual variability**

*Herring larval abundance and jellyfish abundance in spawning areas – support for possible impact by jellyfish on herring survival*

Significant positive correlations were found between the herring larval abundance index (LAI) and the maximum abundance of *Aurelia aurita* in the Buchan ( $R = 0.66 P = 0.04 N = 10$ , Figure 5.4) and Central ( $R = 0.78 P = 0.02 N = 8$ ) regions. In the Orkney/Shetland region, the detrended herring larval

abundance correlated with the detrended  $\ln(\text{median})$  abundance of *Cyanea capillata* ( $R = 0.69$   $P < 0.01$   $N = 14$ ).

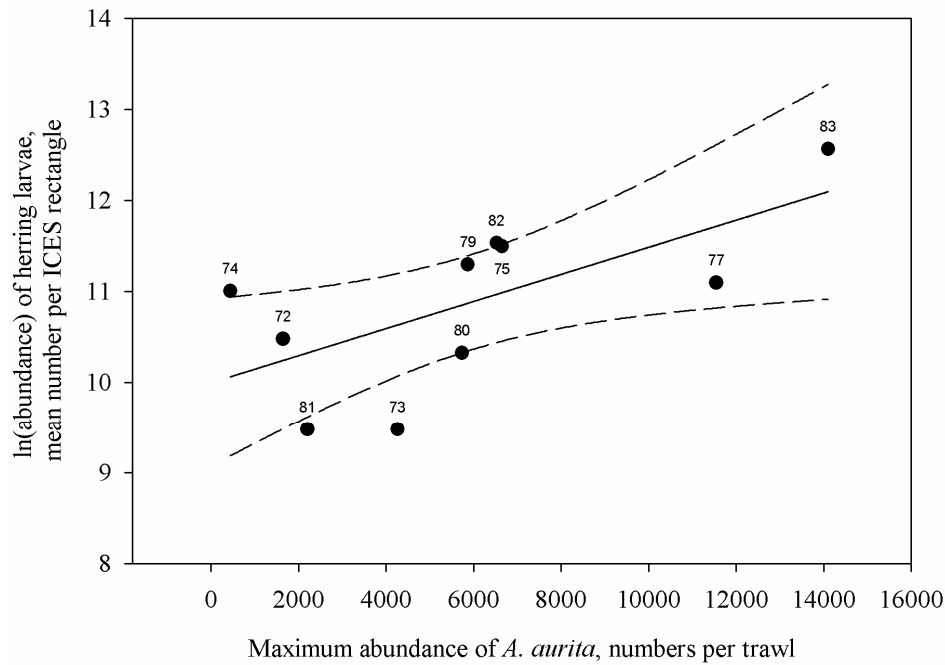


Figure 5.4 Herring and *Aurelia aurita*: Relationship between abundances at the Buchan spawning ground ( $R = 0.66$   $P = 0.04$ ) with 95% confidence interval (dashed lines). Herring larval abundances are mean numbers per ICES triangle and jellyfish abundance are maximum numbers per trawl.

#### *Herring 0-group recruitment, herring stock biomass, and North Sea jellyfish abundance*

A significant positive relationship was found between the detrended herring recruitment time series for the period 1971 to 1986 and the detrended herring spawning stock biomass ( $R = 0.79$   $P < 0.01$   $N = 16$ , Figure 5.5). The maximum abundance of *A. aurita* also correlated significantly with recruitment (*A. aurita*  $R = -0.60$   $P = 0.02$   $N = 15$ ). Significant negative correlations were also found between herring SSB and both the  $\ln(\text{maximum})$  *Aurelia aurita* abundance and the detrended time series of *Cyanea capillata* abundance (*A. aurita*  $R = -0.67$   $P < 0.01$   $N = 15$ , *C. capillata*  $R = -0.68$   $P < 0.01$   $N = 15$ , Figure 5.5).

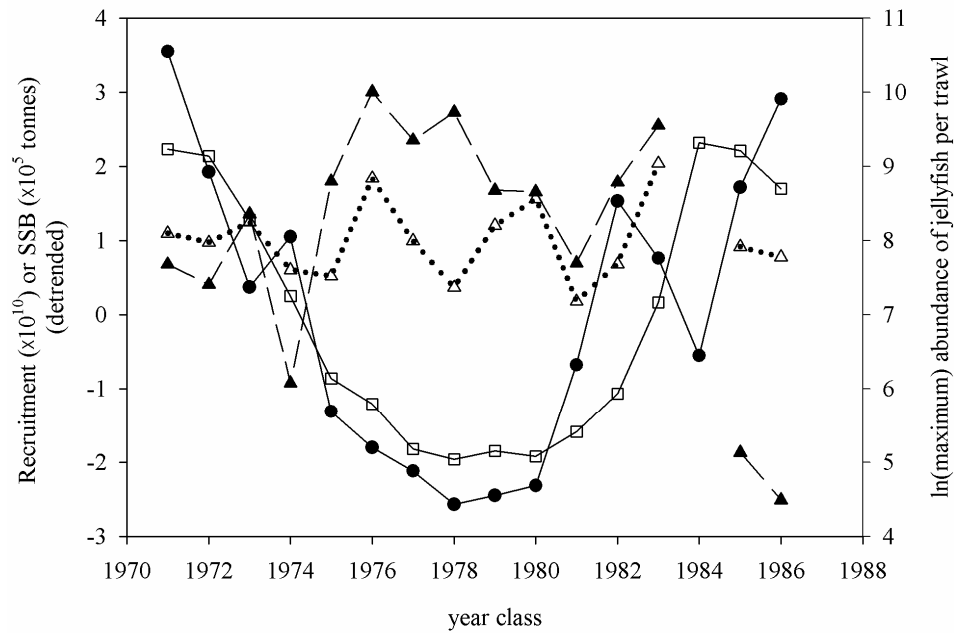


Figure 5.5 Herring, *Aurelia aurita*, and *Cyanea capillata* in the North Sea: Detrended time series of herring recruitment (solid line and closed circles), SSB (solid line and open squares) and the abundance of *A. aurita* (dashed line, closed triangles) and *C. capillata* (dotted line, open triangles). Note that, for ease of comparison, 5 is added to the *C. capillata* ln(maximum) abundance data. Correlation coefficient between herring recruitment and SSB  $R = 0.79$ ; between herring recruitment and medusa abundances: *A. aurita*  $R = -0.67$  and *C. capillata*  $R = -0.68$  (all  $P < 0.01$ ).

#### *Herring residual survival and jellyfish abundance - possible impact by Aurelia aurita on herring survival*

To determine whether or not the changing jellyfish abundance was a significant factor in the recruitment of herring, the component of variability in survival due to the environment (i.e. residual survival) was correlated against the abundance of each jellyfish species. A significant negative relationship was found between detrended residual survival and maximum *Aurelia aurita* abundance ( $R = -0.61$   $P = 0.02$   $N = 15$ , Figure 5.6), suggesting that an abundance of *A. aurita* is associated with lower than expected survival of herring.

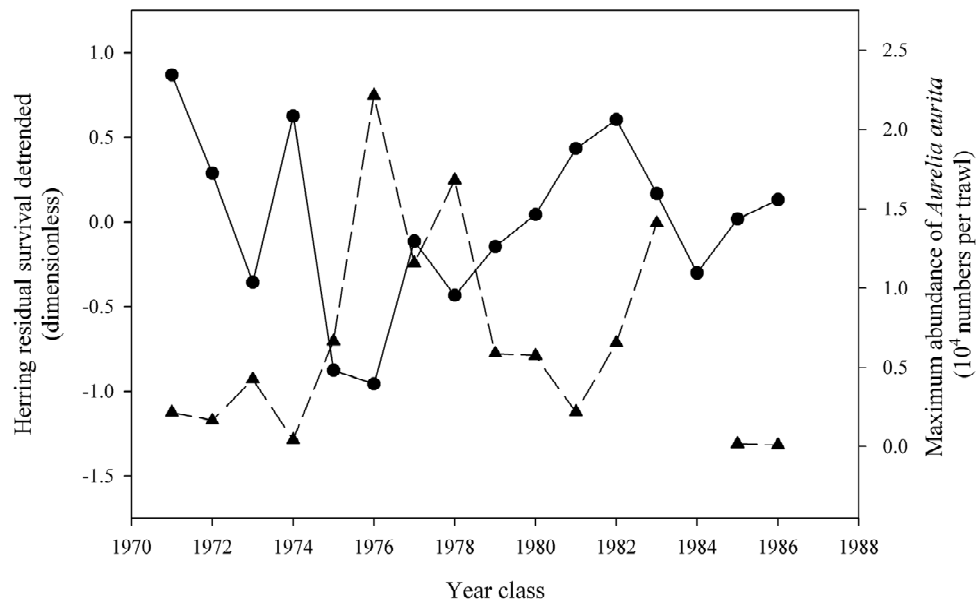


Figure 5.6 Herring against *Aurelia aurita*: Relationship between abundance of *A. aurita* in the North Sea and larval herring residual survival ( $R = -0.61$   $P = 0.02$ ).

#### *Climatic modulation of possible jellyfish impact on survival*

Further multiple regression analyses were conducted to explore the role of climate change in mediating the possible impact of jellyfish on herring residual survival and recruitment. The detrended herring residual survival and recruitment were regressed against medusa abundance with the NAOI as an additional explanatory variable. Maximum abundance of *A. aurita* was included in the model since it was the only measure that correlated with herring residual survival in addition to the LAI in the Buchan and Central regions; *C. capillata* was also included because the  $\ln(\text{abundance})$  of this medusa correlated significantly with the LAI in the Orkney/Shetland region.

An initial model of herring residual survival without interactions between the three explanatory variables suggested that the abundance of *C. capillata* and the NAOI were not significant variables. However, as changes in the NAO could result in shifts in the relative distributions of the jellyfish species, interactions between the explanatory variables were explored. Although there was no significant interaction between the NAOI and the abundance of *A. aurita*, a significant interaction between the abundance of *C. capillata* and the NAOI was found when the interaction was included as an additional

explanatory variable with the abundances of *A. aurita* and *C. capillata* and with the NAOI; the proportion of variability explained increased by 25% over the model with *A. aurita* alone. The detrended residual survival and the observed recruitment were modelled using equation 6 with  $x_1$  = maximum abundance of *Aurelia aurita*;  $x_2$  = ln(maximum) abundance of *Cyanea capillata*;  $x_3$  = NAOI and an interaction between  $x_2$  and  $x_3$ . The model yielded the following results: for  $y$  = detrended herring residual survival  $R^2 = 0.62$   $P = 0.03$   $N = 15$ ; for  $y$  = detrended recruitment  $R^2 = 0.78$   $P < 0.01$   $N = 15$  (Figure 5.7 and Table 5.1). The same model also fit significantly to the detrended recruitment, but not residual survival, with ln(maximum) substituted for maximum *A. aurita* ( $R^2 = 0.82$   $P < 0.01$   $N = 15$ ). In each model all variables were significant at the 0.05 level with the exception of the abundance of *C. capillata* in the model of herring survival, which suggests that this medusa is unlikely to influence survival directly.

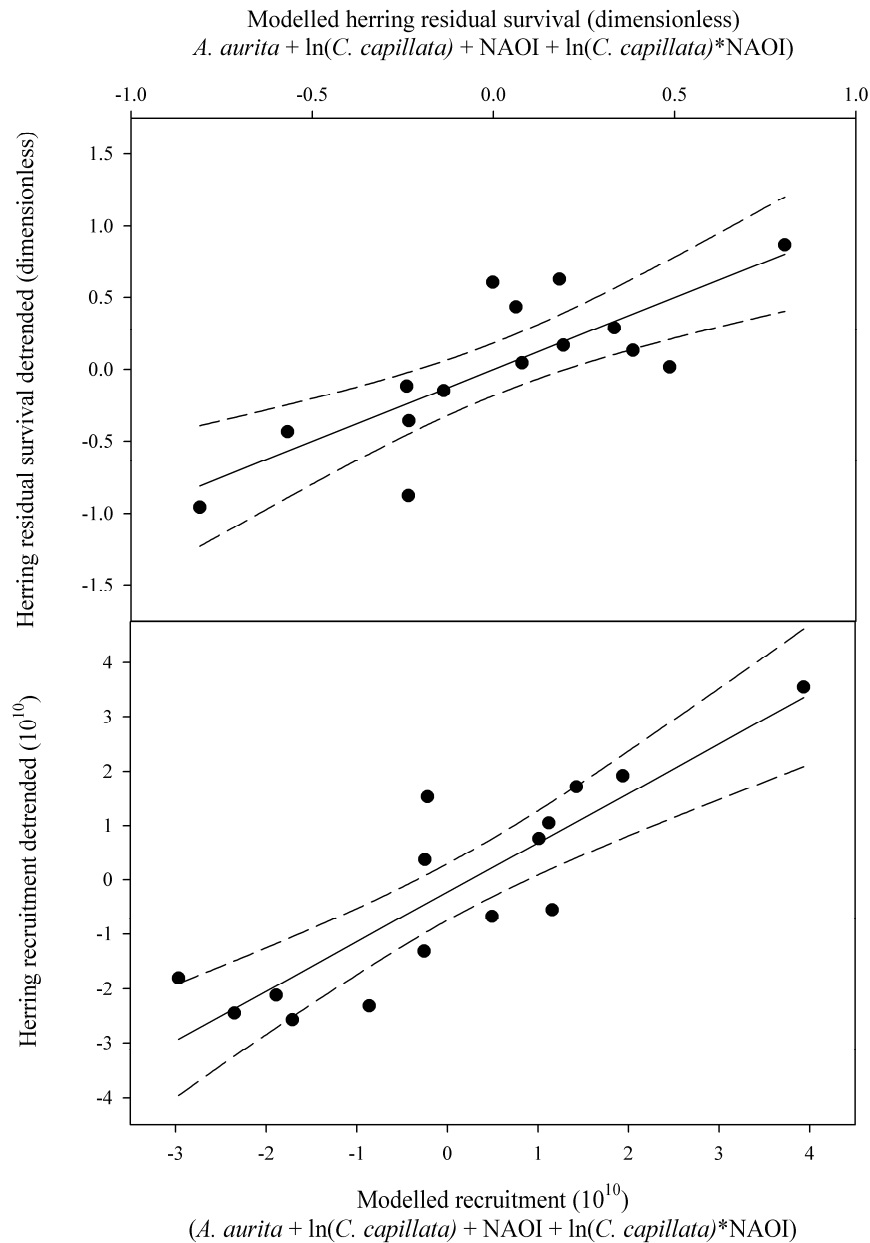


Figure 5.7 Herring, *Aurelia aurita*, and *Cyanea capillata*: Climatic modulation of jellyfish impacts on herring. Linear regression model (solid line with dashed lines for the 95% confidence interval) with the maximum abundance of *A. aurita* ( $x_1$ ), ln(maximum) abundance of *C. capillata* ( $x_2$ ) and the NAOI ( $x_3$ ) with an NAO-*C. capillata* interaction ( $x_2 \cdot x_3$ ) as explanatory variables vs herring residual survival ( $y_s$ ) detrended (top,  $R^2 = 0.62$   $P = 0.03$ ,  $y_s = 91.97 - 5.95 \times 10^{-5} x_1 - 8.76 \times 10^{-2} x_2 - 1.91 x_3 + 0.201 x_2 \cdot x_3$ ), and vs herring 0-group recruitment ( $y_r$ ) detrended (bottom,  $R^2 = 0.78$   $P < 0.01$ ,  $y_r = 8.19 \times 10^4 - 1.78 x_1 - 1.29 \times 10^4 x_2 - 4.95 \times 10^4 x_3 + 8.91 \times 10^3 x_2 \cdot x_3$ ).

No significant relationship was found between the NAOI and either the residual survival or recruitment of herring or the abundance of any medusa in the full



North Sea dataset. Therefore the inclusion of the NAOI as an additional explanatory variable in the linear model (Equation 6) does not violate the assumption of independent variables. Herring residual survival was indeed correlated with the abundance of *A. aurita*, as was herring recruitment; however, herring residual survival does not influence *A. aurita* abundance. *Aurelia aurita* medusae are abundant in advance of, and during, the spawning and hatching season (Figure 5.2). Therefore *A. aurita* is a predictor of herring survival, and not the reverse, and the assumption of independence is upheld.

| Response y = herring recruitment ( $R^2 = 0.82, P < 0.01$ ) |                            |                               |             |        |
|---|----------------------------|-------------------------------|-------------|--------|
| Explanatory variable  | $\beta_{\text{estimated}}$ | $\beta_{\text{standardised}}$ | t-statistic | P      |
| Intercept   | $1.30 \times 10^5$         | -                             | 6.16        | <0.001 |
| $x_1 = \ln(\textit{Aurelia aurita})$                        | $-6.96 \times 10^3$        | -0.557                        | -3.59       | 0.005  |
| $x_2 = \ln(\textit{Cyanea capillata})$                      | $-1.37 \times 10^4$        | -0.565                        | -3.39       | 0.007  |
| $x_3 = \text{NAOI}$   | $-4.31 \times 10^4$        | -3.330                        | -3.41       | 0.007  |
| $x_2.x_3 = \ln(\textit{Cyanea capillata}). \text{NAOI}$     | $7.81 \times 10^3$         | 3.621                         | 3.67        | 0.004  |

| Response y = herring recruitment ( $R^2 = 0.78, P < 0.01$ ) |                            |                               |             |       |
|---|----------------------------|-------------------------------|-------------|-------|
| Explanatory variable  | $\beta_{\text{estimated}}$ | $\beta_{\text{standardised}}$ | t-statistic | P     |
| Intercept   | $8.19 \times 10^4$         | -                             | 3.47        | 0.006 |
| $x_1 = \textit{Aurelia aurita}$                             | -1.78                      | -0.572                        | -3.06       | 0.012 |
| $x_2 = \ln(\textit{Cyanea capillata})$                      | $-1.29 \times 10^4$        | -0.532                        | -2.81       | 0.019 |
| $x_3 = \text{NAOI}$   | $-4.95 \times 10^4$        | -3.827                        | -3.53       | 0.005 |
| $x_2.x_3 = \ln(\textit{Cyanea capillata}). \text{NAOI}$     | $8.91 \times 10^3$         | 4.133                         | 3.77        | 0.004 |

| Response y = herring residual survival ( $R^2 = 0.62, P = 0.03$ ) |                            |                               |             |       |
|---|----------------------------|-------------------------------|-------------|-------|
| Explanatory variable  | $\beta_{\text{estimated}}$ | $\beta_{\text{standardised}}$ | t-statistic | P     |
| Intercept   | 91.97                      | -                             | 1.15        | 0.276 |
| $x_1 = \textit{Aurelia aurita}$                                   | $-5.95 \times 10^{-5}$     | -0.753                        | -3.03       | 0.013 |
| $x_2 = \ln(\textit{Cyanea capillata})$                            | $-8.76 \times 10^{-2}$     | -0.142                        | -0.57       | 0.584 |
| $x_3 = \text{NAOI}$   | -1.91                      | -3.620                        | -2.51       | 0.031 |
| $x_2.x_3 = \ln(\textit{Cyanea capillata}). \text{NAOI}$           | 0.201                      | 3.671                         | 2.52        | 0.031 |

Table 5.1 Regression model results (with the proportion of variability explained by the model  $R^2$  and significance value  $P$ ) for North Sea herring recruitment and residual survival against the maximum abundances of *Aurelia aurita*, and *Cyanea capillata*, and the NAOI, with an interaction between the NAOI and *C. capillata* for the period 1971 to 1986 (excluding 1984). Estimated and standardised  $\beta$  values are shown with  $t$ -statistics and associated  $P$  values, where \*\*\* indicates  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ , .  $P < 0.10$ .

### 5.5. Discussion

Medusae may exert top-down control over marine ecosystems (Schneider and Behrends 1998; Oguz et al. 2001) and previous studies have suggested that jellyfish may impact on herring larval survival both directly and indirectly through predation on ichthyoplankton and crustacean zooplankton (Bailey 1984; Möller 1984; Purcell 2003). Whether or not these interactions between medusae and fish have any measurable long-term impact on populations of either is as yet unknown, but it has been suggested that the over-exploitation of fish stocks could increase prey availability and release jellyfish from competitively imposed restrictions on population abundance, which may exacerbate any detrimental effect (Pauly et al. 1998; 2002). This study is the first to quantify possible interactions between jellyfish abundance and herring recruitment over extended time periods and to account for spawning stock biomass variation and climatic factors. However, correlative studies of this type describe associations and coupled trends that may or may not be causal. Therefore the possible links between herring and jellyfish and the climate suggested here require further study to clarify the causal mechanism. I consider four possible underlying mechanisms for the correlations found between herring residual survival and jellyfish abundance:

1. The abundances of *A. aurita* and *C. capillata* are high during the period of lowest herring SSB due to the release of jellyfish from competition with herring. Herring residual survival is thus lower than expected because at low herring stock and high jellyfish abundances the possible competition and predation impacts of jellyfish are greatest.
2. The correlations describe coupled trends that are a result of NAO-driven environmental change.
3. The relationships describe impacts by jellyfish (*A. aurita* and *C. capillata*) on herring that are mediated by NAO-driven environmental change.
4. The association between herring and jellyfish is the result of more widespread changes in the North Sea ecosystem, e.g. plankton community change or the ‘Gadoid outburst’, possibly due to the ‘Great Salinity Anomaly’.

*Mechanism 1: Release of jellyfish abundance from competition with herring adults resulting in increased competition and predation impacts by jellyfish on herring survival*

Whatever the cause (e.g. overfishing, climate change, or pollution) in the declining herring stock during the 1960s and early 1970s, the indirect effect may have been to increase the food available for jellyfish. The negative correlations between herring spawning stock biomass and the abundance of *A. aurita* between 1971 and 1986 suggest that as the herring stock decreased so the medusa abundance increased, possibly through a release from competition with the herring stock (Figures 5.3 and 5.5). The reduction in the herring stock may also have led to the negative correlation east of Shetland between larval fish prevalence and *A. aurita* prevalence (Figure 4.8, Section 4.4.2.4). The negative correlation between herring residual survival and *A. aurita* abundance suggest that the rise in *A. aurita* abundance may have caused further decreases in the survival of herring larvae irrespective of changes in the adult herring population (Figure 5.4). A similar impact might also explain the negative correlation between larval fish prevalence and *Cyanea capillata* prevalence west of Denmark during August–September (Figure 4.9, Section 4.4.2.4).

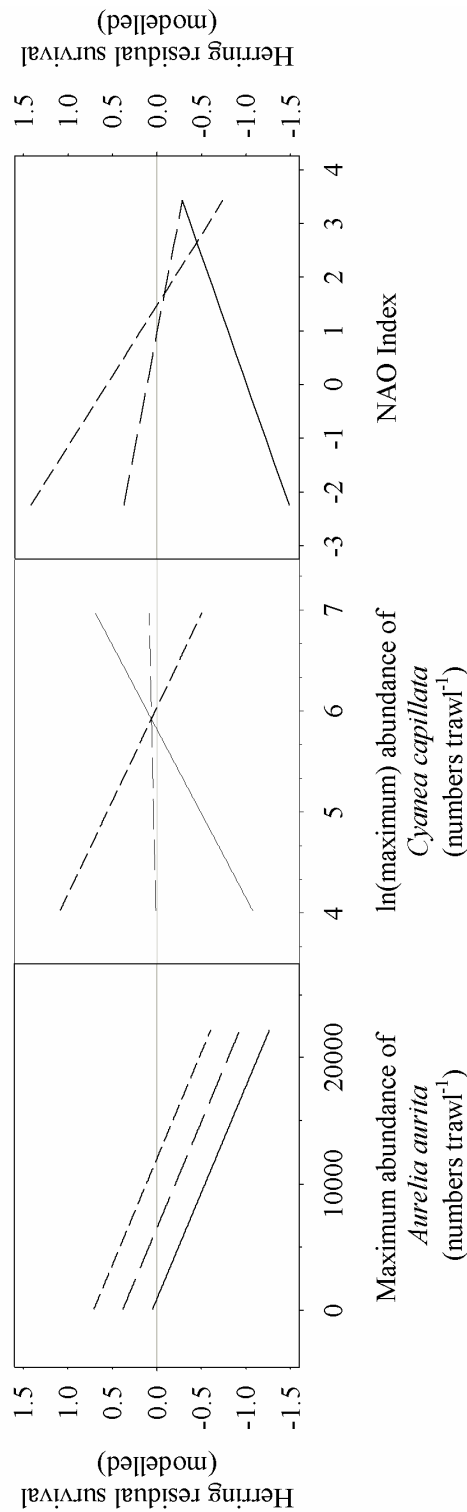


Figure 5.8 Herring, *Aurelia aurita*, and *Cyanea capillata*: The modelled effect on herring residual survival ( $y_s = 91.97 - 5.95 \times 10^{-5} x_1 - 8.76 \times 10^{-2} x_2 - 1.91 x_3 + 0.201 x_2 \cdot x_3$ ) of changes in the NAO and jellyfish abundance over the observed ranges of the NAOI ( $x_3$ ) and the maximum medusa abundance in the period 1971 to 1986: left, change in expected survival due to variation in *Aurelia aurita* abundance ( $x_1$ ) at a constant median abundance of *Cyanea capillata* ( $x_2 = 209$  medusae); centre, *Cyanea capillata* ( $x_2$ ) at median *Aurelia aurita* abundance ( $x_1 = 5736$  medusae), where solid lines represent high NAO ( $x_3 = 3.42$ ); long-dashed lines median NAO ( $x_3 = 0.56$ ) and short-dashed lines low NAO ( $x_3 = -2.25$ ); right, effect on survival due to changing NAO conditions under fixed medusa abundance, where solid lines represent highest abundance of medusae ( $x_1 = 22125$  *A. aurita* and  $x_2 = 1064$  *C. capillata*); long-dashed lines median values ( $x_1 = 5736$  *A. aurita* and  $x_2 = 209$  *C. capillata*) and short-dashed lines lowest abundance of medusae ( $x_1 = 89$  *A. aurita* and  $x_2 = 56$  *C. capillata*).

The positive relationships between abundances of herring larvae and *Aurelia aurita* in the Buchan and Central areas, and *Cyanea capillata* in the Orkney/Shetland area, suggests that both herring spawning success and jellyfish abundance show a similar response to interannual environmental change. Conditions (such as food availability and temperature) that are beneficial for herring hatching success are also favourable for a jellyfish bloom, which increases the likelihood of interactions between jellyfish and herring and minimizes the effect of the environment on either herring or jellyfish. Predation by medusae on herring larvae, and direct competition between medusae and herring, may occur when they overlap spatially and temporally, and indirect competition may arise if a time lag exists. The herring stock considered here spawns during the late summer and autumn (August – September) when medusae are maturing (Figure 5.2). The main period of *A. aurita* and *C. capillata* medusa abundance in the North Sea is during the early summer (May to August) and by September/October these species become scarce in the plankton (Russell 1970). Medusae are therefore most likely to impact directly on herring via competition and predation during August in the spawning areas. Indirect impact via competitive removal of food by medusae during the summer might also result in low prey availability for herring hatchlings in the autumn, and thus poor larval survival (Olesen 1995). The early life stages of herring suffer highest mortality, so much so that the year-class strength is set generally by the time young fish have passed larval and early metamorphosed stages, therefore the possible impact of medusae might occur in the critical period (Axenrot and Hansson 2003; Nash and Dickey-Collas 2005).

This possible mechanism for the release of jellyfish from competition may be exemplified by the ten-fold rise in *Chrysaora melanaster* abundance in the Bering Sea (1979 to 1999), which was negatively correlated ( $R = -0.69$ ,  $P < 0.01$ ) with the decreasing abundance of potentially competitive planktivorous forage fishes (juvenile herring *C. pallasii*, Age-1 pollock *Theragra chalcogramma*, and capelin *Mallotus villosus*) (Brodeur et al. 2002). However, climate change and ‘regime shift’ may also have driven these trends (Brodeur et al. 1999). For example, if climatic changes alter the period and location of highest prey abundance, medusae may be favoured over planktivorous fish or *vice versa*.

*Mechanism 2: Coupled trends resulting from NAO-driven environmental change*

Climatic variation, as encapsulated in the NAOI, may influence the abundance and distribution of herring and jellyfish. Lynam et al. (2004) showed that the abundance of *Aurelia aurita* medusae in regions in the eastern and western North Sea were significantly negatively related to the winter North Atlantic Oscillation Index (NAOI) ( $R^2 > 0.50$  and  $P < 0.01$ ) (Chapter 2). Lynam et al. (2005) (Chapter 2) extended the analysis and found that the abundance of *A. aurita* north of Scotland was positively correlated with the NAOI ( $R^2 = 0.40$  and  $P < 0.05$ ). Whereas east of Scotland, in a region approximating to the Buchan area, both *A. aurita* and *C. capillata* abundances were negatively correlated with the NAOI (Chapter 2). Hydroclimatic change may also have altered the distribution of medusae through a strengthening of the inflow of Atlantic/Arctic waters to the northern North Sea (Chapters 3 and 4).

Climatic variation has been shown to govern alternating periods dominated by Norwegian spring-spawning herring and sardines (*Sardina pilchardus*) in the English Channel and off south-west England, where a high NAOI has been associated with dominance by herring (Alheit and Hagen 1997). Conversely, the Bohuslän herring periods in the Skagerrak appear to benefit from a low NAOI (Alheit and Hagen 1997). The NAOI has also been found to be weakly but significantly positively correlated with the year class strength of spring-spawning herring in the Baltic Sea ( $R^2 = 0.35$   $P < 0.03$   $N = 10$ ), and has been used to improve predictive models of herring recruitment from young-of-the-year densities (Axenrot and Hansson 2003).

NAO variation may be the root cause of changes in both jellyfish abundance and in the distribution of herring spawners and thus regional spawning success. Therefore the correlations found here may merely be coupled trends rather than evidence for an impact by jellyfish on herring survival. However, the NAOI was not significantly correlated with either the herring residual survival or recruitment, therefore if there is a link between NAO-related environmental change and residual survival it is probably mediated by ecosystem changes.

*Mechanism 3: NAO-mediated possible impact by jellyfish on herring survival*

I have suggested that the positive correlations between jellyfish abundance and the LAI indicate that both the spawning success of herring and the regional abundance of jellyfish respond similarly to environmental change. Therefore, as important predators of zooplankton, jellyfish could form an intermediary between NAO-driven change and herring residual survival.

I explored the role that jellyfish and the NAO may play in driving interannual variability in herring residual survival and recruitment through multivariate regression analyses. The models described in this chapter relate both herring residual survival and recruitment to abundances of *A. aurita* and *C. capillata* with an NAOI interaction (Figure 5.7). The interaction term suggests either that jellyfish form an intermediary, linking climatic change to herring residual survival (Figure 5.8, right pane), or that climatic changes mediate the possible impact of medusae on herring (Figure 5.8, left and centre panes). When either herring residual survival or recruitment were regressed (without interactions) against the three explanatory variables, only the abundance of *A. aurita* correlated significantly. This suggests that the interannual change in herring residual survival is linked primarily to the abundance of *A. aurita*. Once an interaction was included between the abundance of *C. capillata* and the NAOI both variables appear to have a significant role. *Cyanea capillata* is a predator on the smaller *A. aurita* and may regulate the abundance of *A. aurita* (Båmstedt et al. 1997). In addition, the NAO may drive environmental changes that alter the spawning success of herring and the relative abundance of the jellyfish species *A. aurita* and *C. capillata* (see Mechanism 2). Thus, both *C. capillata* and the NAO may mediate the possible impact of *A. aurita* on herring survival.

In the models (Equation 6 and Table 5.1) the coefficient of the *A. aurita* variable ( $\beta_1$ ) is negative, suggesting that as the abundance of *A. aurita* medusae increases, the survival of herring decreases. *Cyanea capillata* interacts with the NAOI (the *C. capillata* coefficient  $\beta_2$  and the NAOI  $\beta_3$  are negative, whereas the interaction  $\beta_4$  are positive) so that constant NAOI (or *C. capillata*) conditions must be considered in order to understand the possible impact of *C. capillata* (or NAOI) on herring.

For a high NAOI, as the abundance of *C. capillata* increases the survival of herring also increases (Figure 5.8, centre pane, solid line). In contrast, under low NAOI conditions, an increase in *C. capillata* abundance decreases herring survival (Figure 5.8, centre pane, short-dashed line). Similarly, fixing *C. capillata* abundance can reveal the effect of NAOI variation. For a high abundance of *C. capillata*, as the NAOI increases the survival of herring increases (Figure 5.8, right pane, solid line). Whereas, with a low or median abundance of *C. capillata* an increase in the NAOI appears to be detrimental to herring residual survival (Figure 5.8, right pane, short-dashed line).

If both *A. aurita* and *C. capillata* are at very high abundance, herring larval survival is likely to be lower than expected irrespective of the NAO phase, although it may be much worse at a low NAOI (Figure 5.8, right pane, solid line). However, if both jellyfish species are at median or low abundance, the herring residual survival is only likely to be lower than expected if the NAO is in a high phase (NAOI > approximately 1.5) (Figure 5.8, right pane, dashed lines). This suggests that a high NAO has a largely detrimental impact on the survival of autumn spawning North Sea herring.

The possible negative effect of *A. aurita* medusae on larval survival appears to be enhanced under low NAO conditions if and only if *C. capillata* abundance is high (Figure 5.8, centre pane, short-dashed line). Lynam et al. (2005) found that *A. aurita* and *C. capillata* abundance in the Buchan spawning area is expected to be high during low NAO years, therefore the possible detrimental effect of jellyfish on larval survival may be altered most by the NAO there. When a high NAO prevails, jellyfish are expected to be more abundant north of Scotland and west of the Orkneys (Lynam et al. 2005), and there is likely to be less spatial overlap between the medusae and herring larvae. During these high NAO years, an increase in the abundance of *C. capillata* is associated with a rise in herring residual survival, which again suggests that both *C. capillata* and herring residual survival benefit from similar conditions in the North Sea (Figure 5.8, centre pane, solid line). The apparent increase of the impact on herring residual survival under high NAO conditions, if the abundance of *C. capillata* is median to low (Figure 5.8, left pane, solid line), therefore suggests that high NAO conditions resulted in an additional negative impact on herring that is independent of *A. aurita*. However, this NAO-driven



impact appears to be much weaker than that expected by a high abundance of jellyfish under a low NAO (Figure 5.8, right pane).

The collapse of the herring stock during the 1970s did not happen uniformly over the North Sea. As the whole North Sea population abundance declined, the distribution of spawning activity moved northwards until, during the minimum herring abundance and maximum *A. aurita* abundance period in 1976 to 1978, the population was concentrated at Shetland (Heath et al. 1997). Therefore the herring stocks retreated to the area where *C. capillata* was the most common medusa and the detrimental effect of the generally more abundant *A. aurita* was minimised. The herring stock recovered following a ban on North Sea herring fishing between 1977 and 1981. This coincided with a return to the positive phase of the NAO in 1980 and, perhaps more importantly, a reduction in the abundance of *A. aurita*.

*Mechanism 4: The 'great salinity anomaly', plankton community change, and the 'gadoid outburst'*

The gradual decline in the North Sea herring stock during the 1950s and 1960s may have been caused principally by overfishing, but the eventual collapse of the stock in 1977 may have been triggered by environmental change and low survival of herring larvae. The great salinity anomaly of the 1970s saw a huge volume of cold, low salinity water travel around the North Atlantic gyre from 1968 to 1981 and invade the North Sea during the low NAO period 1977 to 1979 (Dickson et al. 1988; Belkin et al. 1998). In addition, changes in the plankton community contributed to the gadoid outburst of the 1970s, which saw a dramatic rise in the abundance of gadoids in the North Sea (Hislop 1996; Beaugrand et al. 2003). Although initial gains were made in the Buchan herring stock, the herring did not follow the rise in gadoid abundance (Rothschild 1998). The subsequent long-term decreasing trend in the North Sea herring stock appeared to follow a decline in zooplankton abundance, which presumably would increase competition between herring and other planktivores, including jellyfish (Aebischer et al. 1990; Rothschild 1998). Therefore, it is possible that the correlations described here are incidental associations resulting from a period of extensive change in the North Sea.

### 5.6. Concluding remarks

The regional abundance of *Aurelia aurita* and *Cyanea capillata* medusae was generally greatest in years when highest abundances of herring larvae were found in the spawning areas of the Buchan, Central, and the Orkney/Shetland regions of the North Sea. Years of expected high larval survival of autumn-spawning herring coincided with an overall high abundance of *A. aurita* in the North Sea. However, there appears to be a significant negative impact of *A. aurita* on herring residual survival and recruitment in the North Sea, which might result from a combination of predation on herring larvae by medusae and competition between larvae and medusae for zooplankton food. Whether or not jellyfish contribute directly to declines in fish stocks or become more prominent in over-exploited ecosystems is hard to discern, particularly as a reduction in herring stocks may release *A. aurita* and *C. capillata* from competition and exacerbate the possible impact of jellyfish on larval herring survival. I consider the interannual relationships between *A. aurita* abundance and herring residual survival to be evidence for an impact by these common medusae on herring recruitment. This possible impact on herring appears to be climatically modulated via relative shifts in the distribution and abundance of the herring and medusae populations. If jellyfish are consistently abundant, a switch to a low NAOI might result in a greater impact by jellyfish on herring residual survival (Figure 5.8, right panel, solid line). It is therefore important that jellyfish abundance in the North Sea be monitored and that herring recruitment be assessed with respect to ecosystem change. Specifically, management of North Sea herring stocks might benefit from incorporation of predation and competition effects of medusae into forecasting models of herring recruitment.

## Chapter 6

### Shelter for gadoids under a jelly umbrella?



Whiting (*Merlangius merlangus*) safe among the tentacles of a lions mane jellyfish (*Cyanea capillata*)  
Photograph reproduced from Aquascope (2000)

The work described here is in review:

Lynam C.P. and A.S. Brierley (in review). *Shelter for gadoids under a jellyfish umbrella?* Marine Biology

I estimate that I contributed 90% of the effort towards the paper, which can be broken down into the following five equally weighted areas: Data collection/preparation 60 %, I gathered/prepared environmental and fisheries data from ICES and I had already prepared the jellyfish data and NAO data; Inspiration 100 %; Analysis 100 %; Conclusions 95 %; Publication 95 %, the paper was written by me but reviewed by ASB.

## 6. Shelter for gadoids under a jelly umbrella?

### 6.1. Abstract

Young gadoid fish have been observed using medusae as ‘umbrellas’ to provide refugia from predation. Here, I explore the possibility that the high abundance of medusae in the North Sea (up to 34 medusae per 100 m<sup>3</sup>) may improve the survival of larval gadoids. Jellyfish were caught during routine sampling for 0–group gadoids (cod *Gadus morhua*; haddock *Melanogrammus aeglefinus*; Norway pout *Trisopterus esmarkii*; and whiting *Merlangius merlangus*) in the North Sea from 1971 to 1986 and a considerable overlap was found between the distribution of these fish and both *Cyanea lamarckii* and *Cyanea capillata* (Hay et al. 1990). Hay et al. (1990) found positive correlations between the biomass of 0–group gadoids and *Cyanea* spp. in trawl catches for the period 1974 to 1983 when the spawning areas of these fish were fully sampled. In this study, I test correlations between the abundance of medusae in the North Sea and the residual survival of larval fish, as quantified by the deviation in recruitment from the expected Ricker–modelled recruitment. Significant positive correlations were found between whiting residual survival and the ln(maximum) abundance of both *Cyanea* spp. combined for the period 1974–1983 ( $R = 0.71$   $P = 0.02$   $N = 10$ ). If all years are used where data were collected, 1971–1986, then positive correlations are evident for each *Cyanea* spp. and for combined *Cyanea* spp. ln(maximum) abundance (all  $R \geq 0.60$   $P < 0.01$   $N = 15$ ). The abundance of jellyfish may thus be an important factor regulating the mortality of whiting, and should be considered in the development of ‘ecosystem–based’ management of whiting stocks.

### 6.2. Introduction

Commensal associations between *Cyanea* spp. and gadoids (cod, haddock, Norway pout and whiting) have been proposed, whereby young fish shelter among the jellyfishes tentacles so avoiding predation (Section 1.9). In addition the gadoids may steal prey from the medusa and feed on crustaceans (Hyperiidia) that are parasitic on jellyfish (Russell 1970; Hay et al. 1990; Purcell and Arai 2001). Through a correlative analysis, I consider the possible beneficial impact of the proposed shelter relationship on the residual survival of those gadoid fish (cod, whiting, and haddock) that have been suggested to

associate with *Cyanea* spp. ( $\geq 3$  significant  $P < 0.01$  correlations, Table 6.1) (Hay et al. 1990). Norway pout are unlikely to benefit from an association with medusae as the 0-group fish are thought to spend most of the daylight hours close to the seabed, and moving into midwater at night (Bailey 1975).

| Umbrella species        | Year | Whiting  |          |          | Cod      |          |          | Haddock  |          |          | Norway pout |          |          |
|-------------------------|------|----------|----------|----------|----------|----------|----------|----------|----------|----------|-------------|----------|----------|
|                         |      | <i>R</i> | <i>P</i> | <i>N</i> | <i>R</i> | <i>P</i> | <i>N</i> | <i>R</i> | <i>P</i> | <i>N</i> | <i>R</i>    | <i>P</i> | <i>N</i> |
| <i>Cyanea capillata</i> | 1974 | 0.67     | ***      | 39       | 0.50     | **       | 30       | 0.67     | ***      | 41       | 0.60        | ***      | 23       |
|                         | 1975 | 0.32     |          | 33       | 0.33     |          | 19       | 0.17     |          | 28       | 0.33        |          | 22       |
|                         | 1976 | 0.31     |          | 38       | 0.24     |          | 43       | 0.08     |          | 46       | 0.27        |          | 30       |
|                         | 1977 | 0.39     | *        | 35       | 0.36     | **       | 55       | 0.19     |          | 66       | 0.28        |          | 41       |
|                         | 1978 | 0.14     |          | 41       | 0.42     | **       | 54       | 0.15     |          | 55       | 0.21        |          | 34       |
|                         | 1979 | 0.09     |          | 53       | 0.09     |          | 64       | 0.37     | **       | 68       | 0.25        | *        | 62       |
|                         | 1980 | 0.68     | ***      | 60       | 0.40     | **       | 47       | 0.78     | ***      | 52       | 0.55        | ***      | 41       |
|                         | 1981 | 0.41     | **       | 63       | 0.25     | *        | 73       | 0.35     | **       | 73       | 0.32        | *        | 44       |
|                         | 1982 | 0.37     | **       | 57       | 0.25     | *        | 67       | 0.34     | **       | 71       | 0.34        | *        | 42       |
|                         | 1983 | 0.30     | *        | 72       | 0.26     | *        | 78       | 0.30     | **       | 77       | 0.24        |          | 47       |
| <i>Cyanea lamarckii</i> | 1974 | 0.31     |          | 20       | -0.25    |          | 18       | 0.08     |          | 22       | -0.51       |          | 11       |
|                         | 1975 | 0.00     |          | 25       | -0.12    |          | 13       | -0.22    |          | 18       | -0.14       |          | 14       |
|                         | 1976 | 0.36     | *        | 40       | 0.29     |          | 41       | 0.10     |          | 41       | -0.14       |          | 19       |
|                         | 1977 | 0.29     |          | 29       | 0.13     |          | 35       | -0.06    |          | 41       | -0.30       |          | 18       |
|                         | 1978 | 0.75     | ***      | 33       | 0.60     | ***      | 40       | 0.04     |          | 44       | -0.16       |          | 21       |
|                         | 1979 | 0.39     | **       | 49       | 0.41     | **       | 61       | -0.02    |          | 60       | -0.11       |          | 45       |
|                         | 1980 | 0.30     | *        | 44       | -0.07    |          | 35       | 0.19     |          | 36       | 0.12        |          | 26       |
|                         | 1981 | 0.28     | *        | 57       | 0.05     |          | 42       | -0.10    |          | 41       | -0.41       |          | 17       |
|                         | 1982 | 0.17     |          | 44       | -0.07    |          | 44       | -0.37    | **       | 47       | -0.25       |          | 21       |
|                         | 1983 | 0.52     | ***      | 65       | -0.15    |          | 68       | 0.03     |          | 67       | -0.03       |          | 42       |

Table 6.1: Rank correlation coefficients (*R*) and their significance levels where \*\*\* indicates  $P < 0.001$ , \*\*  $< 0.01$ , and \*  $< 0.05$  for correlations between biomass of *C. capillata* (top) and *C. lamarckii* (bottom) with the abundance of 0-group gadoids in those *N* hauls where both fish and medusae were caught together. Reproduced from Hay et al. (1990). Note that correlations were only reported for those years when the distribution of gadoids was surveyed most completely and  $N > 10$ .

Ephyrae (juvenile medusoids) of *Cyanea lamarckii* and *C. capillata* are produced and released during the winter and early spring (from December to March) from benthic scyphistomae (polyps); by May the majority will have metamorphosed into medusae (Russell 1970). The distribution of scyphistomae has not been established; however, as ephyrae and medusae are often found in high abundance in coastal areas, it is probable that shallow waters constitute the

major zone for jellyfish development (see Chapter 4, Figure 4.1 and 4.2, for the distribution of medusae in the North Sea). Large (>10 cm umbrella diameter) jellyfish are particularly abundant in the North Sea during June to August; however, *C. capillata* may be present throughout the year. The young gadoid (0–group) fish considered in this study live in the upper water layers ( $\leq 40$  m) for a period of a few months before migrating to the seabed (Daan et al. 1990; Bjorke and Saetre 1994). Although the gadoids spawn during the same months in which jellyfish are found in the North Sea, the spawning areas and timings are particular to each fish species. Cod spawning in the North Sea takes place between January and April and occurs in most offshore areas, but mainly in the northern and central North Sea (Rogers and Stocks 2001). Newly hatched cod are distributed over a large proportion of this area but are advected towards Jutland, leading to high concentrations of larvae in the shallow Wadden Sea. Haddock release their eggs in a number of batches from March until May in most areas of the North Sea from the Scottish coast to the Norwegian inshore waters. In the northern North Sea most of the haddock larvae do not travel far from the spawning grounds; however, some larvae from spawning grounds off the Scottish western coast can be transported into the northern North Sea (Rogers and Stocks 2001). The spawning season of whiting extends from late January until June, and an individual female will release many batches of eggs over a period of at least ten weeks (Rogers and Stocks 2001). High numbers of immature whiting are found both off the Scottish coast and in the Wadden Sea, where medusae are particularly abundant (Coull et al. 1998).

During the jellyfish survey period, 1971 to 1986, important environmental changes (hydroclimatic and biotic shifts) occurred in the North Sea, which may have impacted upon both the abundance of jellyfish and the survival of larval fish. From 1968 to 1981 a large volume of cold, low salinity water, described as ‘The Great Salinity Anomaly’, travelled around the North Atlantic gyre (Dickson et al. 1988; Belkin et al. 1998). This water entered the northern North Sea during 1977 to 1979, coinciding with a phase shift of the North Atlantic Oscillation Index (NAOI) from high to low and a period of high jellyfish abundance (Dickson et al. 1988; Reid et al. 2003) (Chapters 2 and 3). An exceptionally cold period during 1978–1982 in the North Sea was characterized by a strong decrease in the abundance of dinoflagellates, diatoms, decapods, and

total copepods in the Continuous Plankton Recorder data (Edwards et al. 2002). Subsequent to this cold period, the North Sea zooplankton shifted from a community that had been dominated by cold water species since 1961 to a community of warm water species from 1984 to 1999 (Beaugrand 2004).

Here I will determine a residual survival index for each of three gadoid species (cod, whiting, and haddock) by factoring out from the recruitment data any effect due to changes in spawning stock biomass, as quantified by a Ricker stock–recruitment model. With these survival indices, I will conduct a correlative analysis to determine whether the hydroclimatic variables (temperature, salinity, or NAOI) that appear to have resulted in shifts in the zooplankton community are significant covariates ( $P < 0.05$ ) or whether the abundance of jellyfish is more explanatory of the interannual variability in gadoid species survival.

### 6.3. Methods

#### *Data collection*

Medusa abundance data were collected over 15 years (1971–86, excluding 1984) during the routine summer International Council for the Exploration of the Sea (ICES) International 0–group Gadoid Surveys of the North Sea (Hay et al. 1990). Jellyfish were a bycatch of these surveys. Full survey methods are given in Hay et al. (1990), and Chapters 2 and 3. Mean monthly salinity and temperature data for the surface (top 5 m) layer in one degree by half-degree grid squares throughout the North Sea were supplied by ICES.

Cod (*Gadus morhua*) spawning stock biomass (SSB, tonnes) and 1–group recruitment (individuals), are published by ICES for the North Sea combined with the eastern English Channel for cod and west of Scotland/Rockall for saithe (ICES 2003a). Whiting (*Merlangius merlangus*) SSB, and 1–group recruitment data for the North Sea and Skagerrak are also published by ICES (1996b). Haddock (*Melanogrammus aeglefinus*) SSB, and 0–group recruitment data for the North Sea combined with the Skagerrak and Kattegat were obtained from C. Needle (Marine Laboratory, Aberdeen).

*Residual survival index for fish larvae*

Hay et al. (1990) were unable to determine any influence of *Cyanea* abundance on the survival of 0–group fish to the 1–group. However, they only tried correlations between *Cyanea* biomass and the abundance of 1–group fish in the following years. To identify if there are any external impacts on the recruitment of a fish species either by another species or by the environment, we should first factor out from the recruitment data any ‘internal’ effect due to changes in spawning stock biomass. I have used a Ricker model (Equation 3, Section 5.2) to account for this variation in recruitment due to long–term population change. The external impacts on larval survival (i.e. variability in recruitment not due to changes in SSB) were then measured by the residual survival (Equation 5, chapter 5.2). The constants  $a$  and  $b$  were fitted, for each gadoid species, by non–linear least–squares estimation using the *Gauss–Newton* algorithm in *R Version 1.8.1* (R Development Core Team 2003): for whiting  $a = 6.60 \times 10^{-4}$  and  $b = 1.68 \times 10^{-3}$ ; cod  $a = 3.57$  and  $b = 2.9 \times 10^{-6}$ ; and haddock  $a = 457$  and  $b = 6.54 \times 10^{-6}$ .

**6.4. Results**

The residual survival from 1971 to 1986 of whiting, but not haddock or cod, correlated positively with the  $\ln(\text{maximum})$  abundance of both *Cyanea* species combined ( $R = 0.64$ , Figure 6.1) and individually: *C. lamarckii* ( $R = 0.65$ ) and *C. capillata* (once a long-term rise in *C. capillata* abundance was detrended) ( $R = 0.60$ ) (all  $P < 0.01$   $N = 16$ ); note that *C. lamarckii* abundance did not correlate significantly with *C. capillata* abundance. As fluctuations in temperature and salinity during the early life stages of fish can impact greatly on the development and survival of hatchings, the mean surface salinity and temperature were calculated for the whiting spawning period (from January to August) in the western North Sea, from 5°W to 3°E and between 55°N and 66°N, where these larvae are spawned. No significant correlations were found between the residual survival of whiting and either temperature or salinity. Climatic oscillations can also alter hydrographic conditions (i.e. wind–induced mixing, surface currents and nutrient inflows from rivers) in the North Sea; therefore, whiting residual survival was correlated against the North Atlantic Oscillation Index, but no significant correlations were found.



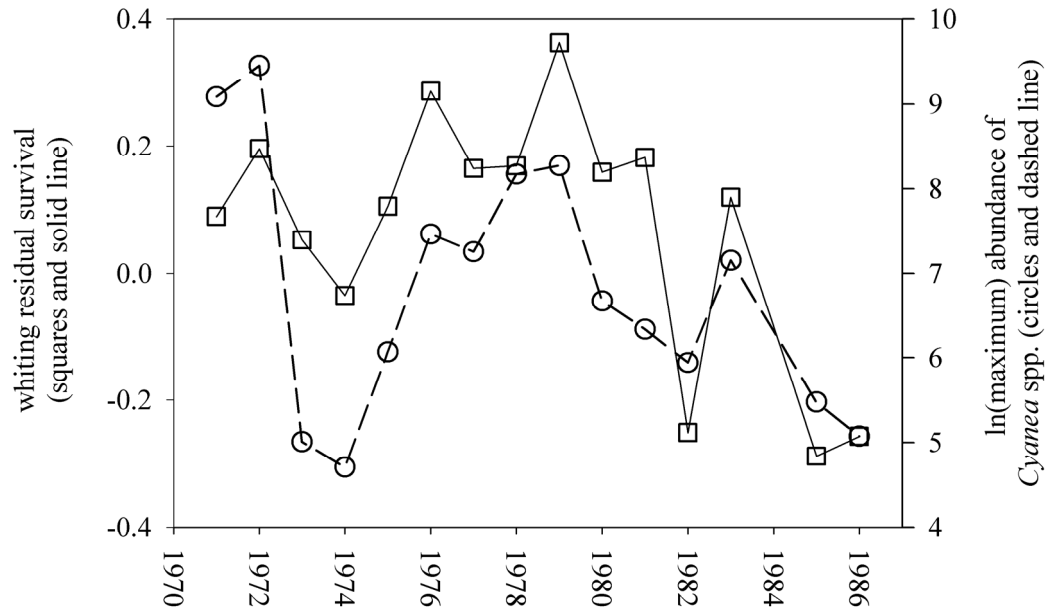


Figure 6.1 Interannual variability in whiting residual survival and *Cyanea* spp. abundance (correlation coefficients, 1971 to 1976  $R = 0.64$   $P < 0.01$  and 1974 to 1983  $R = 0.71$   $P = 0.02$ ).

### 6.5. Discussion

A considerable spatial and temporal overlap exists between jellyfish aggregations and whiting hatchlings (Hay et al. 1990). The survival of whiting appears higher than expected, on the basis of whiting SSB, in years of high *Cyanea* spp. abundance. Whiting are known to use jellyfish for shelter and have a mucus coating that grants them immunity to stinging by the tentacles of *Cyanea* spp. (Russell 1970 and references therein). Although haddock and cod have both been observed sheltering under medusae, the short pelagic phase of haddock and early spawning of cod probably limits any effect of sheltering on the survival of these species (Russell 1970; Hay et al. 1990 and references therein). *Cyanea* spp. are characterised by particularly numerous, long tentacles that may trail for many metres behind even a comparatively small jellyfish (~10 cm diameter). If whiting were to steal prey from the medusae they would forage over the range of the jellyfishes tentacles with relatively little effort; however, there are no observations to verify this hypothesis. Whiting may provide a 'cleaning' service for the medusae under which they shelter by consuming parasitic crustaceans, such as *Hyperia galba*. Although Hay et al. (1990) state

that *Cyanea* spp. were less frequently infested by parasites than *Aurelia*, this hypothesis is also unproven. Russell (1928, cited in Hay et al. 1990) reported that young whiting follow the vertical migration of *Cyanea* closely and Hay et al. (1990) speculated that those whiting spawned inshore may travel offshore under the protection of their jellyfish ‘umbrellas’.

Within shoals, 0–group whiting are highly cannibalistic and individually they are particularly likely to succumb to predation by other fish. Therefore the hypothesis of Hay et al. (1990), that the association of individual whiting with *Cyanea* spp. may improve their chances of survival, would appear to be the most likely explanation of the positive correlation found here between whiting residual survival and *Cyanea* spp. abundance. Whiting is one of the most numerous and widespread fish species in the North Sea and, in addition to preying upon crustacean zooplankton, whiting are predatory on other commercially important fish (gadoids and clupeids) (Knijn et al. 1993; ICES 1996a; Bromley et al. 1997; Rogers and Stocks 2001; Wennhage and Pihl 2002). In order that progress towards the goal of ecosystem–based fisheries management may be made, it is vital that the interactions between fish and the plankton community be understood and further researched.

## **Chapter 7**

### **Sound scattering and the acoustic analysis of medusae**

## **7. Sound scattering and the acoustic analysis of medusae**

### **7.1. Why use acoustics?**

Netting methods are able to produce useful data on the distribution and abundance of medusae. However, to monitor movements of aggregations and interactions between medusae and fish it is important to have real-time continuous data. Acoustic techniques are used with great success to detect pelagic fish (including fish larvae) and crustacean zooplankton and have the ability to reveal both the movements of swarms and schools and their interactions within the water column (Horne 2000). However, because of the high water content of jellyfish and their lack of hard parts (i.e. exoskeleton, shells) or air-filled vesicles they are similar in density to seawater, which makes them weak scatterers of sound. Despite this, theoretical models (Monger et al. 1998) and some limited tank and field observations (Mutlu 1996; Colombo et al. 2003), have shown that acoustic techniques can be used to sample jellyfish quantitatively. Previous work in the Benguela (Brierley et al. 2001) has demonstrated that medusae of Hydrozoa and Scyphozoa can be detected acoustically, and that a relationship does exist between echo strength and jellyfish size. If acoustic techniques are to be used more widely to monitor jellyfish in global marine ecosystems, and to study the interactions of jellyfish with fisheries, knowledge of the acoustic properties of common jellyfish species is required.

Organisms that are monitored through use of an acoustic beam are called the targets of the beam and they are said to have been ensonified if echoes from them are received. If individual targets are distinguishable and separate (not superimposed) echoes are resolvable by the echosounder then animal densities can simply be calculated through echo counting. However, for animals that are densely packed (i.e. separated by less than the acoustic beam width) this is rarely the case and combined (overlapping) echoes are recorded. In order to convert the acoustic densities of the densely packed targets into animal densities we must know the proportion of incident acoustic energy that is backscattered by the individual targets. The species-specific measure of acoustic backscattering strength, or Target Strength (TS) (Section 7.3), is essential for acoustic abundance estimation. The acoustic focus of this project has been to

improve on jellyfish target strength estimation for *Aequorea aequorea* and *Chrysaora hysoscella* and to develop a method by which the biomass of jellyfish can be estimated for a large survey area such as the Benguela Sea. Historically, very little work has been conducted on jellyfish regarding acoustic target identification and measurements of TS. In contrast, fish have been subject to acoustic investigation *in situ* since the early 1940s (Horne 2000, and references therein). Therefore, acoustic discrimination between several discrete frequencies for target identification purposes and measurements of the medusan target strengths of *A. aequorea* and *C. hysoscella* have been the main focus of the 1999 and 2001 Benguela Environment and Fish Interactions and Training (BENEFIT) surveys. In the 1999 survey, the acoustic scattering was measured at 18, 38 and 120 kHz, and back calculations from acoustic densities and animal densities obtained from the pelagic trawl samples provided average TS estimates (Section 7.5, Brierley et al. 2001). In 2001, more acoustic density measurements were carried out, including target strength measurements of tethered medusae at 38 kHz under controlled conditions inside Walvis Bay (Section 8.2, Brierley et al. 2004). The addition of a new 200 kHz transducer to the acoustic instrumentation of the ship and a refit of the transducer arrangement that aligned all the frequencies closely on the vertical axis and maximized the beam overlap, both added considerable discriminatory power and facilitated the development of four-frequency identification algorithms (Sections 8.2 and 8.4, and Chapter 9).

## **7.2. The acoustic beam**

Scientific echosounders transmit sound pulses to, and receive echoes from, the water through piezoelectric transducers, which convert electrically generated signals to sound and also convert sound incident on the crystal to electrical energy. Operating the transducer through several cycles of the chosen frequency produces a pulse or ‘ping’ of sound, projected in a directional beam. The ideal conical beam is shown in Figure 7.1 intercepting an acoustic target and returning a backscattered pulse to the transducer. The received signal is logged with data indicating the time received and the intensity of the echo. These signals may be amplified and displayed as an echogram (Figure 7.2). The range or depth of the target is calculated by the elapsed time between signal emission

and reception multiplied by the speed of sound and divided by two (since the pulse travels to and from the target).

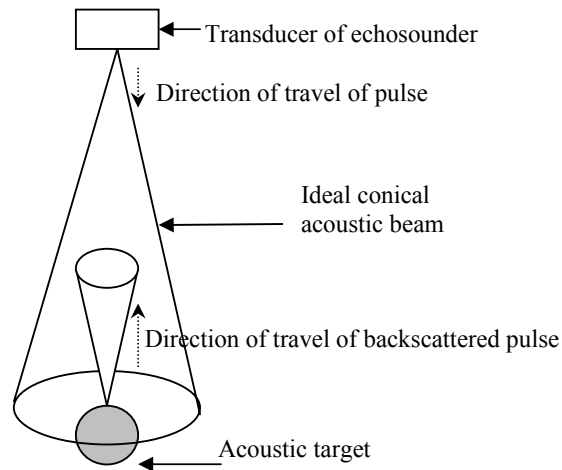


Figure 7.1 An ideal acoustic pulse and backscatter from an acoustic target

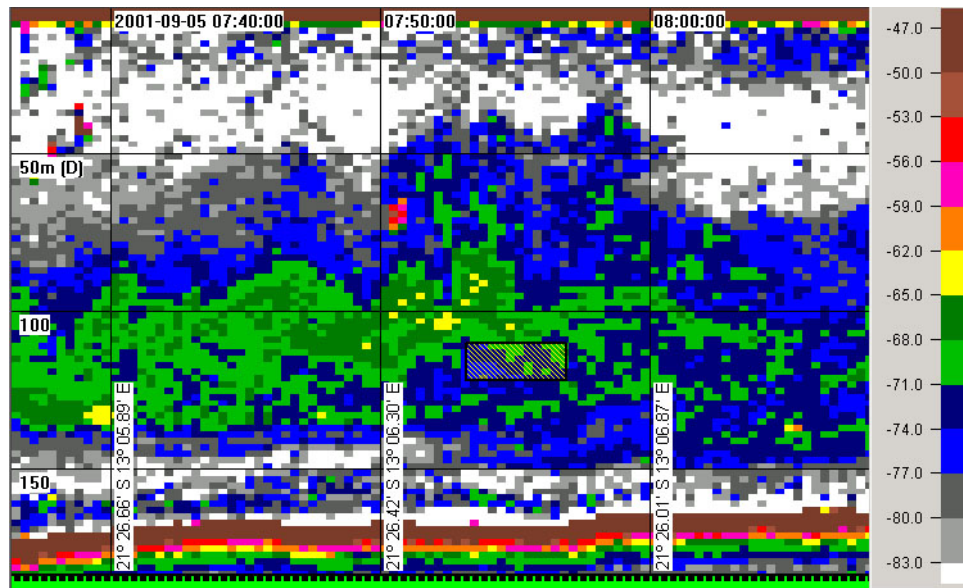


Figure 7.2 38 kHz Echogram of a gelatinous zooplankton aggregation, which when fished in the boxed area was found to be 97.8% *Aequorea aequorea* by weight (outer umbrella diameter 20.2 cm). The echogram shows the seabed at ~160m depth and near-surface transmit zone between 0 to 8 m. The date and local time is shown in the timestamps at the top of the figure and the location is given at each 10 minute interval. These data were collected in the Namibian Benguela from the RV *Dr Fridtjof Nansen*. TS for *Aequorea aequorea* at 38 kHz (inner disk diameter 6.5 cm) = -86.8 dB using the TS to bell diameter relationship found by Brierley et al. (2001). The right panel shows a colour legend in dB where -62 dB indicates ~299 individuals  $m^{-3}$ , -67 dB indicates ~95 individuals  $m^{-3}$ , and -86.8 dB indicates 1 individuals  $m^{-3}$ .

Realistically, the beam will intercept various targets, such as fish, zooplankton, and the seabed, that are not necessarily the targets of interest. In addition, the transducer is not an ideal point source but an array of elements. Therefore the acoustic beam projected is not directionally uniform (Figure 7.3) and some of the transmission will result in echoes from targets not directly below the transducer. The function that describes the change in sensitivity of the beam is known as the beam pattern. By convention, the beam pattern is equal to unity on the axis of the beam, where the beam sensitivity is greatest. If the transducer were an ideal point source the beam pattern would be omni-directional, i.e. equal to unity in all directions. The ideal conical beam can be considered as an ideal ‘searchlight’, with the beam pattern equal to unity inside the beam and zero outside the beam.

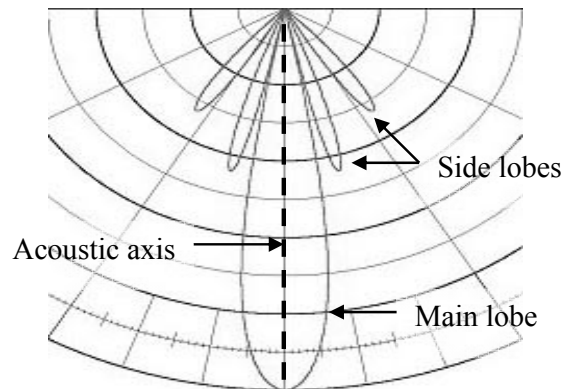


Figure 7.3 Directional sensitivity in the acoustic beam

The beam width is commonly described by the angle between two lines extending outward from the transducer on either side of the main lobe where the beam pattern is equal to  $1/\sqrt{2}$  and the intensity is 3dB lower than that on the acoustic axis, giving this angle the name ‘3dB angle’ (MacLennan and Simmonds 1992). The beam width is dependent on the frequency of the transmitted pulse and the size of the transducer. The higher the frequency of the beam, and the wider the transducer, the narrower the beam width becomes.

As the acoustic beam travels away from the transducer the wavefronts spread over an increasing area (Figure 7.3). As this happens the energy density or intensity of the wavefronts drops. How the intensity of the beam changes is determined by:

- *the medium in which it travels e.g. sea water.* Both frictional losses and the reduction of molecules to ions by the pressure of the acoustic waves on the medium may result in absorption of acoustic energy. The temperature, salinity, and pH of the sea water affect the absorptive properties of the medium through altering the relaxative properties of the molecules and the speed of sound in the medium (MacLennan and Simmonds 1992).
- *the range of the wavefronts from the source.* In the region immediately in front of the transducer and out to a range  $x \approx L^2/\lambda$ , where  $L$  is the diameter of the transducer and  $\lambda$  is the wavelength of the acoustic beam, the intensity of the beam varies rapidly with range in an oscillatory manner. This region is known as the near-field or the Fresnel zone. The properties of the transducer are usually chosen to minimise this region since unpredictable small changes in the transducer elements may result in large changes in intensity. Past this range  $x$ , the beam enters the far-field or Fraunhofer zone and the inverse square law applies such that there is a predictable exponential decrease in intensity with range.
- *the beam pattern and the beam frequency.* The shape of the beam and therefore its spreading with range depends on its beam pattern. The higher the frequency the more rapid the absorption: e.g. absorption is unimportant below 10 kHz for targets at 100 m range in sea water, but at 1 MHz the useful range is only a few metres (MacLennan and Simmonds 1992).

### **7.3. Target strength and aggregation density**

The acoustic echoes returned to the echosounders can be used to determine the sound scattering properties of jellyfish and when combined with data from netting these can be related to species. Echoes from aggregations may then be used to indicate aggregation density and species composition.

Target strength (TS) is the parameter used to relate echo intensity to target numerical density. TS is a logarithmic measure of the proportion of echo energy intensity returned (backscattered) by the acoustic target, e.g. an individual medusa, relative to the incident sound pulse. The greater (i.e. more positive) the TS, the more intense the echo. TS is measured in dB (decibel), which is a logarithmic scale of sound level, where the number of decibels is



$N_{dB}=10\log_{10}(I_2/I_1)$ , where  $I_2$  is the echo intensity and  $I_1$  is the transmitted intensity. The intensity of sound backscattered by a target at a given frequency is a function of the backscattering cross section,  $\sigma_{bs}$ , at that frequency.

$$TS = 10.\log_{10}(\sigma_{bs}) \quad (7) \text{ (Ona 1999)}$$

Assuming a long transmission period, and that the target is in the far-field, then the backscattering cross section  $\sigma_{bs} = R^2 I_b / I_i$  where  $R$  is the range to the target from the transducer,  $I_b$  is the intensity at the midpoint of the backscattered pulse, and  $I_i$  is the intensity at the midpoint of the pulse incident on the target.  $\sigma_{bs}$  is dependent on the frequency of the pulse  $f$  (Hz), velocity of sound  $c$  ( $\text{ms}^{-1}$ ), wavenumber  $k$  ( $=2\pi f/c$ ) and the ‘equivalent spherical radius’  $a$  (m) of the medusa’s umbrella. Generally the larger the target the greater the TS at a given frequency since more of the acoustic pulse will be backscattered. The TS of an individual medusa is dependent on the following physical properties:

- The frequency of the acoustic pulse. At low frequencies and in the Rayleigh scattering regime, where the acoustic wavelength and the target size are of the same order, the TS increases rapidly with target size. At higher frequencies, in the geometric scattering regime where the target is much larger than the wavelength of the pulse, the TS dependence on size is weaker.
- The contrast between sound speed in the water and in the target, and the contrast between the density of the water and the target; the greater the contrasts the more reflective the boundary (see section 8.1).
- The size of the target; larger targets will return stronger echoes than smaller targets of the same composition. As a jellyfish swims, its TS has been proposed to increase as the animal spreads out and decrease as the bell contracts (Mutlu 1996) (see Figure 8.16, Section 8.2.2).

The level of backscattered energy from a jellyfish aggregation is also dependent on the numerical density ( $\rho_v$ ) of the aggregation. The numerical density of a jellyfish aggregation can therefore be calculated from the volume backscattering strength,  $S_v = \Sigma\sigma_{bs}/V$  where the sum is over all discrete targets in the volume,  $V$  (Ona 1999):

$$\rho_v = 10^{(S_v - TS)/10} \quad (8)$$

The mean TS of individuals can be estimated for *in situ* targets through the Comparison Method, as follows. A research vessel equipped with downward pointing scientific echosounders surveys the water column while trawling from the rear of the vessel. The mean volume ( $\langle S_v \rangle$ ) and mean area ( $\langle S_A \rangle$ ) backscattering strength of an aggregation is thus determined immediately prior to trawling. The density of individuals per  $m^3$  in the aggregation can be measured directly from the trawl catch. The mean TS in terms of volume backscattering is:

$$TS = \langle S_v \rangle - 10 \log_{10}(\rho_v) \quad (9)$$

Equation 9 can be reformulated for  $\rho_v$  in terms of  $\langle \sigma_{bs} \rangle$ , the mean species-specific acoustic backscattering cross section ( $m^2$ ):

$$\rho_v = \langle S_A \rangle / (1852^2 \langle \sigma_{bs} \rangle \Delta z) \quad (10)$$

where  $\Delta z$  is the depth over which the acoustic data were integrated (e.g. for jellyfish sampling in the Benguela Sea, the effective opening of the net,  $\Delta z$ , was 12 m) and 1852 is the conversion from nautical miles to metres. The mean TS in terms of area backscattering is thus:

$$TS = 10 \log_{10}(\langle \sigma_{bs} \rangle / 4\pi)$$

$$TS = 10 \log_{10}(\langle S_A \rangle / (1852^2 \rho_v \Delta z 4\pi)) \quad (11)$$

#### 7.4. The split-beam echosounder

Split-beam echosounders have been developed to determine the location of a target in relation to the transducer. The split-beam echosounder utilises a specially designed transducer that is divided into four equally sized quadrants by controlling the electrical gain applied to the signal at each element (MacLennan and Simmonds 1992). The echosounder emits a transmission pulse across the whole transducer at once, but is able to process the signals received by each quadrant separately. Unless the target is directly below the transducer there will be a difference in the length of the path made by the backscattered pulse from the target to the receiving quadrants of the transducer. This path difference results in a phase difference between the signals received by the four quadrants and can be used to determine the angle between the target and the transducer. The time elapsed between signal emission and reception indicates the range to the target and this information, combined with the knowledge of the

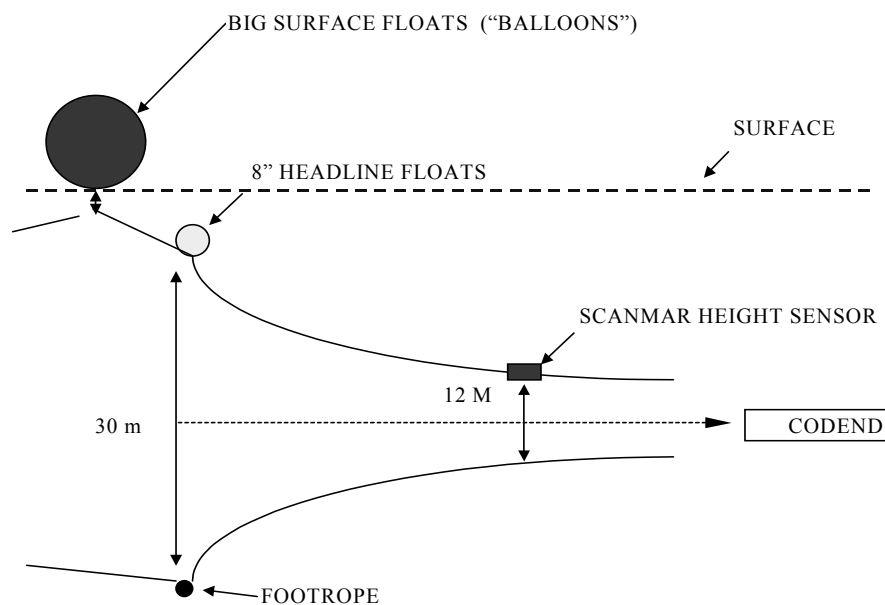
angle to the target and simple trigonometry, allows the location of the target to be identified.

Locating the targets allows off-axis targets to be distinguished from on-axis targets and increases the precision and accuracy of target strength measurements. As the intensity of the beam varies with its angle to the transducer's central axis, echoes from targets off the beam axis will appear of lower strength relative to similar targets on-axis where the beam intensity is greatest. With knowledge of the beam pattern and target location, the off-axis TS may be compensated for and be made directly comparable to on-axis TS.

### 7.5. Acoustic observations of jellyfish in the Namibian Benguela

The first study of a three-stage international project, with the overall aim to identify the biomass of medusae in the Benguela Sea, took place in 1999. The results of the five day investigation into the Target Strength (TS) of *Aequorea aequorea* and *Chrysaora hysoscella* were published by Brierley et al. (2001).

Net samples were taken with 4-pane pelagic trawls (modified Åkrehamn trawl, Valdemarsen and Misund 1994) (Figure 7.4). Net hauls were typically conducted at 3 knots and were of 5 min duration (extending approximately 450 m horizontally). Catches were often very large (several tonnes), and on these occasions random subsamples were taken in 40 litre fish baskets. A SIMRAD EK500 echosounder operating 18, 38 and 120 kHz split-beam transducers (Figure 7.5) was run continuously throughout the cruise.



↑Figure 7.4 Illustration of the large pelagic sampling trawl used in 1999, shown here rigged with floats for surface trawling. The vertical opening of this trawl was 30 m, and the height at the front of the section believed to catch jellies (400 mm panels) was then measured to 12 m; from this point the mesh size reduced to 36 mm.



Figure 7.5 Transducer arrangement of the drop keel of R/V “Dr. Fridtjof Nansen”, during 1999, showing orientation of the transducers on the keel.

From a total of 66 net hauls, 56 could be considered quantitative measures of jellyfish density; 8 hauls burst under the strain of excessive catches of jellyfish and an additional 2 hauls had to be discarded because either the trawl warp broke or the multisampler acoustic release failed. Of the 56 trawl samples, only those that identified a single species were used for the purpose of comparison with acoustic data. 14 samples were dominated by *Aequorea aequorea* (>80% wet mass) and 11 contained >95% wet mass *Chrysaora hysoscella*. For a more detailed description of methods see Brierley et al. (2001).

From the 14 selected samples, the mean umbrella diameters of *Chrysaora hysoscella* and *Aequorea aequorea* (central disk) were 26.8 and 7.4 cm respectively. The central disk of *Aequorea aequorea* was found to contribute 56% ( $\pm 9\%$ ) to total diameter and 44% ( $\pm 12\%$ ) to total wet mass. A significant relationship between target strength at 38 kHz and *Aequorea aequorea* umbrella diameter was found:

$$TS = -329 + 298 \log_{10} \text{umbrella diameter} \quad (R^2 = 0.899, P = 0.014, N = 5) \quad (7)$$

The total catch (or the weight of the subsample) was weighed and the mean wet mass of a medusa was found to be 1.15 kg for *C. hysoscella* and 0.06 kg for *A. aequorea*. Animal tissue density was  $0.996 \text{ kg.l}^{-1}$  for *C. hysoscella* and  $1.014$

$\text{kg.l}^{-1}$  for *A. aequorea* suggesting that any Target Strength differences between the species might be due to differences in animal tissue.

The mean area backscattering strength  $\langle s_A \rangle$  (see Section 7.2) was compared with jellyfish volume density determined from trawl samples and positive relationships were produced at 18, 38 and 120 kHz. The resulting regression statistics and target strength estimates are given in Table 7.1. The mean TS values per individual for the larger *Chrysaora hysoscella* were substantially greater (>16 dB) than the smaller *Aequorea aequorea* TS estimates at each of the 3 frequencies. However, once scaled to TS per kg (Equation 12) the differences between species were less marked, ranging from 3.8 dB  $\text{kg}^{-1}$  at 18 kHz to 6.9 dB  $\text{kg}^{-1}$  at 38 kHz.

$$\text{TS per kg} = \text{TS} + 10 \log_{10} 1/m \quad (12)$$

where  $m$  is the mean mass per individual (MacLennan and Simmonds 1992).

#### *Chrysaora hysoscella* (1.15 kg)

| Frequency                 | 18 kHz  | 38 kHz  | 120 kHz   |
|---------------------------|---|---|---|
| Regression                | $s_A = 11.8 + 2385 \rho_v$<br>( $R^2 = 0.15$ $P = 0.25$ ) | $s_A = 44.8 + 6485 \rho_v$<br>( $R^2 = 0.54$ $P = 0.01$ ) | $s_A = 22.1 + 2658 \rho_v$<br>( $R^2 = 0.39$ $P = 0.04$ ) |
| TS (dB)                   | -51.5   | -46.6   | -50.1   |
| (95% CI)                  | (-48.0 to -?)   | (-45.1 to -48.9)  | (-48.3 to -53.3)  |
| TS (dB $\text{kg}^{-1}$ ) | -52.1   | -47.2   | -50.7   |

#### *Aequorea aequorea* (0.06 kg)

| Frequency                 | 18 kHz   | 38 kHz  | 120 kHz   |
|---------------------------|--|---|---|
| Regression                | $s_A = 0.8 + 78.8 \rho_v$<br>( $R^2 = 0.42$ $P = 0.01$ ) | $s_A = 4.7 + 110.7 \rho_v$<br>( $R^2 = 0.70$ $P < 0.01$ ) | $s_A = 20.8 + 27.0 \rho_v$<br>( $R^2 = 0.30$ $P = 0.04$ ) |
| TS (dB)                   | -68.1  | -66.3   | -68.5   |
| (95% CI)                  | (-65.0 to -?)  | (-64.5 to -69.5)  | (-66.7 to -71.5)  |
| TS (dB $\text{kg}^{-1}$ ) | -55.9  | -54.1   | -56.2   |

Table 7.1 Regression relationships for area backscatter ( $s_A$ ) against medusa density ( $\rho_v$ ) for *Chrysaora hysoscella* and *Aequorea aequorea*.

### 7.6. Acoustic characterization of gelatinous plankton aggregations: four case studies from the Argentine continental shelf

Observations, in the northern and central Argentine continental shelf (35° – 47° S and 52° – 69° W), have shown that backscatter from medusa (*Aequorea* sp. and *Lychnorhiza lucerna*), salp (*Iasis zonaria*) and ctenophore (*Mnemiopsis leidyi*) aggregations may be as great as that from pelagic fish such as hake, sardines and horse mackerel (Colombo et al. 2003).

*Aequorea* sp. (Hydrozoa)

The species was acoustically sampled using a calibrated SIMRAD EK500 with a 38 kHz split-beam transducer at the southern spawning area for hake off Isla Escondida and Golfo San Jorge (44° – 47°S). This species was caught in a modified Isaacs-Kidd midwater trawl (10 m<sup>2</sup> mouth opening, mesh size reducing from 50 mm to 1500 mm). Catches reached up to 76 kg (8 – 20 cm umbrella diameter), representing a numeric density of 2 *Aequorea* per 100 m<sup>3</sup>. Dense scattering layers (with average S<sub>v</sub> values of up to –62.1 dB) were found to mask the presence of adult hake. The average TS for *Aequorea* sp. was estimated from the *in situ* echo recordings obtained from the most dispersed organisms in the aggregation. An average of –64.53 dB was determined for the upper 50 m layer (*N* = 4374). Fifty individual target traces were also isolated from the echograms and their individual TS distributions were found to be similar with average TS of –64.15 dB.

*Lychnorhiza lucerna* (Scyphozoa)

These medusae were caught (35°10'S, 56°-10' W) by net sampling with a small bottom trawl (2.4 m<sup>2</sup> mouth opening, 6 m total length, 6 m headrope and groundrope, 25 mm wing-mesh size, 10 mm in the codend, 10 m bridles, and 80 cm vertical opening) and an Hydro-Bios Multi-Plankton Sampler Type B Multinet (0.25 m<sup>2</sup> mouth opening, 300 mm mesh size) sampler. A catch of 137 kg of *L. lucerna* (3 – 31 cm bell diameter, mode = 11 cm) was obtained, representing a density of 14 individuals per 100 m<sup>3</sup>. Some juveniles of demersal fish species (mainly *Paralichthys brasiliensis* and *Micropogonias furnieri*) ranging from 2 to 6 cm (density = 5 per 100 m<sup>3</sup>) and two *Chrysaora lactea* (Scyphozoa) were also found in the sample. Echo recordings were obtained at 120 kHz using a SIMRAD EY500 echosounder and a split-beam transducer; however, no TS measurements were obtained due to the difficulty of partitioning detections by species from a mixed layer.

## Chapter 8

### Measurements of acoustic backscatter from jellyfish

The work described in Section 8.3 has been published as part of the following:

Brierley A. S., Axelsen B. E., Boyer D.C., Lynam C.P., Didcock C.A., Boyer H. J., Sparks C.A.J., Purcell J.E. and Gibbons M.J. (2004) *Single-target echo detections of jellyfish*. ICES Journal of Marine Science **61**, 383-393.

I estimate that I contributed 10% of the effort towards the paper due to my analysis of the *in-situ* data, which involved much data handling and programming in Matlab.

Brierley A.S., Boyer D.C., Axelsen B.E., Lynam C.P., Sparks C.A.J., Boyer H.J. and Gibbons M.J. (2005). *Towards the acoustic estimation of jellyfish abundance*. Marine Ecology Progress Series **295**, 105-111.

I estimate that I contributed 10% of the effort towards the paper, because I built a zooplankton backscatter model and suggested a method to determine the zooplankton backscatter component in previous jellyfish Target Strength measurements.

The work described in Section 8.5 has been published as:

Lynam C.P., Brierley A.S. and Axelsen B.E. (2004). *Pinging down the food web: multi-frequency acoustic discrimination of jellyfish and fish*. ICES report CM2004/R:06.

I estimate that I contributed 60% of the effort towards the paper: Data collection/preparation 65 %, the acoustic data were gathered by CPL and BEA equally and prepared by CPL; Inspiration 0 %; Analysis 75 %, where the remainder is attributable to valuable guidance from ASB and BEA; Conclusions 75 % with suggestions from ASB; Publication 85 %, the paper was written by me but reviewed by ASB.

## 8. Measurements of acoustic backscatter from jellyfish

### 8.1. Introduction

In order to estimate the biomass of medusae from acoustic data, we must know what proportion of the sound energy incident on an individual will be backscattered to the transducer, i.e. the animal's Target Strength (TS, Section 7.3). When many species are ensonified together the acoustician must also use a method that will allow echoes to be attributed to particular species. In this chapter the following four sections describe the work that I have undertaken so that I may calculate the biomass of medusae *in situ* from acoustic survey data. In Section 8.2, I report observations of the speed of sound in jellyfish tissue and density measurements that may be used to develop a model of jellyfish TS. Sections 8.3 and 8.4 describe estimates of medusae TS from *in situ* detections using three methods: single target identification from the triangulation of four acoustic beams (Section 8.3); detections from tethered medusae (Section 8.3); and the comparison method (Section 8.4). A jellyfish species independent mass-TS relationship is determined in Section 8.4, using all TS estimates reported for *Aequorea aequorea* and *Chrysaora hysoscella* (Sections 7.5, 8.3, and 8.4). Using multifrequency acoustic data (18, 38, 120 and 200 kHz), an algorithm is developed in Section 8.5 that will allow the automatic discrimination of echoes due to medusae from fish. The techniques developed here are subsequently applied successfully to acoustic survey data in Chapter 9.

### 8.2. The speed of sound in seawater, *Aurelia aurita*, and *Cyanea capillata*

The Target Strength (TS) of an individual organism is dependent on the contrast between the speed of sound in seawater and in the animal's tissue ( $h$ ) and also the contrast between the densities of two materials ( $g$ ). For gas bladdered fish, knowledge of the geometric shape of the animal and its orientation in the water column has often been considered sufficient to parameterise models of acoustic backscatter (Hazen and Horne 2003). For weakly scattering zooplankton, however, the material properties ( $g$  and  $h$ ) are often the most important parameters (Chu and Wiebe 2005). For example, the modelled dorsal aspect TS of an amphipod (Equation 13) would increase by  $\sim 20$  dB if either contrast were to increase from 1.01 to 1.15 (Figure 8.1).



$$TS_{\text{amphipod}} = 10 \log_{10} \left( \frac{\pi L^2 (ka)^4 \alpha^4 c G}{1 + \left( \frac{\pi (ka)^3 \alpha^2 c}{R^2 F} \right)} \right) \tag{13}$$

where  $L$  is the length in m of an amphipod (measured as the length from the rostrum to the telson) once modelled as a straight fluid filled cylinder with radius  $a$ ,  $k$  is the wavenumber,  $g$  is the density contrast,  $h$  is the sound speed contrast,  $\alpha = ( (1-gh^2) / (2gh^2) ) + ( (1-g) / (1+g) )$ ,  $c$  is the speed of sound in water in  $\text{ms}^{-1}$ ,  $G = 1 - 0.8 \exp( -2.5 (ka - 2.0)^2 )$ ,  $R = (gh - 1) / (gh + 1)$  and  $F = 3.0 (ka)^{0.65}$  (Trevorrow and Tatanka 1997).

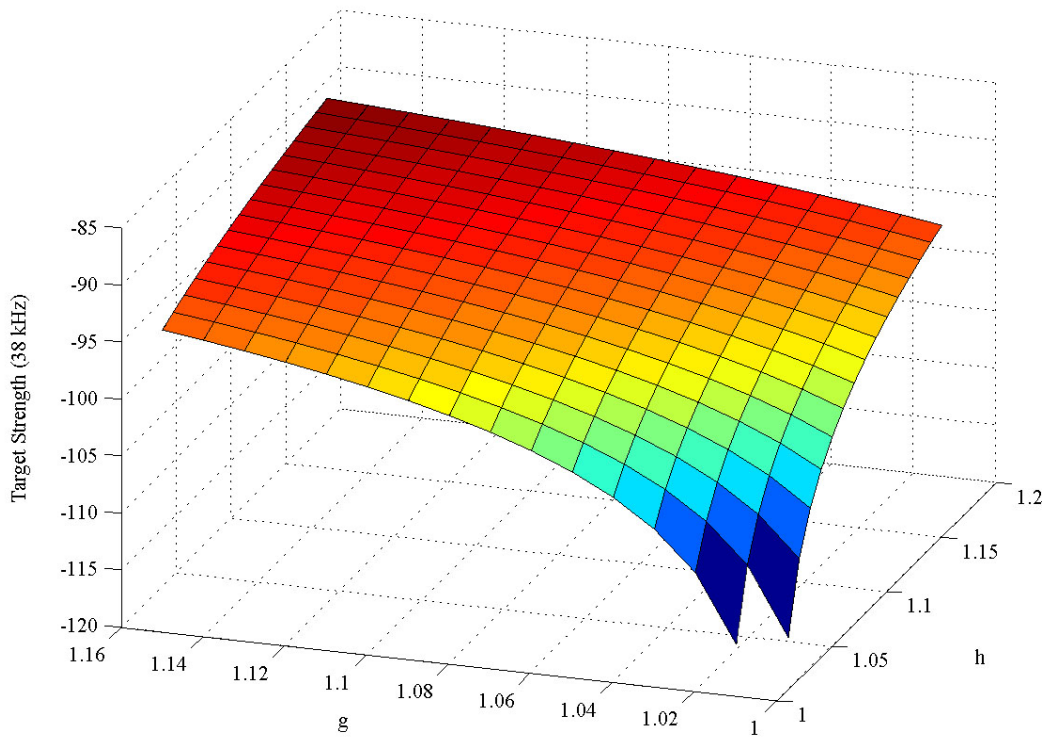


Figure 8.1 An example of the dependence of target strength (TS) on the sound speed contrast  $h$  and density contrast  $g$  for amphipods.

Here I report measurements of both the speed of sound (using a 500 kHz acoustic pulse) and density in seawater, mesoglea ('jelly'), and tentacular matter of the scyphozoans *Aurelia aurita* and *Cyanea capillata*. No significant difference was found between the density of jellyfish and that of seawater. Sound speed measurements were made over a range of temperatures (9 °C to 21°C) and significant linear relationships were found between temperature and

sound speed in both seawater and jellyfish tissues. The sound speed contrast for whole *A. aurita* and *C. capillata* umbrella tissue was not significantly different from seawater; however, for *C. capillata* tentacles the sound speed contrast ranged between 0.997 and 0.999 (mean value 0.998). These results suggest that the dense tentacular matter is a stronger scatterer than the mesoglea; this information will be of use for incorporation into sound scattering models of jellyfish.

### 8.2.1. Methods

The time of transit for the acoustic pulse within each material was measured using the following equipment (Figure 8.2):

- two Perspex tubes combined to form an inverted ‘T’ (the T-tube) with two 500 kHz transducers sealed at each end of the horizontal tube. The vertical tube was used to funnel the sample into the horizontal tube and act as a barrier to other material.
- a digital thermometer to measure sample temperature
- a control unit incorporating a signal generator.
- an accurate oscilloscope (*Agilent 54624A*).

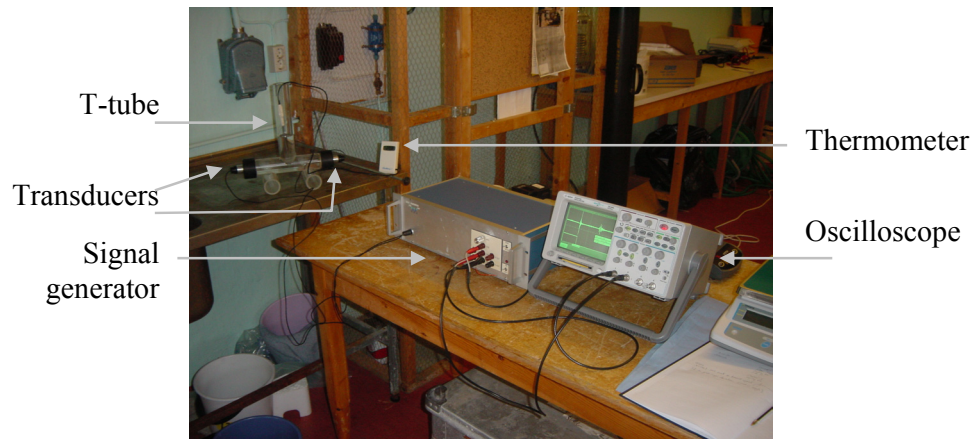


Figure 8.2 The arrangement of the equipment used to measure speed of sound within seawater and jellyfish tissue

#### *Biological material*

*Fresh specimens were collected during August 2004 in Hopavågen Bay, Norway, as they were being washed toward the beach and also from the adjacent tidal lagoon by using a dip-net to herd the animal into a plastic bucket. Foote (1989) noted that sound speed changed as biological material*

*deteriorated, and recommended that measurements be made within 12 hours of collection. Even including the time taken to remove animals of other species from samples, it was possible to undertake all measurements within 12 hours of collection. The two jellyfish species investigated were *Cyanea capillata* and *Aurelia aurita*. The density of each animal material was estimated as accurately as possible at the end of each measurement series. *A. aurita* has fragile tentacles that are generally shed during capture and oral arms in equal consistency to the umbrella. *Cyanea capillata*, in contrast, is characterised by its frilled oral arms and numerous trailing tentacles that contain many nematocysts, which consist of tightly coiled stinging cells of greater density than the mesoglea ('jelly'). Therefore for *C. capillata*, additional density and sound speed measurements were made for tentacular matter.*

#### *Sound speed analysis*

Samples of seawater or chopped up medusa tissue were added to the T-tube and when possible the samples filled the horizontal section of the T-tube completely. If too much air was present the acoustic pulse was scattered and no signal was detected at the receiver. However, if only a few bubbles were present then sound was able to pass the length of the tube by the shortest path (i.e. through the water or tissue) and a useful signal could still be detected.

The signals to and from the T-tube were regulated by the control unit so that discrete square wave transmit pulses were produced intermittently and received individually (Figure 8.3). Precise measurements of the time taken for the sound to travel the length of the horizontal section were obtained from the oscilloscope. The square wave was not perfect but its characteristic irregularities were constant (Figure 8.4) and an initial peak was isolated and used to locate a comparable 'beginning' of the transmission on the oscilloscope (Figure 8.4). As previously noted by scientists at the British Antarctic Survey, the rise and fall of the square wave and also an internal peak were found to interfere with the received signal (Figure 8.5); the received sound pulse was easily isolated nonetheless (Figures 8.5, 8.6 and 8.7).

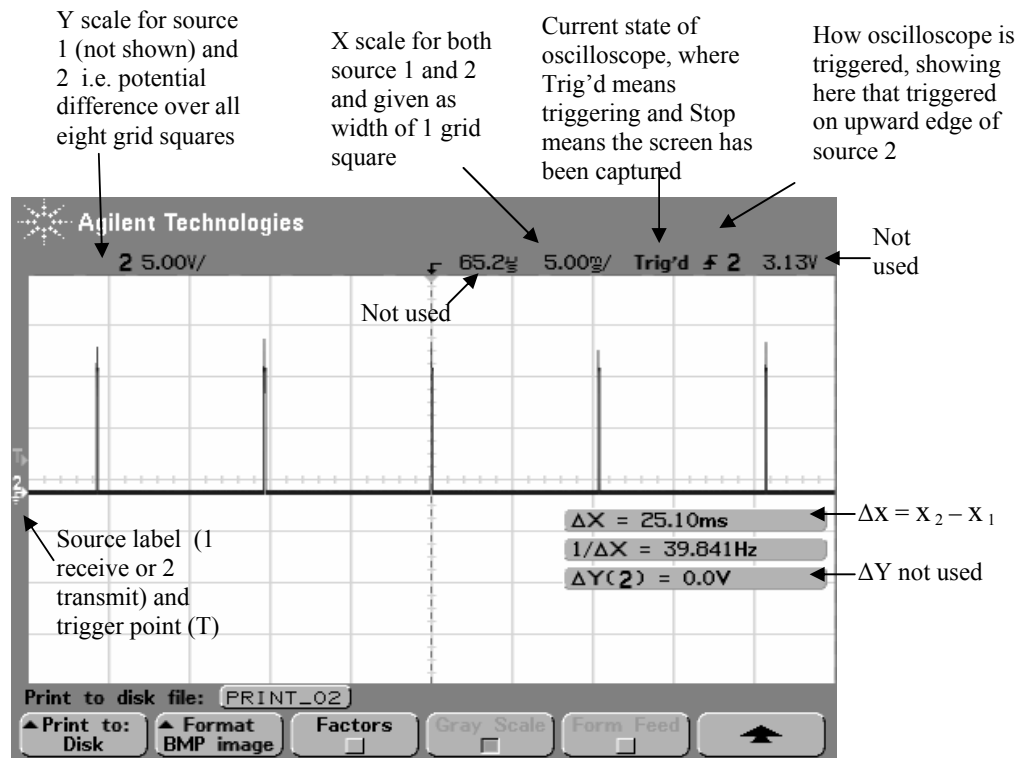


Figure 8.3 Five transmitted sound pulses over a period of 50 ms. x scale, 1 grid square = 5 ms, y scale 5V

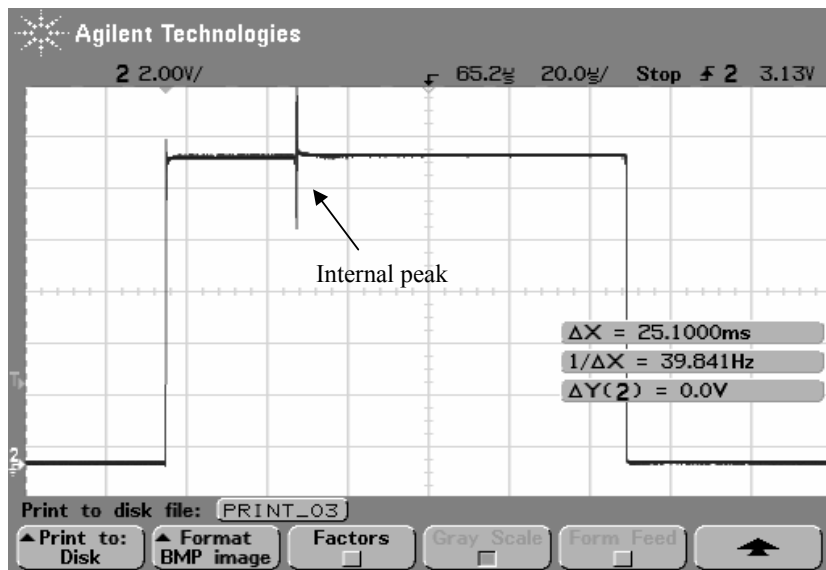


Figure 8.4 A single transmit pulse lasting approx 110  $\mu\text{s}$  showing internal peak

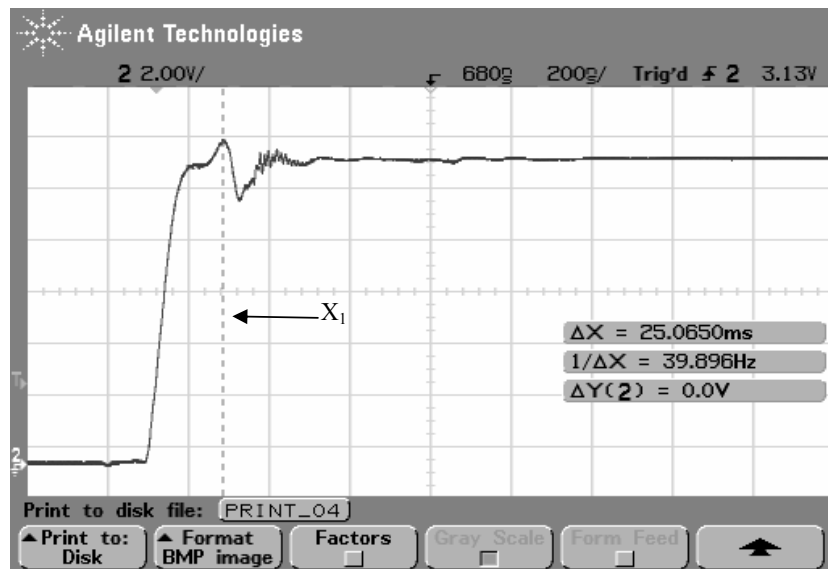


Figure 8.5 The rise of the square pulse showing the constant peak used as a reference point and marked with the dashed reference line ( $x_1$ ).

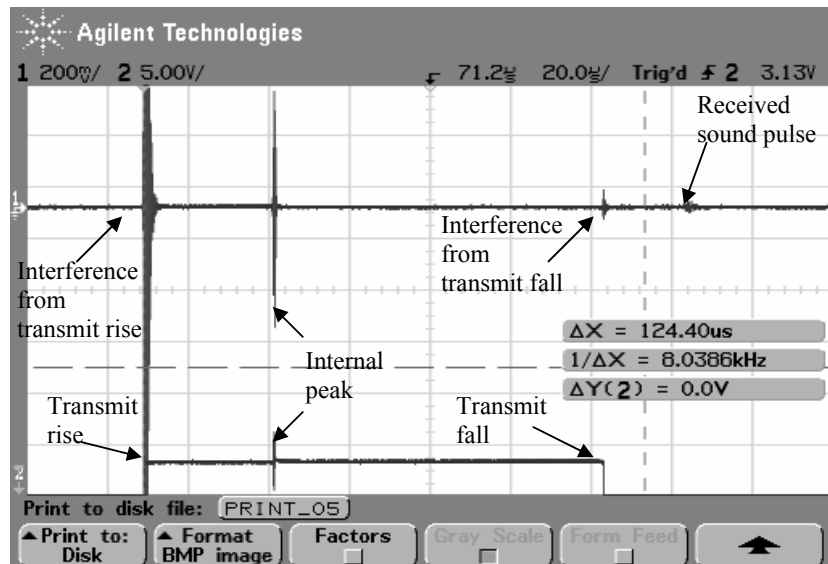


Figure 8.6 The square transmit pulse (at bottom of screen below horizontal dashed line) and the received signal (above horizontal dashed line). Note that three pulses are received that match almost instantaneously with the rise and fall of the square wave and also the internal peak (see Figure 8.4) produced during its progress. A smaller additional wave is also received (to the right of the vertical dashed line) marking the arrival of the acoustic pulse that has passed through the medium in the T-tube.

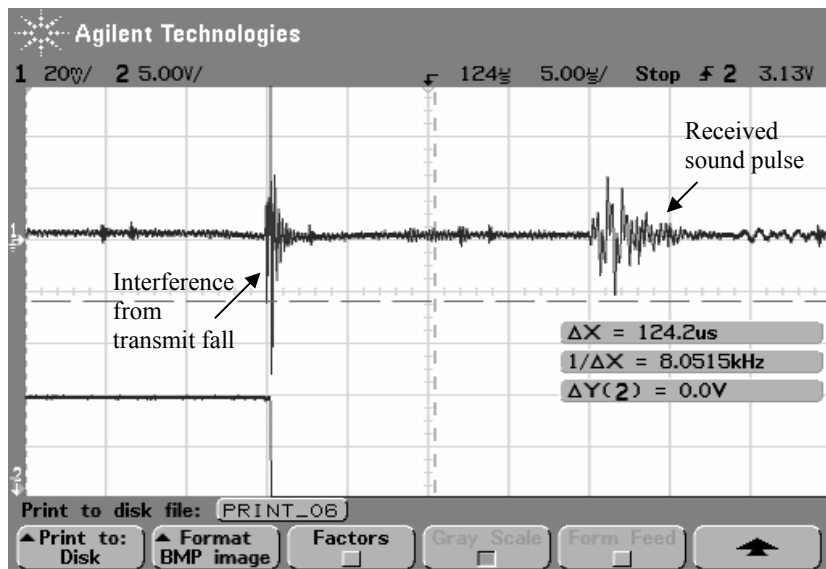


Figure 8.7 As Figure 8.6 but zoomed in to the fall of the square transmit pulse (below horizontal dashed line) and the received signal (above horizontal dashed line), note that there is a received pulse that matches with the fall of the square wave. The actual received signal is shown to the right of the vertical dashed line.

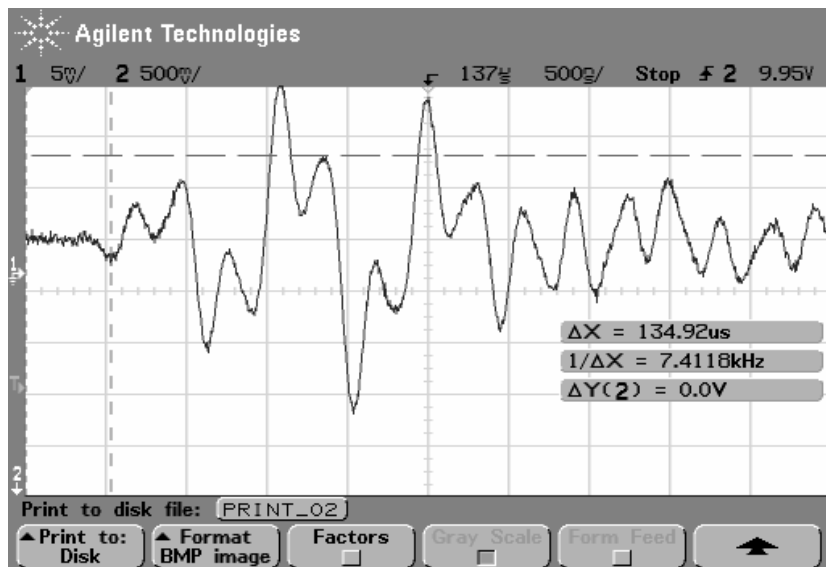


Figure 8.8 Close up view of the actual received signal (this example was passed through jellyfish tentacles) showing the initial trough with the measurement line ( $x_2$ )  $\Delta x = x_2 - x_1 = 134.92 \mu s$  on the display shows the time between the reference ( $x_1$ , see Figure 8.4) and measurement lines.

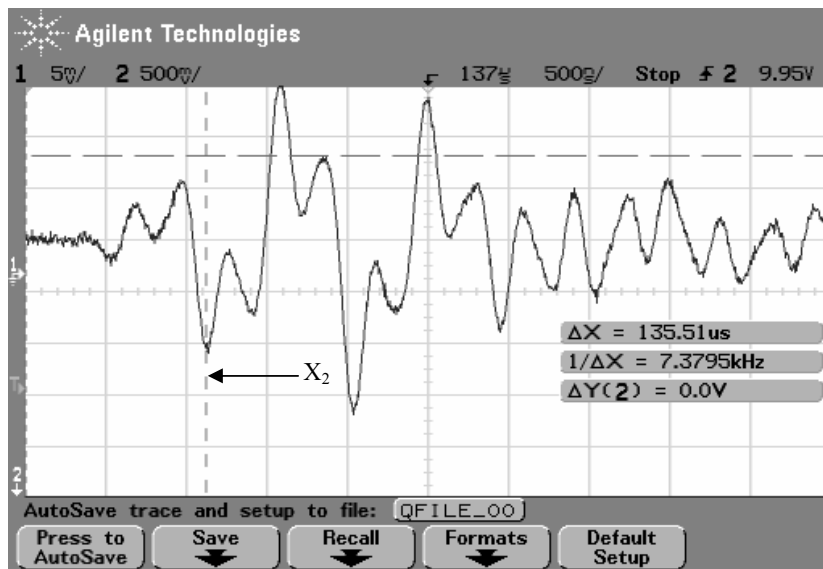


Figure 8.9 As Figure 8.8 but with the measurement line ( $x_2$ ) located on the first major trough (which was used since in umbrella-only samples the first trough was so small that it became unreliable as a measurement point.  $\Delta x$  on the display shows the time between the reference ( $x_1$ , shown on Figure 8.5) and measurement lines ( $x_2$ ). The difference between the above  $\Delta x = x_2 - x_1$  and that shown in Figure 8.8 is  $0.59 \mu\text{s}$ , a constant characteristic of the signal when passed through either jellyfish and seawater.

The oscilloscope was configured as follows:

- Autoset – returns settings to those required except:
- Edge – Trigger on upward edge of source 2
- Channel 2 – y-scale set to 5mV
- Channel 1 – y-scale set to 500mV and adjusted as required
- Layout of the screen was controlled by using horizontal and vertical arrowed knobs.
- The horizontal time interval was set to 500ns

Cursor mode set to time and measurements made as follows: the cursor arrow controls were used to fix the reference point,  $x_1$ , at the initial peak of the square wave and the measurement,  $x_2$ , at the beginning of the received sound pulse (Figure 8.5). The feature chosen on the received sound pulse was the first major deviation, which was the first trough in the wave (Figure 8.8). However, this became hard to find accurately for jellyfish umbrella-only measurements therefore the second trough (Figure 8.9) was used since it had a greater amplitude and was always distinguishable. The second trough was found to follow the first by  $0.59 \mu\text{s}$  in both seawater and jellyfish

measurements. This delay was constant since it is a function of the generated signal only. The travel time ( $\Delta x = x_2 - x_1$ ) of the acoustic pulse between the two selected points was then read directly from the oscilloscope screen.

| Material                | Min density<br>kg.l <sup>-1</sup> | Mean density<br>kg.l <sup>-1</sup> | Max density<br>kg.l <sup>-1</sup> | Standard<br>deviation kg.l <sup>-1</sup> |
|-------------------------|-----------------------------------|------------------------------------|-----------------------------------|--|
| Seawater                | 1.004                             | 1.007                              | 1.010                             | 0.002                                    |
| <i>Aurelia</i> whole    | 0.990                             | 1.010                              | 1.027                             | 0.010                                    |
| <i>Cyanea</i> umbrella  | 0.975                             | 1.002                              | 1.035                             | 0.015                                    |
| <i>Cyanea</i> tentacles | 0.982                             | 1.008                              | 1.039                             | 0.017                                    |

Table 8.1 Measured densities of jellyfish tissues and seawater

It was not possible to fix the temperature of the biological samples therefore sound speed measurements were made of a range of temperatures. Seawater, over a range of 9 to 22°C ± 0.1°C, was used as a comparative reference for jellyfish measurements. Expected sound speeds in seawater were also calculated from the relationship below to verify and calibrate the measured values.

$$c = 1448.96 + 4.591 T - 0.05304 T^2 + 2.374 \times 10^{-4} T^3 + 1.34 (S-35) + 0.0163 D + 1.675 (10^{-7}) (D^2) - 0.01025 T (S-35) - 7.139 (10^{-13}) T (D^3) \pm 0.07 \quad (14)$$

where  $c$  = speed of sound (ms<sup>-1</sup>),  $T$  = temperature (°C),  $S$  = salinity (ppt) and  $D$  = depth (m), the relationship holds over the following ranges  $-2 < T < 30$ ,  $25 < S < 40$ ,  $0 < D < 8000$ , (MacKenzie 1981)

The time taken for the signal to cross the T-tube, when the tube was filled with either seawater or jellyfish tissue, was read directly from the oscilloscope. This measurement was used to calculate the sound speed in metres per second, these values were then regressed against temperature for both seawater and jellyfish material.

### 8.2.2. Results

Seawater temperatures (and therefore the temperature of medusae) were measured *in situ* by CTD and ranged from 8.21 to 19.74 °C. However, during transit to the laboratory the jellyfish tissue warmed to about 15 °C. Sound speed measurements were taken intermittently as the jellyfish temperature increased to 21 °C. Using a waterbath, the animals were subsequently cooled to 9 °C.



*Calibration*

The sound speed measurements for seawater, calculated on the basis of the nominal T-tube length, were found on average to be  $24.66 \text{ ms}^{-1}$  lower than expected when compared with the values computed using equation 14. Figure 8.9 shows the calculated and measured speed of sound in seawater, with salinity of 31.40 ppt, over a range of temperatures. The measured speed of sound in seawater should equal that of the calculated value; since this was not the case either the measurement of time of flight or of path length was incorrect. The measured travel time was a constant  $2.2 \times 10^{-6}$  seconds longer than expected over the temperature range, therefore the error was systematic. It is possible that the oscilloscope readings are delayed by this amount; however, any constant delay would affect the reading of both time of transmit and of time of receive so the time difference would still be accurate. My measurements of travel time were sufficiently precise (to within  $\pm 2 \times 10^{-9}$  seconds) that I am able to conclude that the error must reside in the measurement of path length and not of travel time. Although the measured length of the T-tube was 20.00 cm, the transducers were mounted an unknown distance back from the face of the unit. To account for the difference in measured and calculated sound speed, the effective path length of the transmitted sound from transmitter to receiver must be greater. So the effective path length across the T-tube was 20.33 cm and this value was used in the following calculations for speed of sound in jellyfish tissue.

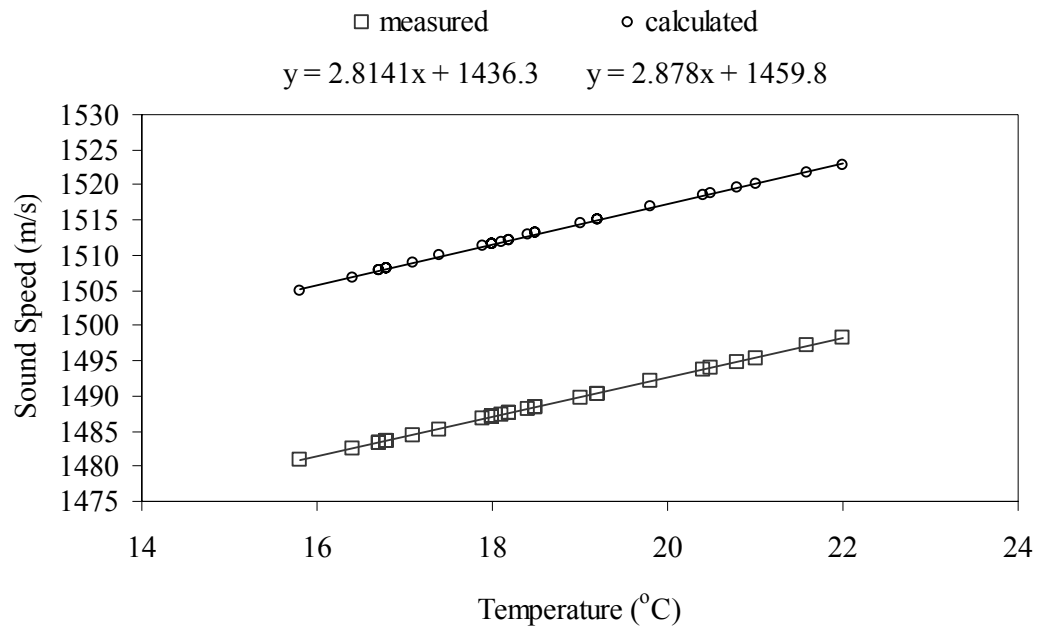


Figure 8.10 Temperature dependence of sound speed in seawater (salinity = 31.40 ppt), where the squares show the values calculated using time intervals measured from the oscilloscope and distance travelled = 0.20 m and the circles are the values computed using the formula of MacKenzie (1981).

#### *Measurements of density and sound speed*

Samples of seawater and chopped up jellyfish umbrella were weighed (accurate to 4 significant figures) and their volumes were measured (accurate to 3 significant figures), by adding each sample to a measured volume of water and recording the resulting increase in volume. With these measurements the density (to the nearest  $0.01 \text{ g.ml}^{-1}$ ) of each material could be calculated (density = mass/volume). No significant difference was found between the density of jellyfish (of either species) and seawater ( $t$ -test, all  $p > 0.10$  and  $N = 10$  for each material). However, it is notable that the maximum measured densities of each jellyfish tissue was greater than the maximum seawater measurement (Table 8.1). The following significant,  $P < 0.0001$ , linear regressions of speed of sound ( $c_{\text{material}}$ ) against temperature ( $T$ ) (Figure 8.11) were found:

$$c_{\text{seawaterR}} = 1463.1572 + 2.7730 T \quad (R^2 = 0.975 \quad N = 28)$$

$$c_{\text{whole Aurelia}} = 1456.8159 + 3.1536 T \quad (R^2 = 0.993 \quad N = 51)$$

$$c_{\text{Cyanea umbrella}} = 1460.0064 + 2.9300 T \quad (R^2 = 0.997 \quad N = 48)$$

$$c_{\text{Cyanea tentacles}} = 1467.5924 + 2.7283 T \quad (R^2 = 0.981 \quad N = 29)$$

At the midrange temperature,  $T = 15^\circ\text{C}$ , the sound speed ( $c_{\text{seawater}}$ ) in seawater based on the above regression relationship was 1504.7522, and therefore the sound speed contrasts ( $SSC = c_{\text{seawater}}/c_{\text{material}}$ ) for jellyfish tissues are as follows:

$$c_{\text{whole Aurelia}, T=15^\circ\text{C}} = 1504.1199 \rightarrow SSC_{\text{whole Aurelia}, T=15^\circ\text{C}} = 1.000$$

$$c_{\text{Cyanea umbrella}, T=15^\circ\text{C}} = 1503.9564 \rightarrow SSC_{\text{Cyanea umbrella}, T=15^\circ\text{C}} = 1.001$$

$$c_{\text{Cyanea tentacles}, T=15^\circ\text{C}} = 1508.5169 \rightarrow SSC_{\text{Cyanea tentacles}, T=15^\circ\text{C}} = 0.998$$

The regression lines presented here are near parallel and the lines for whole *A. aurita* and for *C. capillata* umbrella tissue fall within the 95% confidence interval of the regression relationship for seawater (Figure 8.11). However, at every temperature, the measured sound speed within *C. capillata* tentacular matter was greater than the sound speed in seawater.

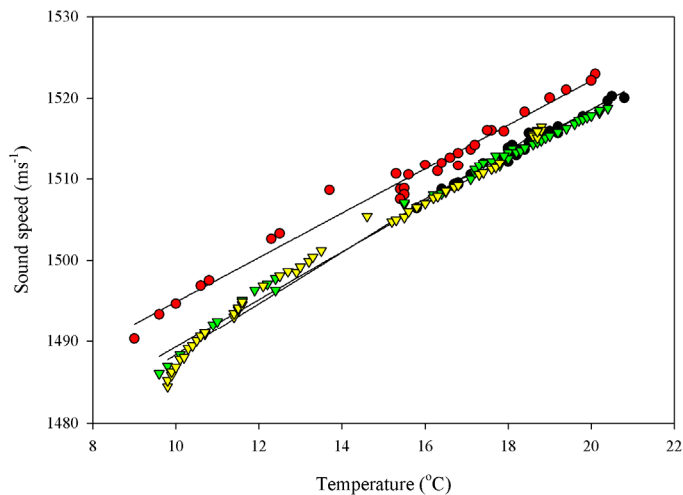


Figure 8.11 Sound speed measurements for *Cyanea* tentacles (red circles), yellow *Cyanea* umbrella (yellow triangles), seawater (black circles), *Aurelia* whole (green triangles) and regression lines (black).

### 8.2.3. Discussion

The similar densities of seawater and jellyfish and low sound speed contrasts suggest that if medusae are acoustically detectable then they will be weak targets and the strongest echoes may be expected to arise from tentacular matter such as the densely packed nematocysts. The great sensitivity of modern acoustic instruments, e.g. the dynamic range of the SIMRAD EK60 echosounder is 150 dB, facilitates the detection of weak targets and gelatinous organisms have been shown to be detectable (Sections 7.5 and 7.6).

### **8.3. Single target discrimination and target strength estimation for *Aequorea aequorea* and *Chrysaora hysoscella***

Previous work in the Benguela (see Section 7.5) (Brierley et al. 2001; 2005) has demonstrated that *Aequorea aequorea* and *Chrysaora hysoscella* can be detected acoustically, and that there is a relationship between echo intensity and jellyfish size. Acoustic surveys combined with net sampling, to determine species composition and size (diameter or mass) distributions, can provide a rapid and cost-effective estimate of the biomass and distribution of species. However, to convert acoustic density estimates into biomass values, accurate knowledge of the Target Strength (TS)–size relationship is required. Here, I show that, through the triangulation of multiple-frequency acoustic beams by the method developed by Demer et al. (1999) (Figure 8.12), estimates of TS calculated using single target detections from free-swimming medusae may be improved. These TS estimates are compared to those based on detections from tethered medusae and also to TS estimates calculated by the comparison method. The results were published in the co-authored publication Brierley et al. (2004) and show that TS estimates are consistent across methods.

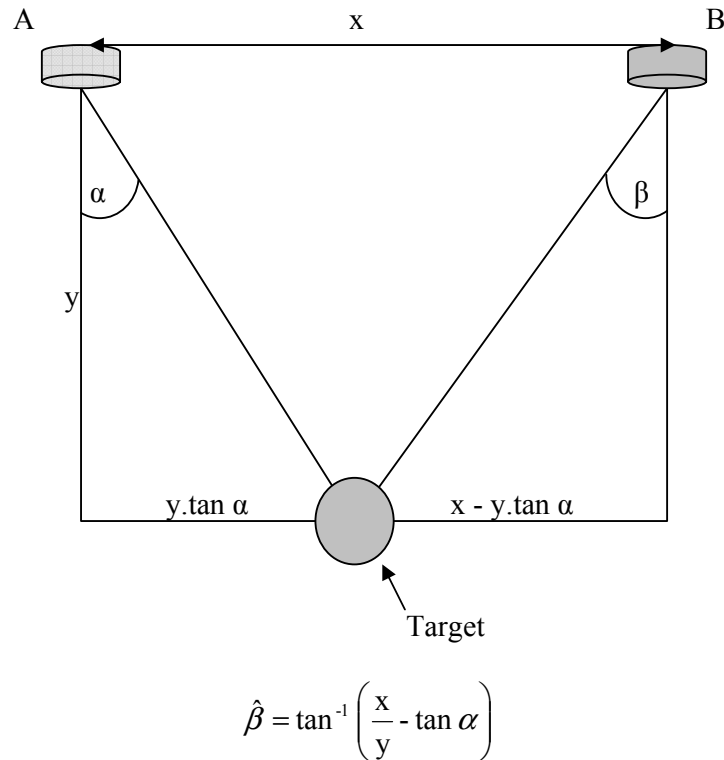


Figure 8.12 Position matching of a single target using two transducers (A and B). If transducer A is a split-beam instrument (Section 7.4) then angle  $\alpha$  can be measured and angle  $\beta$  estimated using the offset  $x$  between transducers A and B and the target depth  $y$ . If transducer B is also split-beam then angle  $\beta$  can be measured and compared to the expected value. If the measured value agrees with the estimated value then the echo can be accepted with greater confidence to arise from a single target.

### 8.3.1. Methods

The SIMRAD EK500 scientific echosounder was used to identify single targets during a seven-day cruise on the RV *Dr Fridtjof Nansen* in September 2001 that sailed to and from Walvis Bay, Namibia. Jellyfish were insonified by four overlapping acoustic beams (18, 38, 120 and 200 kHz) (Figure 8.13). The 18, 38 and 120 kHz split-beam transducers were able to determine the location of a target in relation to the transducer. The fourth (200 kHz) was a single-beam transducer without this capability. Soule *et al.* (1995) raised doubts over the reliability of the standard EK500 single target detection algorithm, suggesting that echoes from closely located targets could be incorrectly identified as arising from a single target. To overcome the possible inaccuracy of the EK500

algorithm Demer et al. (1999) proposed a technique to triangulate the beams (Figure 8.12). By this method single targets are only accepted as such if detected by multiple beams simultaneously at the same point, thereby increasing the likelihood that the single targets are actually from individual scatterers.

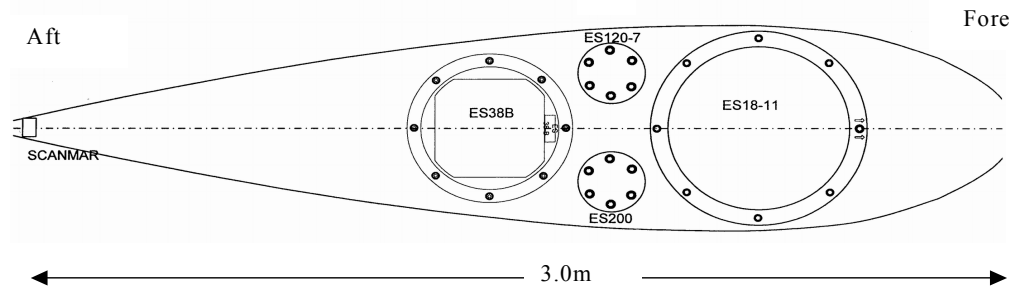


Figure 8.13 Transducer arrangement of the drop keel of RV *Dr Fridtjof Nansen* showing schematic illustration of the new orientation of the transducers on the keel.

During the first six days of the cruise, pelagic trawls (Figure 8.14) were undertaken to catch jellyfish (for details of fishing activities see Section 7.5 and Brierley et al. 2001). A typical trawl lasted around five minutes. Species composition, size and mass distributions were determined for all trawls so that acoustic targets could be identified as belonging to particular species. For each trawl where medusa catches were >99.5% by mass, single target data were exported using *SonarData Echoview (Version 3.2)* and analysed in *Matlab (Version 5.2)*. Targets were matched initially by time of detection and target depth using the time and depth stamp for each datapoint. Targets were further discriminated by angular position in the beam: for the split-beams (18, 38 and 120 kHz) the target position relative to the transducer is known and the expected position of the targets relative to the other transducers (including the 200 kHz) could be calculated using simple trigonometry (Figure 8.12). Targets were thus matched temporally and spatially.

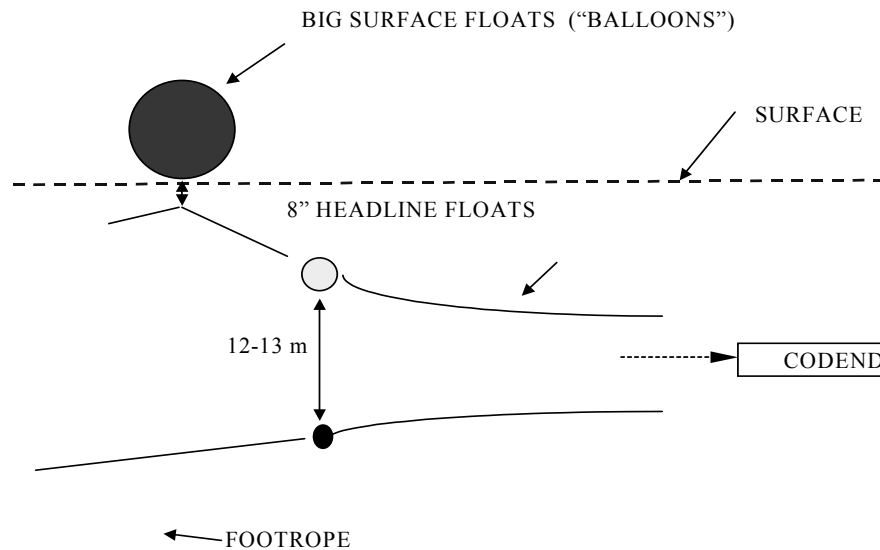


Figure 8.14 Illustration of the large pelagic sampling trawl used in 2001 and 2003, here rigged with floats for surface trawling. The vertical opening of this trawl was 30 m, and the height at the front of the section believed to catch jellies (400 mm panels) was then measured to 12 m.

As echo intensity is dependent on position within the beam, the EK500 software was used to provide compensated TS values, for split-beam measurements, that would have been exhibited by the target were it to lie on the beam axis (at highest intensity in the beam). The 200 kHz single-beam transducer was unable to determine the angular location of single targets, so compensated TS could not be calculated directly. However, since the transducer position relative to the other transducers was known, I was able to determine (in a similar manner to the position matching between split beams) where the previously collated matches would lie in the 200 kHz beam. The single targets detected by the 200 kHz beam (and that matched with targets in each of the other three beams) could then be used with knowledge of the beam pattern of the 200 kHz transducer (SIMRAD, 1996) to provide compensated (equivalent on axis) TS values at 200 kHz.

Single target TS distinguished in this way can then be reliably compared across frequencies to give measurements of frequency-specific TS for jellyfish. Peaks in the TS distributions can be allocated by comparison with bell

diameter–frequency data as similarly shaped size and TS distributions are expected. Histograms of medusa diameter for each trawl and of single target echo intensities for those targets that matched by time, depth and angular position were constructed for each species.

### 8.3.2. Results

23 of the 73 trawls fished contained >99.5% jellyfish by mass and contained few (<0.26% by mass) or no fish. Of these 23, 15 were dominated by *Aequorea aequorea* and 8 by *Chrysaora hysoscella*. For all 23 trawls, 3489 single target echo detections were made at 38 kHz. When these 3489 targets were matched to single target echo detections made at 120 kHz 93% were rejected, leaving 235. A further 156 (66% of the 235) were rejected when compared to the 18 kHz single target echo detections leaving 79 matched across the three split beams by time, depth and angular position. 46 of these 79 single target echo detections were simultaneously detected by the 200 kHz beam and matched on depth. Of the 46 targets, 23 were detected within *A. aequorea* dominated trawls and the remaining 23 were from *C. hysoscella* dominated trawls. For the 23 matches for each species, (matched on time and depth across the four frequencies and collated by angular position for the 3 split–beam transducers), histograms of the compensated TS values at 18, 38, 120 and 200 kHz are presented by species in Figure 8.15 with histograms of medusa diameter (diameter distribution from measurements of 122 *C. hysoscella* and 1053 *A. aequorea* medusae caught by netting).



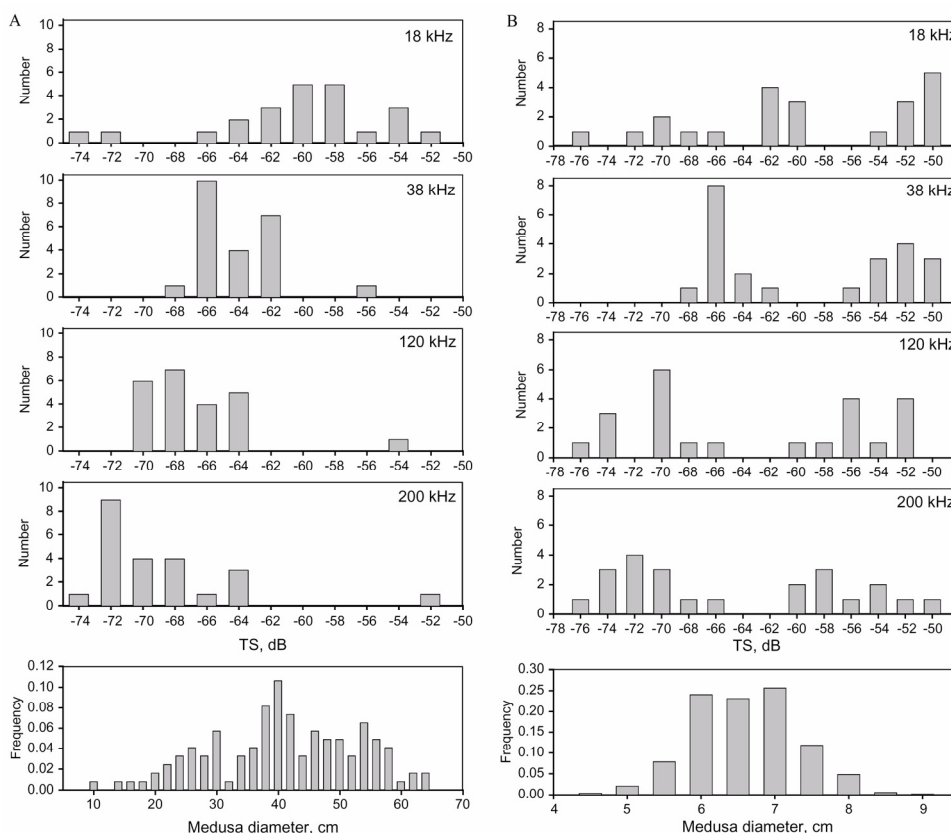


Figure 8.15 A) *Chrysaora hysoscella* and B) *Aequorea aequorea*. Histograms of single target TS detections at 18, 38, 120 and 200 kHz, and histograms of umbrella diameters of jellyfish collected in trawls through sections of the water from which the single target’s echoes were recorded.

Compensated TS from tethered medusae are shown in Figure 8.16; significant positive relationships (at the 10% level) were found for A) *C. hysoscella* umbrella diameter and observed mean TS and B) *A. aequorea* log(outer diameter) and maximum TS at 38 kHz. The single target detections at 38 kHz of free-swimming medusae were compared to echoes collected from tethered medusae (Figure 8.16) and were found to be of a similar magnitude. A simple visual analysis of the TS time series for a *C. hysoscella* medusa (Figure 8.17) suggests that the TS may vary cyclically by 20 dB.

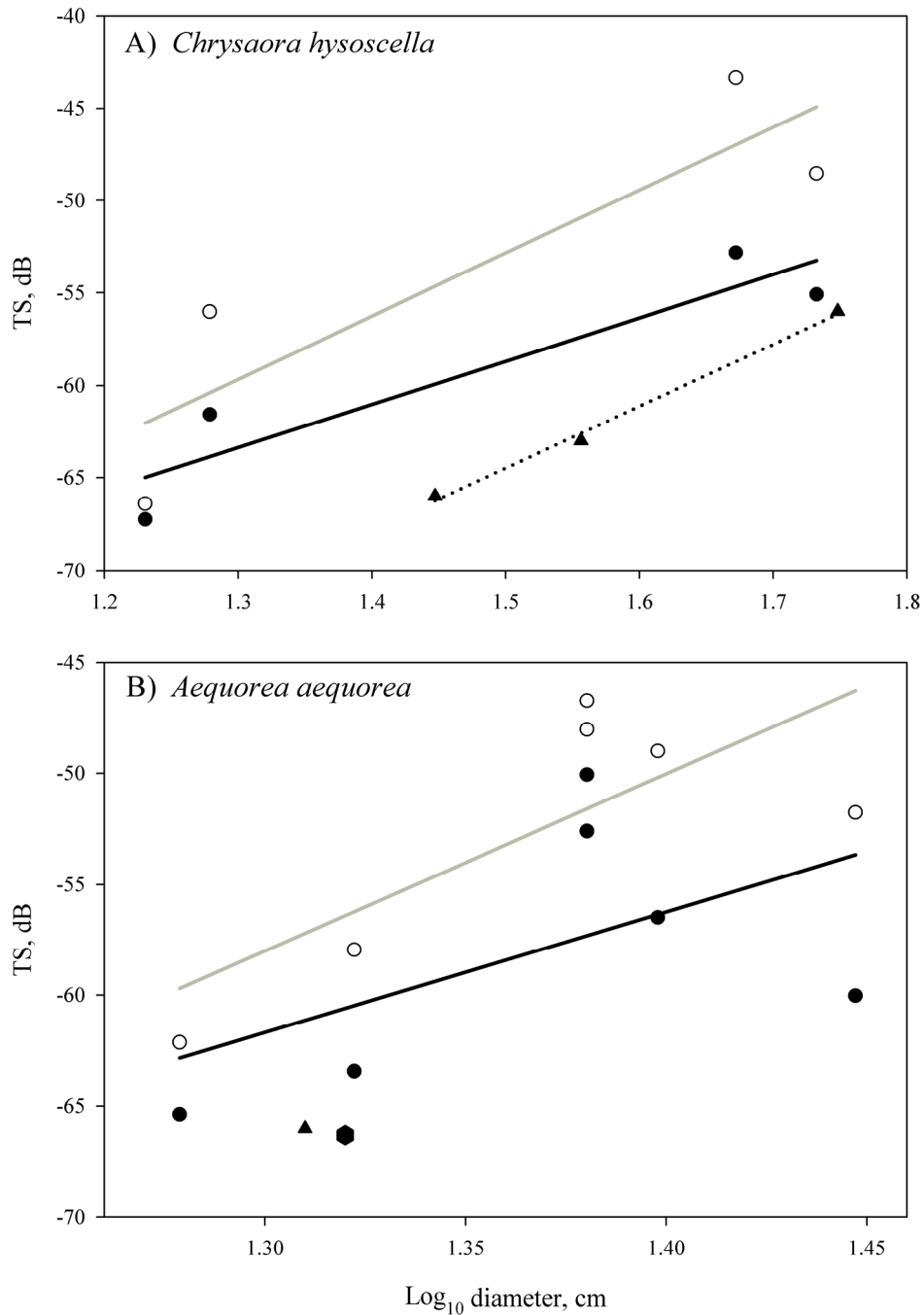


Figure 8.16 *Chrysaora hysoscella* and *Aequorea aequorea* TS-total medusa diameter relationships The filled triangles and dotted line (A only) show the TS against size as determined from *in situ* single target detections (free swimming medusae detected from beam triangulation). Also plotted are the maximum TS per tethered individual (open circles, grey lines) and mean TS per tethered individual (filled circles, black lines). The filled hexagon shows the mean TS for the mean sized *A. aequorea* as reported by Brierley et al. (2001). For comparison method calculations see Brierley et al. (2004). Note the differing x axes.

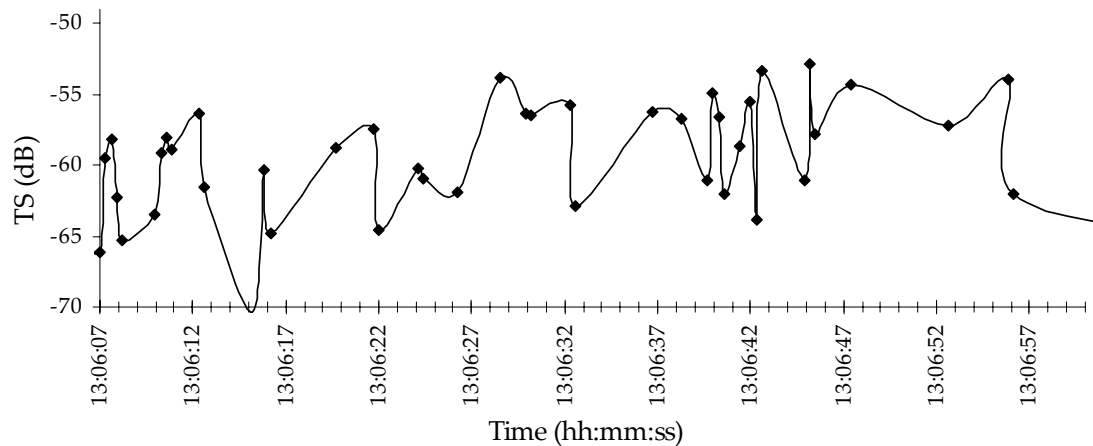


Figure 8.17 Variation in target strength over a 50 second period for an individual *C. hysoscella* medusa with bell diameter 54 cm. This jellyfish was attached by a line to the hull of a small boat, on 7 September 2001, and detected with a 38 kHz SIMRAD EY500 echosounder.

### 8.3.3. Discussion

My finding of comparable measurements of *in situ* TS by multi-frequency beam triangulation and TS from tethered medusae provides strong support for our application of the method proposed by Demer et al. (1999). When vertically orientated (along its long axis) the medusa's umbrella presents a better scattering surface than at any other angle (Figures 8.18 and 8.19), so the mean TS from randomly orientated free-swimming medusa is expected to be a few dB lower than that from the animals tethered vertically.

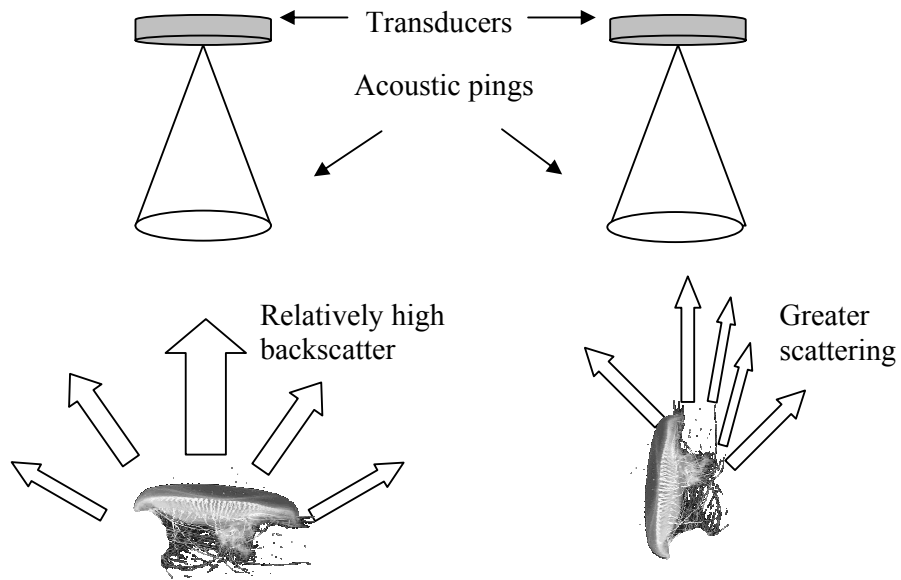


Figure 8.18 Representation of the effect of rotation of *A. aequorea* on acoustic backscatter. If the medusa is orientated along the acoustic axis (left diagram) the umbrella faces the transducer. The umbrella is the best component of the jellyfish as its surface is smoother and more spherical relative to the tentacles and oral arms. If the jellyfish is orientated in any other direction (at the most extreme depicted in the right diagram) the backscatter will be lowered and there will be more destructive interference due to scattering from the oral arms and many tentacles.

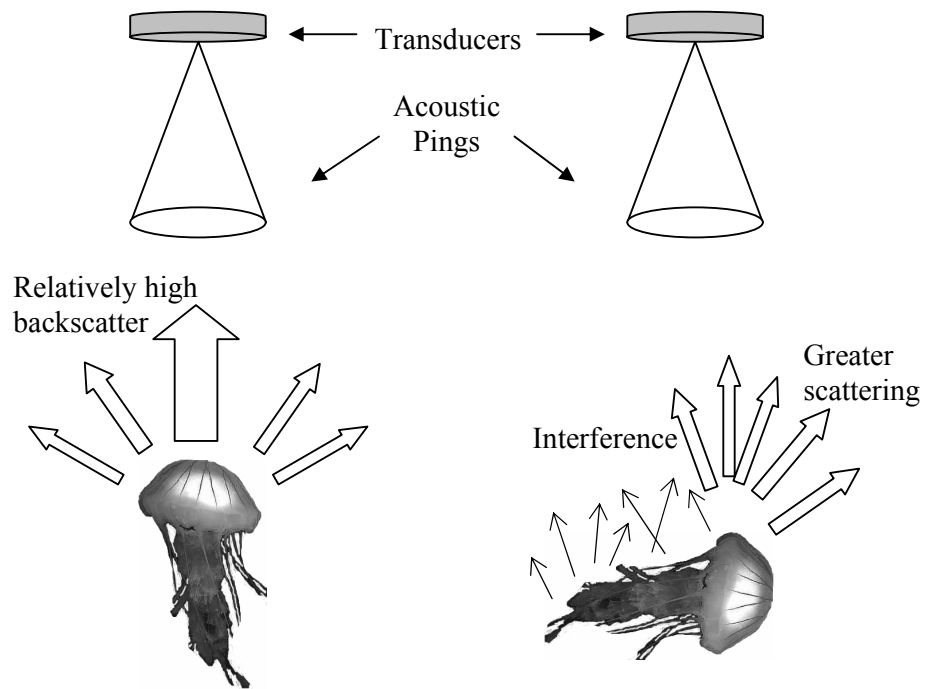


Figure 8.19 Representation of the effect of rotation of a *C. hysocella* medusa on acoustic backscatter, as Figure 8.18.

Preliminary inspection of *C. hysoscella* medusae diameter distributions (Figure 8.15A) ( $N = 122$ ) reveals trimodality. This trimodality is reflected in the TS distributions, but is less apparent due to the lower sample size ( $N = 23$ ). The modal TS values at 38 kHz (-66 dB, -63 dB and -56 dB and corresponding modal diameter values (28, 36 and 56 cm) are plotted in Figure 8.15A (triangles and dotted line). These TS values fall (approx. 4 dB) below the regression of mean TS for tethered medusae, as expected, and have a comparable gradient to both the mean and maximum TS relationships for tethered medusae.

The size frequency distribution of *A. aequorea* (Figure 8.15B) is unimodal ( $N = 1053$ ), however, the TS histograms ( $N = 23$ ) show evidence of multimodality. This discrepancy could be either a reflection of the difference in sample sizes or a result of 'contamination' of the samples by fish or other targets undetected by the trawls. An *Aequorea aequorea* medusa of 7.0 cm central disc diameter (the modal class of trawled samples, Figure 8.15B) would have a log outer diameter of 1.31 and extrapolation for mean TS for tethered medusae at 38 kHz, from Figure 8.16B, would suggest a value of approx. -62 dB. As the corresponding TS for a randomly orientated medusa is expected to be lower than that for a vertically orientated animal, then the -66 dB mode in Figure 8.16 for 38 kHz TS appears to correspond to the modal size class. This point, with  $\log(\text{diameter}) = 1.31$  cm and  $\text{TS} = -66$  dB, is plotted in Figure 8.16B (triangle marker) and does appear close to both the measured mean TS for similarly sized tethered medusae and the value (hexagonal marker) reported by Brierley et al. (2001). We may suppose further that the remaining modes in the TS histograms are therefore due to fish rather than *A. aequorea* medusae, since the size distribution of *A. aequorea* from the same volume of water as was acoustically sampled is unimodal.

As a jellyfish swims, its target strength (TS) has been proposed to increase as the animal's umbrella spreads and decrease as the bell contracts (Mutlu 1996). Our analysis of echoes from tethered jellyfish supports Mutlu's conclusion that the pulsation of the bell may result in the substantial variability (20 dB) in the TS detected (Figure 8.17). In summary, the *in situ* measurements of TS of free-swimming *C. hysoscella* and *A. aequorea* medusae were obtained by multi-frequency beam triangulation and are consistent with TS values determined for tethered medusae.

#### **8.4. A species independent target strength–mass relationship for medusae**

Target strength (TS) estimates for *Aequorea aequorea* and *Chrysaora hysoscella* have been calculated using *in situ* acoustic detections, by the comparison method (see Sections 7.3 and 7.5, Brierley et al. 2001), from acoustic detections of tethered medusae (Section 8.3, Figure 8.16) (Brierley et al. 2004), and through the application of a multifrequency single target detection algorithm (Section 8.3, Brierley et al. 2004). These three techniques produced similar TS estimates, which can be combined to create robust TS–mass or TS–umbrella diameter relationships (based on multi–year measurements) over a range of sizes. Here, I calculate new TS estimates using the comparison method with data (from trawl and acoustic sampling) collected in the Benguela during 2003. These new TS estimates are compared with previously calculated TS estimates for *A. aequorea* and *C. hysoscella*, and indicate that a species independent TS–mass relationship exists for these medusae (Figures 8.21 and 8.22). This simple relationship facilitates the conversion of mean volume backscattering data ( $S_v$ ) into medusa densities (individuals  $m^{-3}$ ).

##### *Previous estimates of jellyfish TS*

Data for *A. aequorea* and *C. hysoscella* have been gathered during cruises to the Benguela on the RV *Dr Fridtjof Nansen*. The first cruise (September 1999) yielded TS estimates through the comparison method (Sections 7.3 and 7.5) (Brierley et al. 2001); TS estimates were subsequently improved using data from the second cruise (September 2001) through i) multifrequency single target matching (Section 8.3), ii) the analysis of backscatter from tethered medusae (Brierley et al. 2004) and iii) correction of TS values estimated by the comparison method, using the 2001 survey data, for the contribution due to zooplankton (Brierley et al. 2005) .

The triangulation based identification of multifrequency single targets presented in Section 8.3 exposed the inadequacies of the EK500 single target detection algorithm to identify targets from individual medusae in dense (0.1 to 0.4 individuals  $m^{-3}$ ) aggregations and in dispersed aggregations (0.01 to 0.1 individuals  $m^{-3}$ ) amidst a background of plankton (98.7% of single targets identified by the EK500 software were most likely, in fact, due to multiple

echoes based on multifrequency acceptance criteria). Identification of jellyfish size-specific TS values via the triangulation technique proved problematic since the resulting small TS sample sizes were difficult to attribute robustly to particular size classes of medusae; (to minimize error) Brierley et al. (2004) chose to compare modal TS values with the modal medusae diameters (Chapter 8.2.3). However, if large (or any particular size class of) medusae occupy a less densely packed area of the water column then single targets would most likely be detected from this region, rendering the modal group comparison flawed. In contrast, the comparison method takes into account the density of jellyfish in a trawled region and the integrated acoustic backscatter from that region. I would therefore argue that the comparison method may be a more robust method when seeking to determine a TS–mass relationship for aggregated jellyfish.

#### 8.4.1. Methods

Here I extract medusa TS values from the August 2003 survey data using the comparison method (Section 7.3) and compare these TS estimates with those collected on previous surveys (Sections 7.5 and 8.3). Fishing activities during 2003 essentially followed those described in a previous investigation of jellyfish in Namibian waters from the RV *Dr Fridtjof Nansen* (Brierley et al. 2001; Buecher et al. 2001; Brierley et al. 2004). Here, I will attempt to determine a mass–TS relationship based on 38 kHz data, which is the frequency used commonly in acoustic surveys of fisheries, so that acoustic data can be converted into estimates of jellyfish biomass.

##### *Trawling*

Two *Åkrehamn* pelagic sampling trawls were used, the larger trawl (12 m opening) was fitted with a remote operated (by acoustic trigger) codend multisampler that enabled three discrete samples to be obtained in each deployment (Figure 8.14, Section 8.3.1) (Skeide et al. 1997; Brierley et al. 2001); the smaller trawl, with a vertical mouth opening of about 10 m, was fitted with 3 or 4 large floats attached to the top panel at the head rope for sampling near the surface (0–10 m depth). The trawls had 180 cm meshes in the mouth opening, gradually decreasing in size towards the aft of the trawl. The codend mesh size was 22 mm. A *Gisund Super* demersal sampling trawl was also deployed twice in order to check for demersal occurrence of jellyfish and

fish during daytime (5 m opening). All trawls were towed using *Thyborøen 125" Combi* otter boards (7.41 m<sup>2</sup>, 2,030 kg) and were equipped with *Scanmar* trawl monitoring sensors providing real time information about depth of the trawl headrope, distance between the trawl doors, trawl mouth opening and clearance from the bottom.

The multisampler trawl was operated in midwater, but in shallow water towards the end of the survey (in the Lüderitz area) two floats, normally used for surface tows ('balloon hauls'), were attached during midwater deployments in order to provide extra lift over the bottom. Although the floats partly collapsed due to the compression they provided enough lift to bring the mouth opening up to 16 m. Splits were cut both in the bottom panel of the extension piece in front of the multisampler and in the front part of each of the codends in order to reduce net tearing. The splits were sewn lightly together using thin twine and each end of the splits greatly enforced, allowing for "controlled" bursts should medusae fill up the codends and threaten to tear the nets, as was the case in 1999 and 2001.

After departure from Walvis Bay 20 August at 16h00 local time (UTC +1), the ship steamed northwards to the border at 17° 15' S. The first of 22 sections was started inshore at 17° 15'S at 20 m depth at 22 August at about 04.00 LT, heading south-west. The subsequent sections similarly covered the depth range of 25 to 350 m (see Figure 9.1, Section 9.1). Monitoring of the scattering layers at two 24 hour stations was conducted in order to study the diel cycle of the jellyfish. It was aimed to keep the effective tow time (time elapsed between opening and closing of each codend) to a constant 5 min for each pelagic and surface haul ( $N = 96$ ), and to 10 min for demersal tows ( $N = 2$ , qualitative hauls checking for demersal fish during the 24 hour stations), due to previous experiences with high densities of jelly causing the trawl extension pieces and codend to tear badly both in 1999 and 2001. However, problems with the acoustic communication from the ship to the multisampler release unit sometimes delayed the closing of the pelagic nets, causing some samples to be towed for up to 12 minutes. It was attempted to keep towing speed for surface and pelagic trawls at 3.5 knots, but actual speeds varied between 3.0 and 4.0 knots depending on the local current strength. In total, 98 trawl stations, 217



length samples, and 32 CTD stations were worked, and a total of 1794 nautical miles (n.mi) were surveyed acoustically.

#### *Sampling scheme and catch analyses*

Random net sampling was undertaken during the survey. However, in addition, targeted sampling was conducted to catch medusae on occasions when medusae were observed at the surface and/or when the echograms suggested that medusae were present at depth. Two 24-hour stations were also selected west of Walvis Bay, near the experimental areas of 1999 and 2001. The first station was worked at about 60 m water depth at 22° 19'S 14° 12'E. The second station was worked south-east, further offshore, at 140 m water depth (22° 49'S 13° 42'E). Each sampling cycle throughout the survey was initiated by a multisampler deployment, hence obtaining 3 discrete pelagic trawl samples, followed by a surface trawl, and ended with a CTD cast. The CTD *Seabird 911+* probe was fitted with temperature, salinity, and oxygen sensors. The oxygen sensor was calibrated using water samples obtained at the surface (5 m depth) and near the bottom (5 m above) in order to ensure proper calibration range. The water samples were titrated and the oxygen level measured using the *Winkler* method.

The samples were analysed as soon as the catches were recovered. The total wet weights of each jellyfish and finfish species were measured to the nearest 0.01 kg for all animals (if total catch  $\leq$  100 kg), or for a subsample ( $\approx$  100 kg of medusae) for larger catches of up to several tonnes. Umbrella diameters of every medusa sampled were measured for both jellyfish species: for *C. hysoscella*, the total umbrella diameter was measured to the nearest 1.0 cm; for *A. aequorea*, the thick, central lens of the umbrella was measured to the nearest 0.5 cm as most of the recovered specimens had lost or damaged umbrella margins (Figure 8.20). For *A. aequorea*, the total umbrella diameter (cm) can be estimated from: (*central lens diameter* x 0.95) + 14.0 ( $R^2 = 0.69$ ) (Brierley et al. 2004). The central lens was estimated to constitute 44 % ( $\pm 12$  %) of the total wet weight (kg) (Brierley et al. 2004).

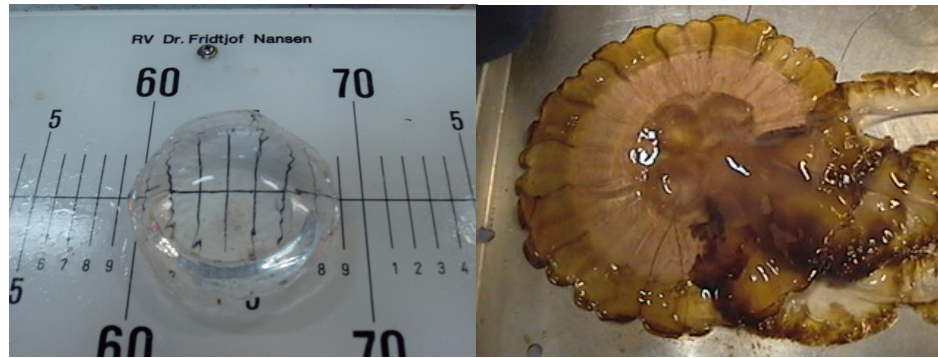


Figure 8.20 *Aequorea aequorea* measurement (left, 8.5 cm bell diameter, photograph by L. Nøttestad) and *Chrysaora hysoscella* (right,  $\approx$  30 cm bell diameter, photograph by C. Sparks) onboard RV *Dr Fridtjof Nansen* in Benguela Sea, 2003.

#### *Estimation of volume trawled*

By not actively avoiding nets nor being herded by trawl bridles, jellyfish enter the trawl passively by floating through it and be retained if the meshes are small enough. However, when particularly dense aggregations are sampled even the large nets employed here may become clogged effectively turning the trawl into a bucket; the short tow times (5 mins) used here were chosen to minimise this effect. In the present study, the sampling volume of the trawl was calculated from the vertical opening ( $O = 12$  m) of the trawl mouth of the multisampler trawl:

$$V = \pi(0.5 \cdot O)^2 \cdot d_t \quad (\text{m}^3) \quad (15)$$

Where  $d_t$  is the towed distance in m. This assumes circular opening of the trawl, and that all jellyfish that enter the mouth opening are retained in the codend. Some jellyfish may, however, be filtered through the trawl meshes, particularly in the fore large-mesh sections of the trawl. During the 1999 survey, an appreciably larger pelagic trawl was utilized (Section 7.5). This trawl was identical to that used in the present study from the belly backwards, but the panels just aft of the mouth had larger meshes: 3200 mm rather than the 1620 mm panels of the trawl used here. The vertical opening of the former trawl was 30 m. From the extension and backwards, the meshes are the same for all sampling trawls (400 mm, stretched), and in 1999 it was assumed that the sampling trawl only caught jellyfish effectively from the 400 mm panels and backwards. The opening in this section was measured using a *Scanmar* height

sensor and was found to be 12 m (Figure 8.14). This opening is nearby to the opening of the multisampler trawl used on the present cruise, and it is reasonable to assume that the smaller-meshed fore panels of this trawl (1620 mm) will retain the medusae effectively (Figure 8.14).

#### *Acoustic calibration*

The transducer arrangement on the drop keel is illustrated in Figure 8.13. Two SIMRAD EK500 echo sounders running split-beam transducers operating at nominal frequencies of 18, 38, 120 kHz (EK 1) and a single-beam transducer at 200 kHz (EK 2) were utilized. Data were logged continuously during the survey utilizing *SonarData Echolog EK (version 2.20.05)*. Settings used as shown in Table 8.2. Note that the pulse length and bandwidth settings were optimised in order to obtain similar and high sampling resolution of all frequencies (Table 8.2). *SonarData Echoview (Version 3.00.75.05)* was used for post-processing. Calibration of all four transceivers was carried out on 17 August 2003, at the end of the previous survey (ANG 2 2003). The calibrations were carried out north of Walvis Bay. The drop-keel was submerged 2.0 m below the hull for the duration of the survey due to relatively rough weather conditions (Section 8.3, Figure 8.13), giving an effective transducer depth of 7.5 m.

| <b>Echosounder</b>                            | <b>EK500 I</b> |            |            | <b>EK500 II</b> |
|---|----------------|------------|------------|-----------------|
|   | ES 18          | ES 38 B    | ES 120-7   | 200-28          |
| Transducer model                              | ES 18          | ES 38 B    | ES 120-7   | 200-28          |
| Transducer type                               | Split-beam     | Split-beam | Split-beam | Single beam     |
| Carrier frequency (Hz)                        | 17 986         | 37 879     | 119 047    | 200 000         |
| Range to sphere (m)                           | 16.2           | 16.2       | 16.1       | 15.3            |
| Theoretical sphere TS (dB)                    | -42.70         | -42.35     | -39.54     | -39.06          |
| Absorption coefficient (dB km <sup>-1</sup> ) | 3              | 10         | 38         | 53              |
| Pulse length (ms)                             | 0.7            | 1.0        | 1.0        | 0.6             |
| SIMRAD annotation                             | SHORT          | MEDIUM     | LONG       | LONG            |
| Bandwidth (kHz)                               | 1.8            | 3.8        | 1.2        | 2.0             |
| SIMRAD annotation                             | WIDE           | WIDE       | NARROW     | NARROW          |
| Transmit Power (W)                            | 2 000          | 2 000      | 1 000      | 1 000           |
| Two-way beam angle (dB)                       | -17.2          | -21.0      | -20.6      | -20.5           |
| S <sub>v</sub> Transducer gain (dB)           | 23.73          | 27.19      | 25.74      | 24.08           |
| TS Transducer gain (dB)                       | 23.45          | 27.22      | 25.96      | 24.80           |
| Angle Sensitivity Alongship                   | 13.9           | 21.9       | 21.0       |                 |
| Angle Sensitivity Athwartship                 | 13.9           | 21.9       | 21.0       |                 |
| 3 dB Beamwidth Alongship                      | 11.1           | 6.9        | 7.2        | 7.0             |
| 3 dB Beamwidth Athwartship                    | 11.0           | 6.8        | 7.3        | 7.0             |
| Off-axis deviation Alongship                  | -0.21          | -0.01      | -0.07      |                 |
| Off-axis deviation Athwartship                | 0.09           | 0.03       | 0.22       |                 |
| Estimated S <sub>v</sub> noise re. 1 m (dB)   | -146.0         | -150.0     | -143.3     | -140.4          |
| Wavelength (m)                                | 0.0833982      | 0.0395998  | 0.0126001  | 0.0075000       |
| Resolvable pulse length (m)                   | 0.525          | 0.75       | 0.75       | 0.45            |
| Half Beamwidth (rad)                          | 0.0964         | 0.0598     | 0.0631     | 0.0611          |
| Solid angle Ω (Srad)                          | 0.0292         | 0.0112     | 0.0125     | 0.0117          |

Table 8.2 Echosounder technical specifications and settings applied during the survey. Calibration parameters were obtained in Langstrand, Namibia prior to the cruise on 17 August 2003, using a WC 38.1 mm tungsten carbide sphere. The depth of the transducer was 5.5 m. The temperature and salinity were measured at 12.5 °C and 35.2 psu, respectively. Average sound speed in the depth range of the calibration was estimated at 1500 m s<sup>-1</sup>.

#### 8.4.2. Results

Of the 94 trawled areas, 14 were found to contain  $\geq 95\%$  by mass of *Aequorea aequorea* and 4 had  $> 89\%$  by mass *Chrysaora hysoscella*. Target Strength (TS) estimates from these areas, determined by comparison of the jellyfish density in the water column inferred from the trawled samples and mean volume backscattering (S<sub>v</sub>) data (Section 7.3), are plotted in Figures 8.21 (triangles) and compared to comparison method estimates from previous surveys (circles 1999

data and squares 2001 data). The following significant relationships (equations 14 and 15) between  $\log_{10}(W)$ , where  $W$  is the wet-weight (grams) of a whole medusa and 38 kHz TS (dB), was found by regression for *C. hysoscella* and *A. aequorea* data (estimates from 1999, 2001, and 2003) combined:

Data from comparison method only (Figure 8.21),

$$\text{TS (dB)} = -76.1960 + 9.5145 \log_{10}(W) \quad (R^2 = 0.33 \ N = 49 \ P < 0.0001) \quad (16)$$

and for all the available data (Figure 8.22),

$$\text{TS (dB)} = -80.9568 + 10.2428 \log_{10}(W) \quad (R^2 = 0.28 \ N = 81 \ P < 0.0001) \quad (17)$$

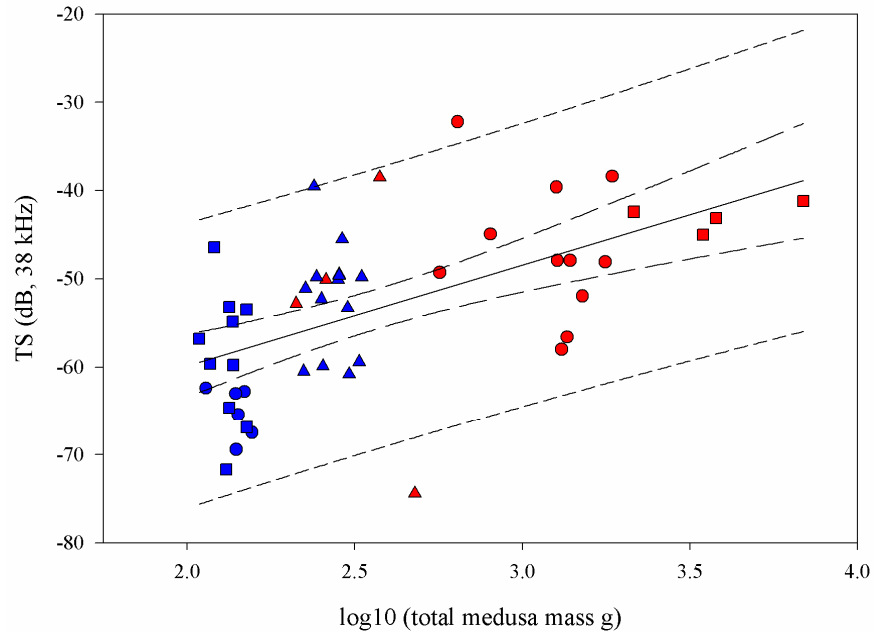


Figure 8.21 Medusae TS (38 kHz) versus total mass, where solid circles (1999 data), squares (2001 data) and triangles (2003 data) are computations using the ‘comparison method’ for *Chrysaora hysoscella* (red points) and *Aequorea aequorea* (blue points). The solid black line is the regression, the long dashed lines show 95% confidence interval for the regression line and the short dashed lines are the 95% prediction interval for individual points.

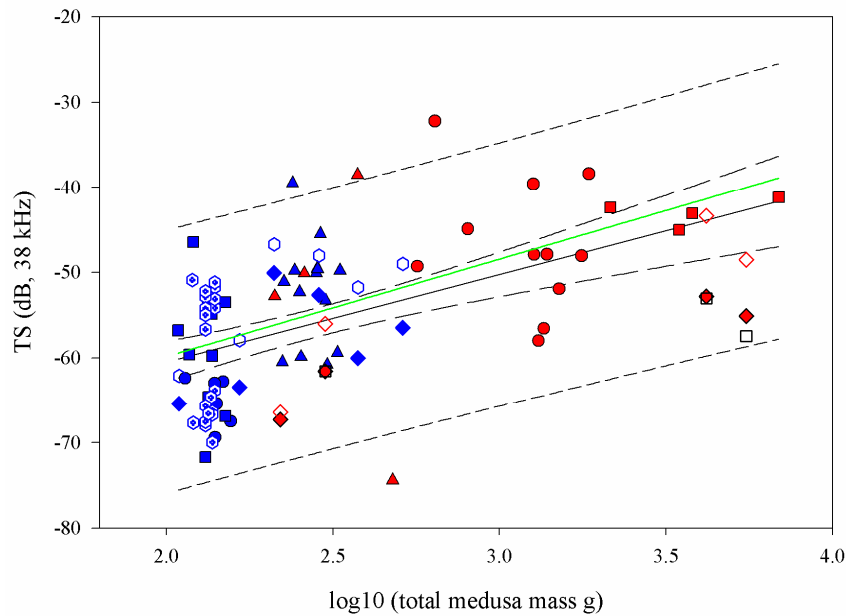


Figure 8.22 As Figure 8.21 but also showing values from: tethered medusae, open diamonds mean measurements and solid diamonds maximum measurements; the mean TS value for tethered *Chrysaora hysoscella* once amphipods had been removed, black square; *in situ* detections from triangulation (Section 8.3), blue dotted diamonds. The solid black line is the regression for all data points, the long dashed lines show 95% confidence interval for the regression line and the short dashed lines are the 95% prediction interval for individual points. The solid green line is the regression from Figure 8.21 for TS values calculated by the comparison method only.

#### 8.4.3. Discussion

The comparison method involves the integration of all acoustic backscatter originating from a specific trawled area of the water column (Sections 7.3 and 7.5). Assuming that the organisms are not in such a high state of flux that the community has altered greatly between trawling and ensonification, the acoustic data should derive from those animals collected by the net samples. However, as there is a time delay (average delay  $\approx 4$  mins) between ensonification and trawling there may indeed be a mismatch between the sampled volumes due to drifting of the net and advection of the plankton. The pelagic trawl used in this study caught a range of marine creatures from large zooplankton (krill and medusae) to fish (e.g. horse mackerel and Cape hake). Although many small zooplankton were not sampled, Brierley et al. (2005) have shown that TS estimates from the comparison method are not biased by

mesozooplankton. The TS–mass relationships derived here suggest that the differences in TS reported previously for the two species of medusae are largely due to differences in mass between individuals and are not species–specific (or, in this case, not even order–specific). The single relationship, shown in Figures 8.21 and 8.22, can now be used to transform acoustic based density estimates into biomass estimates for medusae of *Chrysaora hysoscella* and *Aequorea aequorea*. Unfortunately there is great variability in the regression relationship such that TS predictions span a 40 dB range (parallel short dashed lines). This large range would not be unexpected for individual medusae, since jellyfish detected *in situ* may be in various orientations (Figures 8.18 and 8.19) and swimming states (where the umbrella alternates between contracted and flattened, see Section 8.3.3). However, the majority of the points in the relationship were calculated by the comparison method, which considers the backscatter from an aggregation by comparing net catches with ensonified volumes and is thus dependent on the validity of the assumption of comparable non–biased catches between techniques. Within an aggregation, individual medusae are likely to be randomly orientated and in a variety of swimming states; therefore the variability caused by changes in orientations and swimming behaviour should be included in the relationship. For a swarm of similarly sized jellyfish, we can assume that a typical medusa will have the mean TS, as determined from the regression relationship, and thus have an associated variability in the TS estimate dependent on size:  $\pm 2.5$  for small medusae and up to  $\pm 10$  dB for large medusae (Figure 8.22 long dashed lines).

### **8.5. *In situ* species discrimination using multifrequency acoustics**

Many organisms create backscatter at differing intensities dependent on the frequency of the incident acoustic pulse (MacLennan and Simmonds 1992; Horne 2000). Scientific echosounders emit acoustic pulses of a particular frequency, dependent on the transducer used, and record backscatter from organisms (targets) in the water column. When multiple transducers, with differing frequency beams, are used in synchrony multifrequency backscatter can be gathered from a single target. The use of multifrequency techniques to identify fish and zooplankton species has increased in recent years and it is expected that these methods will enable the development of automatic detection

algorithms (Coyle 2000; Horne 2000; Kloser et al. 2002; Fernandes 2004; Santos et al. 2004). Sound scattering by jellyfish (*Chrysaora hysoscella* and *Aequorea aequorea*) has been shown to be dependent on the frequency of the incident acoustic pulse and the size (umbrella diameter and mass) of the medusa (Sections 7.5 and 8.4) (Brierley et al. 2001; 2004). Here the discrimination of echoes due to medusae, from those from zooplankton and fish, using multifrequency acoustic data (18, 38, 120 and 200 kHz) is shown to enable the reliable identification of jellyfish. An algorithm is successfully developed and tested with the aim of facilitating the automatic identification of acoustic backscatter due to medusae and that due to other organisms. The difference in mean volume backscattering ( $S_v$ , dB) between pairwise comparisons of 18, 38, 120 and 200 kHz data is analysed using *in situ* detections of the two common species of large (> 10 cm diameter) jellyfish (*C. hysoscella* and *A. aequorea*) in the Benguela Sea. The two species are shown to be acoustically discriminable; however, this is likely due to the mass differences (*C. hysoscella* were up to 1 kg heavier than *A. aequorea*) found between individuals of each species during the sampling period.

#### 8.5.1. Methods

For sampling activities see Section 8.4.1. Here I aim to use species-specific multifrequency data to discriminate between jellyfish and finfish species. The most reliable acoustic data will be those echoes that have been produced by dense aggregations with uniform species composition. For schooling fish, individual shoals can often be distinguished from the echogram recordings. However, jellyfish aggregations are not so obvious. During the 10 day survey of the Benguela (Section 8.4.1), two particularly dense aggregations of jellyfish were sampled and at these locations 24-hour sampling cycles were conducted to monitor the dense acoustical scattering layers. Multifrequency acoustic measurements of mean volume backscattering strength ( $S_v$ ) (Section 7.3) were collected from the scattering layers at the stations with the aim to attribute the echoes, with high likelihood, to particular species of jellyfish. The data should then be useful as a reference against which other data (from non-trawled areas) could be evaluated and allocated to species.



*Vertical alignment – electronic transceiver delay*

The data underwent a series of correction steps prior to multifrequency analysis (Figure 8.23). The first step was to align the data vertically, correcting for the electronic delay in the EK500 transceivers, causing a vertical mismatch of the data (Table 8.3) (Korneliussen 2002). All the post-processing was done using *SonarData Echoview (Version 3.25.55.14)*, and the matching was made by simply adjusting the logged draft setting of the various telegrams, before exporting the data, according to Table 8.3.

| <b>EK500 Transceiver</b> | <b>ES 18</b> | <b>ES 38 B</b> | <b>ES 120-7</b> | <b>200-28</b> |
|--------------------------|--------------|----------------|-----------------|---------------|
| Frequency                | 18 kHz       | 38 kHz         | 120 kHz         | 200 kHz       |
| Vertical offset (m)      | 0.46         | 0.30           | 0.24            | 0.17          |

Table 8.3 Electronic delays in the EK500 transceivers.

*Frequency matching*

The next step was to match the two datasets; one set per EK500 echosounder, where EK1 ran 3 transducers (18, 38, and 120 kHz) and EK2 ran the fourth transducer (200 kHz). The two echosounders had to be operated with their separate internal clocks due to a problem with the EK2 resetting the date to a default value (20 April 2000) if operated continuously on an external clock (i.e. the GPS). Although pinging synchronously, corresponding ping returns in the two datasets will have slightly different time stamps (hh:mm:ss.000) due to clock drifting. The two internal clocks of the EK's were therefore synchronised 4 times per day (00.00, 06.00, 12.00 and 18.00 LT) in order to minimise deviance. Synchronisation was achieved by running both echosounders on external clocks for a brief period. For multifrequency comparisons the timestamps must match exactly and this was achieved by first resampling all echograms, and then matching the EK2 data (200 kHz) to the EK1 data (38 kHz was chosen, but 18, 38 and 120 have identical time stamps) using the '*match ping times*' feature in *Echoview* (Figure 8.23).

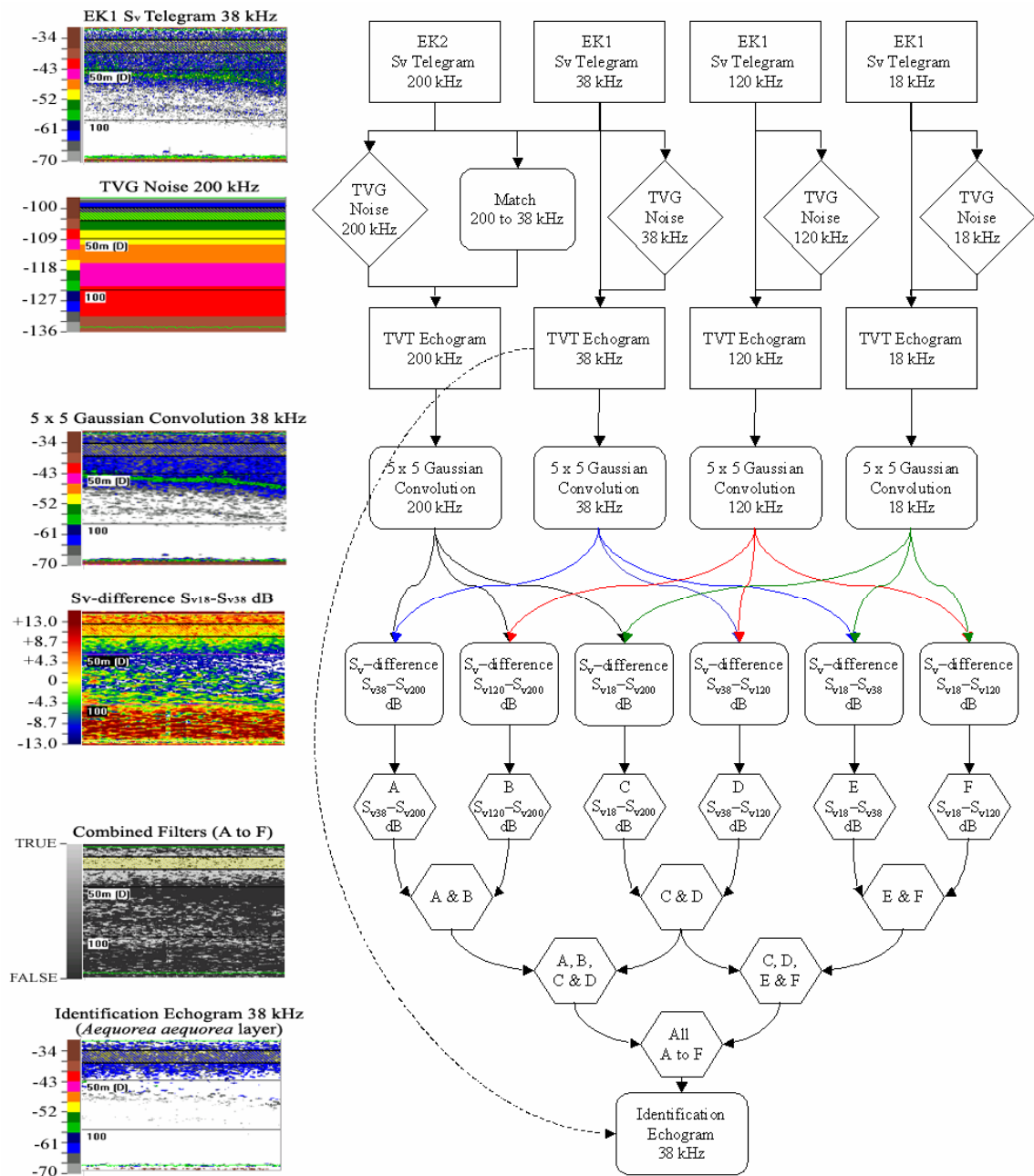


Figure 8.23 (caption on following page)

← Figure 8.23 Multifrequency data correction steps and the process by which species-specific information is generated and applied, with example echograms showing a trawled layer that when sampled by the pelagic trawl (yellow boxed area) was found to be 98% *Aequorea aequorea* and 2% *Chrysaora hysoscella* by mass: the two echosounders (EK1 18, 38 and 120 kHz data and EK2 200 kHz data, top row) are matched using the ‘*Match ping times*’ feature in *Echoview*; the modelled noise (at 1 m) is perpetuated to the depth of the echogram recording using a Time Varied Gain (TVG) function in a ‘*Data generator*’;  $S_v$  data is noise corrected through the creation of a Time Varied Telegram (TVT) using the ‘*Linear minus*’ function;  $S_v$  data are then smoothed using a the gaussian ‘*5x5 convolution*’ feature;  $S_v$ -difference echograms are generated using the ‘*Minus*’ function from which data are exported and species-specific information is gained; data filters (A to F) are created using the ‘*Data range bitmaps*’ and combined using the ‘*And*’ function; finally echoes are allocated to species using the identification echogram, which is created by overlaying the combined filter on the TVT 38 kHz data using the ‘*Mask*’ feature that sets all bins marked FALSE to -999 dB.

#### *Noise estimation and removal*

Background noise levels will vary between frequencies; lower frequencies (particularly 18 kHz) will pick up more propeller and engine noise, but, even so, will generally be less dominated by noise than the higher frequencies (120 and 200 kHz) due to the much higher signal to noise ratio (SNR) at short ranges. Removal of estimated noise from the data has two functions: increasing the SNR at all frequencies, and facilitating comparison of non-biased recordings. The background noise (dB at 1 m) was removed by matching a noise model to the observed noise levels and subtracting this from the data (Watkins and Brierley 1996) (Figure 8.23).

#### *Data smoothing*

There are different ways to improve the match between data recorded at the different frequencies. The most straightforward method would be to average a number of bins (the pixels in the echogram) in the horizontal and vertical planes, i.e. to simply reduce the resolution of the data. The disadvantage of this method is that while averaging improves the spatial overlap of the compared bins, it also reduces the amount of information in the original signal. Another approach, which has been employed here, is to apply a smoothing of each datapoint, acquiring a weighted contribution from the neighbouring cells. This procedure will essentially smooth out the mismatch between neighbouring cells with a small loss of information. I applied a 5 x 5 convolution matrix weighted

according to a Gaussian fit (standard deviation  $\sigma = 5$ ) in both horizontal and vertical planes (Table 8.4) (Figure 8.23).

|       |       |       |       |       |
|-------|-------|-------|-------|-------|
| 0.091 | 1.738 | 6.569 | 1.738 | 0.091 |
| 1.738 | 3.385 | 8.216 | 3.385 | 1.738 |
| 6.569 | 8.216 | 13.05 | 8.216 | 6.569 |
| 1.738 | 3.385 | 8.216 | 3.385 | 1.738 |
| 0.091 | 1.738 | 6.569 | 1.738 | 0.091 |

Table 8.4 5 x 5 Gaussian convolution matrix (weights in %) applied during smoothing of the acoustic data (centre bin in grey).

### *Reference measurements*

The species composition and density in the water column was identified through trawling, while the area of the echogram that the trawl related to was determined through consideration of the depth sampled and the distance/time of the trawled sample behind that of the transducers (a function of ship velocity, and the length of wire cast out for the trawl). Throughout the survey, the most frequently caught species in the pelagic trawl (excluding the 24 hour stations that were dominated by jellyfish and repeatedly sampled) were the jellyfish *Aequorea aequorea* (25 % of total biomass of all organisms sampled, caught in 72 % of trawls) and *Chrysaora hysoscella* (43 % of biomass, in 42 % of trawls) and two finfish species: Cape horse mackerel (*Trachurus trachurus capensis*) (14 % of biomass, in 17 % of trawls), and Cape hake (*Merluccius capensis*) (10 % of biomass, in 19 % of trawls). Each of the other species sampled formed <2 % of total biomass caught, the greatest of which were clupeid species (sardines *Sardinops ocellatus*, anchovy *Engraulis capensis*, and round herring *Etremus whiteheadi*) each at 1.5 % of the total biomass caught. Dense scattering layers that were dominated by the four main species were obtained from the acoustic data where the corresponding pelagic trawl was dominated by a single species (i.e. where *Chrysaora hysoscella* contributed >89% or where fish or *Aequorea aequorea* contributed >95% by mass to the total catch). Weaker criteria had to be chosen for *C. hysoscella* relative to *A. aequorea* and fish due to the tendency for aggregations of *C. hysoscella* to be mixed with other species. Those samples where the density of individuals was high in both catch (i.e. *C. hysoscella*  $\geq 0.4$

individuals per 100 m<sup>3</sup>, while fish or *A. aequorea*  $\geq 1$  individuals per 100 m<sup>3</sup>) and acoustic data (mean  $S_v = TS + 10 \cdot \log_{10}(\text{density}) > -77$  and  $-70$  dB respectively, where the TS of each species was determined from the regression presented in Figure 8.22, Section 8.4.2, and the mean mass per medusa, see 8.4.1) were chosen as reference samples. The noise corrected acoustic data was also analysed to identify fish schools, in order to provide comparable data for the fish reference data, using *Echoview's School's Detection Module* with settings (Table 8.5) proposed by Lawson et al. (2001).

| <b>Detection parameter</b>          | <b>Value (m)</b> |
|-------------------------------------|------------------|
| Total school length                 | 15               |
| Total school height                 | 3                |
| Minimum candidate length            | 10               |
| Minimum candidate height            | 3                |
| Maximum horizontal linking distance | 10               |
| Maximum vertical linking distance   | 2                |

Table 8.5 Settings for the *School's Detection Module*

No catch was dominated by the three clupeid species, either individually or combined. However, calibrated reference data for each clupeid species was supplied by J. Coetzee of Marine and Coastal Management (MCM) Cape Town, South Africa. Clupeids are routinely surveyed by MCM using a SIMRAD EK60 with 38, 120 and 200 kHz transducers. The reference data for round herring and anchovy was collected in the Benguela (latitude 34.74°S, longitude 18.59°E) by the *RS Africana* on 06 November 2004. Reference data for sardines were obtained on 07/11/04 (latitude -34.65°S, longitude 18.82°E), 09/11/04 (latitude -34.47°S to -34.45°S, longitude 19.02°E to 19.03°E) and 23/11/04 (latitude -36.03°S to -36.12°S, longitude 21.78°E to 21.81°E).

#### *Calculation of linear $S_v$ ratio distributions*

Difference echograms (Figure 8.23) were generated between all four frequencies (three for clupeids) using the 5 x 5 convoluted (see *Data smoothing*) volume densities ( $S_{v \text{ kHz}}$ ) for all six possible combinations (for clupeids there was no 200 kHz data therefore there was only three combinations):  $S_{v18} - S_{v38}$ ;  $S_{v18} - S_{v120}$ ;  $S_{v18} - S_{v200}$ ;  $S_{v38} - S_{v120}$ ;  $S_{v38} - S_{v200}$ ; and  $S_{v120} - S_{v200}$ . Since all subtractions were carried out in the log domain, the

resulting  $S_v$ -differences (in dB) express the linear domain ratios. The probability distributions of these  $S_v$ -differences hence represent the 6 available signals, and the hypothesis is that the acoustic information in these signals provides an acoustic signature that can be used as a species identifier. The reference sample probability density functions resemble normal distributions closely (Figure 8.25), so the expected range of  $S_v$ -differences can be expressed in terms of simple confidence intervals (CIs) of the sample data. The 66.7% CI was calculated from the mean  $\pm 1$  standard deviation and the 95% CI from mean  $\pm 2$  standard deviations).

#### *Bitmask filter construction*

In order to separate jellyfish from other scatterers, I created bitmasks (binary echograms) where the selection criteria were based upon the selected reference  $S_v$ -difference data (see *Reference measurements* and Figure 8.23).  $S_v$ -difference data for the reference areas were exported and pooled by species and the means, standard deviations, 95% and 67% CIs were calculated for each pooled distribution (Figures 8.25 and 8.26). The many bitmasks applied here consider one argument, such as the difference in  $S_v$  between 18 kHz and 38 kHz, that should fall within a specified range (the chosen CI, 95% or 67%) and produce the value 1 for bins that are within the range and the value 0 for bins that are not. For each species, bitmasks were produced for all 6  $S_v$ -difference echograms and combined to give one acoustic data filter (where TRUE indicates that the specified range is met in every difference echogram and FALSE means that one or more of the criteria are not met) (Figure 8.23).

#### *Tests of filter performance*

For jellyfish, multifrequency TS estimates have previously been reported at those frequencies used here in the creation of  $S_v$ -difference data (Sections 7.5, 8.2, and 8.3). If correctly estimated, TS-differences should be consistent with  $S_v$ -differences. If the acoustic data filters are performing accurately then estimates of individual densities based on acoustic data should be equal to trawl-based estimates; assuming of course that the trawl does provide unbiased density estimates and that the volume of water insonified does indeed match the trawled volume. Therefore, I test the acoustic data filters by simple regression

of acoustic-based density estimates on trawl-based density estimates. In addition, I calculate the Similarity ID Index (Fernandes 2004),

$$s_{id} = 1 - |(\Phi_t - \Phi_a)| \quad (15)$$

where:  $\Phi_t = \rho_{t(sp\ x)} / \sum \rho_{t(spp)}$ ;  $\Phi_a = \rho_{a(sp\ x)} / \sum \rho_{a(spp)}$ ;  $\rho$  = density estimate, where subscript  $t$  indicates trawl-based and  $a$  indicates acoustic-based estimate of density;  $sp\ x$  = the target species for the identification algorithm;  $spP$  = alternative species and the summation is over all alternatives.

## 8.5.2. Results

### 8.5.2.1. *Aequorea aequorea*

Three of the areas trawled were found to contain dense *A. aequorea* aggregations (mean mass per medusa = 0.12 kg) and no fish (average density of jellyfish from trawl samples > 3 individuals per 100 m<sup>3</sup>) (Figure 8.24). The S<sub>v</sub>-difference data from this subset were pooled, histograms were constructed (Figure 8.25), and the 66.7% and 95% confidence intervals calculated (Figure 8.26, Tables 8.6 and 8.7). The mean S<sub>v</sub>-differences for *Aequorea aequorea* matched the frequency differences found previously in Target Strength (TS) measurements for both *in situ* single target detections and TS values estimated by the comparison method and corrected for the zooplankton contribution to backscatter (Table 8.8) (Brierley et al. 2004; 2005).

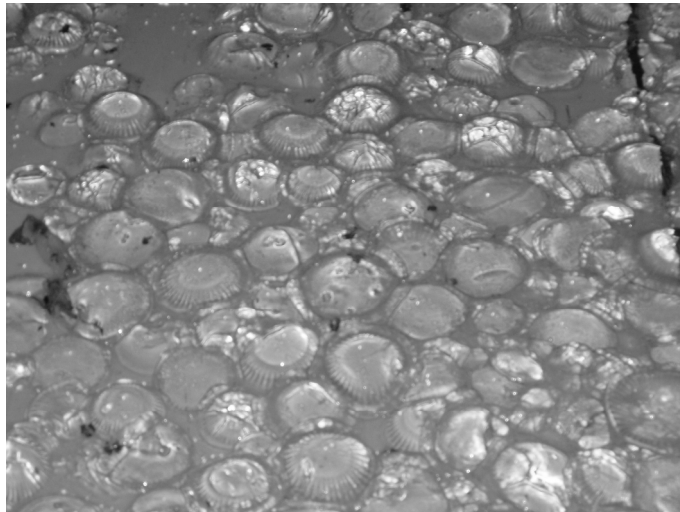


Figure 8.24 *Aequorea aequorea* catch on deck. Photographed by L. Nøttestad onboard RV *Dr Fridtjof Nansen* in Benguela Sea, 2003.

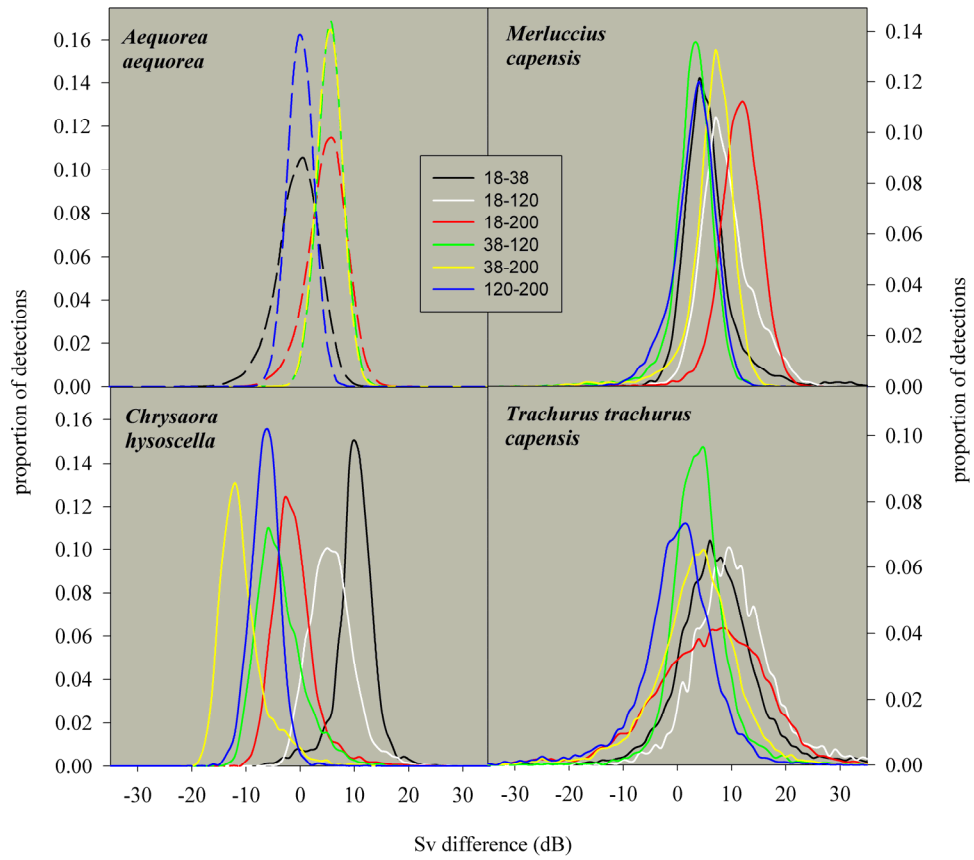


Figure 8.25 Mean  $S_v$  differences in dB by pairwise frequency comparisons for the medusae *Aequorea aequorea* (top left), *Chrysaora hysoscella* (bottom left), Cape hake (*Merluccius capensis*) (top right) and horse mackerel (*Trachurus trachurus capensis*) (bottom right).



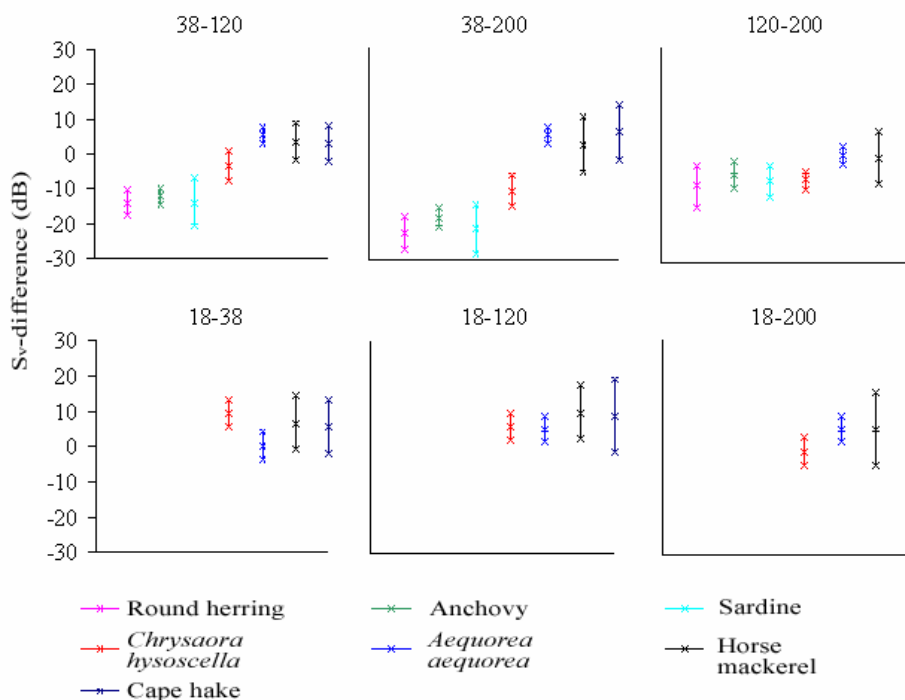


Figure 8.26 Mean Sv differences in dB  $\pm$  1 standard deviation by pairwise frequency comparisons for the medusae *Chrysaora hysoscella* and *Aequorea aequorea* and the following fish species: round herring (*Etrumeus whiteheadi*); anchovy (*Engraulis capensis*); sardine (*Sardinops ocellatus*); horse mackerel (*Trachurus trachurus capensis*) and hake (*Merluccius capensis*).

| $S_v$ -difference $\pm 1SD$ (dB) | 18-38 | 18-120 | 18-200 | 38-120 | 38-200 | 120-200 |
|----------------------------------|-------|--------|--------|--------|--------|---------|
| <i>Chrysaora hysoscella</i>      | 13.13 | 10.05  | 2.99   | 0.93   | -6.11  | -4.31   |
|                                  | 5.84  | 1.89   | -5.03  | -7.97  | -14.91 | -9.66   |
| <i>Aequorea aequorea</i>         | 4.02  | 8.89   | 8.89   | 7.65   | 7.58   | 2.42    |
|                                  | -3.83 | 1.72   | 1.72   | 2.78   | 2.85   | -2.42   |
| Clupeids                         | nd    | nd     | nd     | -6.68  | -13.65 | -2.26   |
|                                  | nd    | nd     | nd     | -20.66 | -27.74 | -11.13  |
| Horse mackerel and hake          | 15.83 | 21.29  | 19.89  | 9.23   | 12.73  | 7.65    |
|                                  | -2.73 | -1.87  | -3.86  | -2.45  | -3.59  | -4.75   |

Table 8.6 Range of  $S_v$ -differences mean  $\pm$  1 standard deviation for the jellyfish, *Aequorea aequorea* and *Chrysaora hysoscella*, and the two groups of fish species: clupeids (anchovy, sardine and round herring) and horse mackerel/hake. Note: nd = no data.

| $S_v$ -difference $\pm 2SD$ (dB) | 18-38           | 18-120          | 18-200          | 38-120         | 38-200          | 120-200         |
|----------------------------------|-----------------|-----------------|-----------------|----------------|-----------------|-----------------|
| <i>Chrysaora hysoscella</i>      | 16.78<br>2.20   | 14.12<br>-2.19  | 7.01<br>-9.05   | 5.38<br>-12.42 | -1.70<br>-19.31 | -1.63<br>-12.34 |
| <i>Aequorea aequorea</i>         | 7.94<br>-7.76   | 12.47<br>-1.87  | 12.47<br>-1.87  | 10.08<br>0.34  | 9.94<br>0.48    | 4.84<br>-4.84   |
| Clupeids                         | nd<br>nd        | nd<br>nd        | nd<br>nd        | 0.31<br>-27.66 | -6.61<br>-34.78 | 2.18<br>-15.56  |
| Horse mackerel and hake          | 25.12<br>-12.02 | 32.87<br>-13.45 | 31.77<br>-15.74 | 15.06<br>-8.29 | 20.89<br>-11.74 | 13.84<br>-10.94 |

Table 8.7 Range of  $S_v$  differences mean  $\pm 2$  standard deviation for the jellyfish, *Aequorea aequorea* and *Chrysaora hysoscella*, and the two groups of fish species: clupeids (anchovy, sardine and round herring) and horse mackerel/hake. nd = no data.

| Frequency difference | Mean $S_v$ | <i>In situ</i> TS detections by triangulation (Brierley et al. 2004) | Comparison method TS zooplankton corrected (Brierley et al. 2005) |
|----------------------|------------|--|---|
| 18-38                | 0.09       | 0.50   | -1.50   |
| 18-120               | 5.30       | 5.50   | 4.60  |
| 18-200               | 5.30       | 7.00   | 4.80  |
| 38-120               | 5.21       | 5.00   | 6.10  |
| 38-200               | 5.21       | 6.50   | 6.30  |
| 120-200              | 0.00       | 1.50   | 0.20  |

Table 8.8  $S_v$ -differences (shown in Figure 8.26 with  $\pm 1$  SD range) and TS differences in dB for *Aequorea aequorea*.

### 8.5.2.2. *Chrysaora hysoscella* and horse mackerel

A relatively high-density swarm of *C. hysoscella* (mean mass per medusa = 1.04 kg) was identified by the trawl (0.4 individuals per 100 m<sup>3</sup>) and echosounder simultaneously. However, a layer of horse mackerel (mean mass per fish = 0.011 kg) was also sampled and the resulting  $S_v$ -difference histograms for the trawled area were bimodal. During the survey, two trawled areas were found to contain pure samples (100% by mass) of horse mackerel. Distinct fish schools were observed in the echograms in and between these two trawls. A total of 63 schools were identified by the *Echoview School's Detection Module* (settings as in Table 8.5). The  $S_v$ -difference data for these schools, and the two trawled areas, were found to match the data arising from the fish layer identified in association with the *C. hysoscella* swarm (i.e. one of the two modes). To create an  $S_v$ -filter for *C. hysoscella* only, data were

exported from the trawled area with the horse mackerel layer masked out using the ‘bad data’ function in *Echoview* resulting in a unimodal distribution of  $S_v$ -differences (Figure 8.25). Acoustic data from three further areas where the trawls were dominated by *C. hysoscella* (>89% by mass), but the catch was low (density < 0.3 individuals per 100 m<sup>3</sup>), were considered for comparison with the data from the high density *C. hysoscella* area. The peaks in the relatively broad  $S_v$ -difference histograms resulting from the low-density trawled areas were found to match the peaks from the histograms based on the high density *C. hysoscella* area with the horse mackerel layer excluded. So, (i) the  $S_v$ -difference data from the horse mackerel layer matched the horse mackerel schools data and (ii) the  $S_v$ -difference data from the dense *C. hysoscella* area, once the horse mackerel contamination was removed, matched the  $S_v$ -difference data for the areas associated with low density *C. hysoscella* trawls. However, the mean  $S_v$ -differences did not match the frequency differences found previously in Target Strength (TS) measurements estimated from either *in situ* single target detections or by the comparison method (Table 8.9)

| Frequency difference (kHz) | Mean $S_v$ -difference (dB) | <i>In situ</i> TS-difference (dB) for detections by beam triangulation (Brierley et al. 2004) | Comparison method TS-difference (dB) for zooplankton corrected data (Brierley et al. 2005) |
|----------------------------|-----------------------------|---|--|
| 18-38                      | 9.49                        | 5.50  | -4.40  |
| 18-120                     | 5.97                        | 8.00  | -0.50  |
| 18-200                     | -1.02                       | 10.50   | 17.10  |
| 38-120                     | -3.52                       | 2.50  | 3.90   |
| 38-200                     | -10.51                      | 5.00  | 21.50  |
| 120-200                    | -6.99                       | 2.50  | 17.60  |

Table 8.9  $S_v$  and TS differences in dB for *Chrysaora hysoscella*.

### 8.5.2.3. Others: hake; anchovy; sardine; and round herring

Cape hake were found in high densities in one demersal trawl (87% by mass, density 11 individuals per 100 m<sup>3</sup>, mean mass per fish = 0.043 kg); histograms of  $S_v$ -difference data from this region were unimodal and similar to the chart of horse mackerel data (Figure 8.25). No trawls contained >65 % by mass (and had a density > 0.1 individuals per 100 m<sup>3</sup>) of either anchovy, sardine or round herring; for these clupeids, single species data collected in the southern Benguela Sea was utilised (Section 8.5.2).

#### 8.5.2.4. $S_v$ -data filters and tests of performance

By inspection, it is apparent that the  $S_v$ -difference histograms for the two species of medusae are sufficiently different from each other to enable discrimination between the species (Figure 8.25). Although *Chrysaora hysoscella* do appear discriminable from each fish species, *Aequorea aequorea* may not be discriminable from horse mackerel or Cape hake by  $S_v$  differencing alone with the available frequencies (Figure 8.26). Horse mackerel and Cape hake appear to have a similar acoustic signature to each other, since there are substantial overlaps between the ranges of their mean  $S_v$ -differences (Figure 8.26). The  $S_v$ -difference data for anchovies, round herring and sardines is also similar across species, rendering these species acoustically indistinguishable from each other; however, these clupeid species do appear discriminable from both horse mackerel and Cape hake (Figure 8.26). Acoustic data filters, based on both 67% and 95% CIs, were therefore created for each jellyfish species, for horse mackerel and Cape hake combined and for all clupeids combined. The data filters were applied to the noise corrected 38 kHz  $S_v$  data and estimates of medusa and fish densities from the filtered data were calculated using the target strength (TS) relationship for medusae given by equation 17 (Section 8.4.3) and the TS relationships for each fish species reported by Barange et al. (1996).

The performance of each filter was examined through calculation of the mean similarity index ( $s_{id}$ , Equation 15, Section 8.5.1, Fernandes 2004) for every area in which one of the species of interest was found to dominate (>87% by mass) regardless of density (Table 8.10). For each group no significant (all  $p > 0.4$   $N = 28$ ) difference was found between the mean similarity index for filters based on either CI (67% and 95%); however, all performed adequately ( $s_{id} \geq 0.7$ ). Regression analyses, using data from every pelagic trawl, indicated that there was no significant relationship between trawl-based and acoustic-based estimates of densities for any group with either (67% or 95%) acoustic filter (all  $p > 0.10$ ). When the two jellyfish filters were applied only to those areas where the trawl catch was dominated by jellyfish ( $N = 19$ ) positive relationships between trawl and acoustic estimates of density were found; however, the only significant relationship was that for *Chrysaora hysoscella* data with the acoustic filter based on the 67% CI ( $R^2 = 0.61$   $P < 0.01$   $N = 19$ ). The acoustic estimates of jellyfish density did not agree with the trawl-based

estimates for either species: for *A. aequorea* the acoustic estimates (using either CI) were an order of magnitude greater than those estimates from the trawl samples; for *C. hysoscella* the acoustic estimates were between one and three orders of magnitude lower than those estimates from the trawl samples, with the exception of one sample where the acoustic estimate (using the 95% CI) gave a value three orders of magnitude greater than the trawl-based estimate.

| Group                       | $s_{id}$ 67% CI | $s_{id}$ 95% CI | $t$ -statistic | $P$ -value |
|-----------------------------|-----------------|-----------------|----------------|------------|
| <i>Chrysaora hysoscella</i> | 0.75            | 0.72            | 0.34           | 0.73       |
| <i>Aequorea aequorea</i>    | 0.80            | 0.78            | 0.20           | 0.84       |
| Horse mackerel and hake     | 0.89            | 0.93            | -0.84          | 0.41       |
| Clupeids                    | 0.91            | 0.84            | -0.89          | 0.38       |

Table 8.10 Similarity index ( $s_{id}$ ) between trawl samples and filtered acoustic data (using either the 67% or 95% CI,  $t$ -test to test for a significant difference between  $s_{id}$  based on either CI) for the jellyfish, *Aequorea aequorea* and *Chrysaora hysoscella*, and the two groups of fish species: clupeids (anchovy, sardine and round herring) and horse mackerel/hake.

### 8.5.3. Discussion

The histograms of  $S_v$ -difference data and plots of 67% CI for the jellyfish species and fish groups (Figures 8.25 and 8.26) suggest that *Aequorea aequorea* and *Chrysaora hysoscella* are acoustically distinguishable from one another and from clupeids, and that clupeids and *C. hysoscella* are distinguishable from Cape hake and horse mackerel. *Aequorea aequorea* may not be discriminable from Cape hake or horse mackerel through  $S_v$ -differencing alone; nevertheless, with the addition of density information and fish school characteristics (Lawson et al. 2001), the fish may be automatically distinguished from medusae since these schooling fish form dense discrete schools ( $S_v > -50$  dB) (Coetzee 2000) quite different to the relatively dispersed aggregations of medusae ( $S_v$  typically between  $-50$  and  $-80$  dB). Cape hake and horse mackerel are not acoustically discriminable at the available frequencies; however, behavioural differences between the species may allow for discrimination since Cape hake are a demersal species and the juvenile horse mackerel surveyed here are generally found in mid-water (Boyer and Hampton 2001).

The similarity index (all  $s_{id} \geq 0.7$ , Fernandes, 2004) suggests that the fraction of biomass found for each species from the trawled samples is representative of the proportion of acoustic backscatter allocated by the acoustic data filters for each species. However, the actual estimates of density do not appear to match across methods. This mismatch suggests that either: the acoustic technique is estimating jellyfish density incorrectly; the trawl is a biased sampler for jellyfish aggregations; or that the trawled volume of water did not match the insonified volume. Mismatching between acoustic/net density estimates is a common problem, most frequently encountered during surveys of highly mobile fish (McClatchie et al. 2000). However, from the data collected here, it is not possible to determine where the inaccuracy lies and further data should be collected to verify and improve the technique.

Filters that are based on  $S_v$  data, such as those developed here, will only be completely reliable if the data are homogeneous, i.e. the area insonified relates to a single species. The reference areas were chosen to be the densest areas for each species in order to maximise the proportion of detections within the reference area that are in fact from the chosen species. However, as the distribution of organisms in the water column is not homogeneous, it is likely that background detections from plankton will have been incorporated in the filter construction step through those echoes where medusae/fish were not detected; particularly so in the 95% CI for *Chrysaora hysoscella* as that species was not found in densities (based on trawl samples) exceeding 0.4 individuals per 100 m<sup>3</sup>. In addition, the great  $S_v$ -differences found at the extremities of the 95% CI (up to 19 dB) might result from detections at only one of the pair of frequencies compared. To reduce the chances of misallocation of acoustic backscatter to medusae or fish (i.e. Type II error), through the use of the data filter for  $S_v$ -difference data, I suggest that the acoustic data filter should be based on the 67% CI, as this should prove more reliable than the wider acoustic data filter, based on the 95% CI. The 67% CI includes detections that are found most frequently within the reference areas for the chosen species/groups and excludes some relatively infrequent values that are included in the 95% CI. Therefore, the allocation of acoustic backscatter to species/groups based only on the most probable  $S_v$ -differences should result in the most robust estimates of numerical density possible using this multifrequency technique.

The attribution of echoes to medusae that have actually been backscattered by fish will greatly bias any estimate of medusa biomass, since medusae are much weaker scatterers of sound and a strong fish echo would be transformed into a high biomass of medusae. For example, a horse mackerel echo with volume backscattering strength  $S_v = -50\text{dB}$  would suggest a fish density of  $0.01 \text{ kg m}^{-3}$  but this would convert to  $1.1 \text{ kg m}^{-3}$  of *A. aequorea* or  $2.2 \text{ kg m}^{-3}$  of *Chrysaora hysoscella*. To minimise this risk, I propose that the ‘schools detection algorithm’ in *SonarData Echoview* be used in conjunction with acoustic data filtering so that dense school-like areas of the echogram are allocated to fish species prior to the allocation of backscatter to medusae. To date, this two-layered approach is the most reliable way developed to discriminate between acoustic backscatter from medusae and from schooling fish.

## Chapter 9

### **An acoustic estimate of jellyfish biomass in the northern Benguela**



*Chrysaora hysoscella* (red medusae), *Aequorea aequorea* (clear medusae) and horse mackerel. Photographed by L. Nøttestad onboard RV *Dr Fridtjof Nansen* during the acoustic survey of the Benguela Sea, August 2003.



## 9. An acoustic estimate of jellyfish biomass in the northern Benguela

### 9.1. Abstract

Here, I report the world's first acoustic estimate of the biomass of *Chrysaora hysoscella* and *Aequorea aequorea* in the northern (Namibian) Benguela Sea; estimates of mean along-track jellyfish densities (binned in 1 nautical mile along track sections) were 55 and 1278 tonnes n.mi<sup>-2</sup>, for *C. hysoscella* and *A. aequorea* respectively and from a Bayesian analysis the most likely distribution in the survey area as a whole had a mean densities of 1 and 360 tonnes n.mi<sup>-2</sup>. In comparison, mean densities of *clupeids* (*Sardinops ocellatus*, *Engraulis capensis* and *Etrumeus whiteheadi*), horse mackerel (*Trachurus trachurus capensis*) and Cape hake (*Merluccius capensis*) were in the whole survey area were 23, 33, and 50 tonnes n.mi<sup>-2</sup> respectively. The total biomass of medusae was estimated at 12.2 million tonnes (99% *Aequorea aequorea*), for the 33,710 n.mi<sup>2</sup> surveyed, and was found to be much greater than the estimated total biomass of fish: clupeids (0.8 million tonnes) juvenile horse mackerel (1.1 million tonnes) and Cape hake (1.7 million tonnes).

### 9.2. Introduction

Following many years of intensive fishing, Namibian sardine (*Sardinops ocellatus*) stocks collapsed during the 1970s in the northern Benguela Sea, (Figures 9.1 and 9.2). Catches by the purse-seine fishery for sardines peaked at approximately 1.4 million tons in 1968, but fell to a record low of ~2000 tons in 1996 (Boyer and Hampton 2001). Sardine catches have since increased, but only to 1-3% of the peak catch of 1968. Few anchovy (*Engraulis capensis*) were caught before the collapse of the sardine stock. However, during the 1970s and 1980s anchovies were targeted heavily by the purse-seine fishery and this exploitation, coupled with environmental changes (increased wind anomalies and upwelling) in the mid-1990s, has resulted in the virtual local extinction of anchovy stocks in the northern Benguela Sea (Boyer and Hampton 2001). Juvenile horse mackerel (*Trachurus trachurus capensis*) have also been targeted by the Namibian purse-seine fishery. After an initial record catch of 140 thousand tons in 1971, horse mackerel catches have declined to around 20 thousand tons per annum today and are comparable to the highly fluctuating sardine catch. In addition to the purse-seine catches of juvenile horse mackerel,

pelagic trawlers fish the adult stock and this fishery is now the largest in Namibia. Catches of adult horse mackerel declined from approximately 0.5 million tons per annum during the 1980s, to between 0.20 and 0.25 million tons per annum between 1999 and 2001. Cape hake, targeted by demersal trawlers, is the most valuable fishery to Namibia. Yet, due to overfishing in the late 1960s and early 1970s (peak landings in 1972 of  $1.1 \times 10^6$  tons), the stock declined gradually until conservation measures were put in place in 1990; landings were then limited to  $5.5 \times 10^4$  tons per annum, but this limit was increased year on year so that almost  $2 \times 10^5$  tons were landed in 2000 (Boyer and Hampton 2001).

The reduction in biomass of commercial fish stocks in the Benguela has resulted in an increase in the primary production available to the unexploited organisms such as jellyfish (Cnidaria and Ctenophora), pelagic gobies (*Sufflogobius bibarbatus*) and lantern fish (*Myctophids*) (Cury et al. 2005). Conversely, these ecosystem changes have been largely detrimental to higher predators, since large pelagic fish are an important prey for seals and seabirds (Cury et al. 2005; Underhill and Crawford 2005). Prior to the collapse of the fish stocks in the Benguela Sea, a comprehensive zooplankton study evaluated the ecosystem but did not mention the occurrence of medusae (Hart and Currie 1960). An early zooplankton study of the waters of Walvis Bay (from the coast to  $12.58^\circ\text{E}$  and from  $21.75^\circ\text{S}$  to  $23.92^\circ\text{S}$ ), throughout the period from January 1959 to December 1962, describes two peaks in the abundance (during June–July and October–December) of the trachymedusan *Lirope tetraphylla* and the ctenophores *Beroë* and *Pleurobrachia* spp. (Kollmer 1963, 1964), but again no mention was made of the jellyfish *Chrysaora hysoscella* (Scyphozoa) and *Aequorea aequorea* (Hydrozoa) that are caught commonly in these waters today. However, after the collapse of the pelagic fish stocks in 1972, the jellyfish *C. hysoscella* and *A. aequorea* were found to form a greater proportion of the landings by purse-seine fishermen and were considered a nuisance (Venter 1988). *Chrysaora hysoscella* and *A. aequorea* are now widespread throughout the northern Benguela Sea and are often caught in such high abundance that fishing nets burst under the weight of medusae when brought aboardship (Fearon et al. 1991; Pagès 1992; Brierley et al. 2001; Sparks et al. 2001). From this limited evidence, we can only conclude that either *C.*

*hysoscella* and *A. aequorea* were not present in the Benguela ecosystem until fairly recently (early 1970s) or that they were in such low abundance relative to fish stocks prior to the 1970s that they did not interfere with normal fishing operations in the region and were thus not perceived to be worthy of comment.

Recent studies of the acoustic properties of medusae have resulted in the formulation of a species independent mass–target strength relationship for the common jellyfish, *Aequorea aequorea* and *Chrysaora hysoscella*, found in the Benguela Sea (Section 8.4) and a novel method for the automatic discrimination of jellyfish backscatter from that arising from other common macro–pelagics (clupeids, horse mackerel, and Cape hake) has also been developed (Section 8.5). These advances facilitate the attempt made here at the world’s first biomass estimate for jellyfish (and comparable fish biomass estimates), based on acoustic data collected during a full–scale survey of the Namibian shelf in August 2003 (Figure 9.1 and Section 8.4.2).

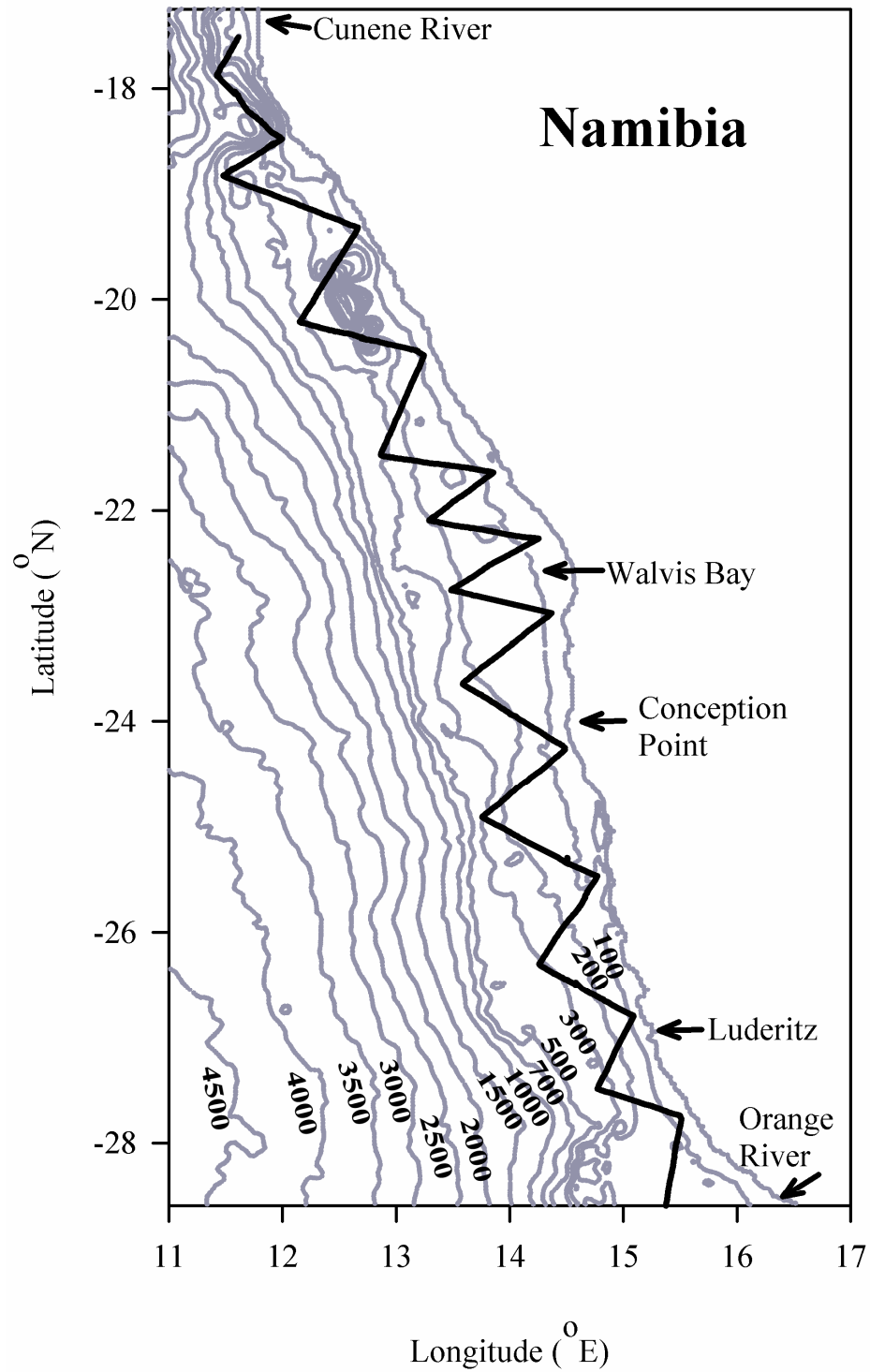


Figure 9.1 Map of the northern Benguela Sea showing bathymetry (grey contour lines) and the cruise track (solid black line) followed southward from the Angola–Namibia border to the South Africa–Namibia border.

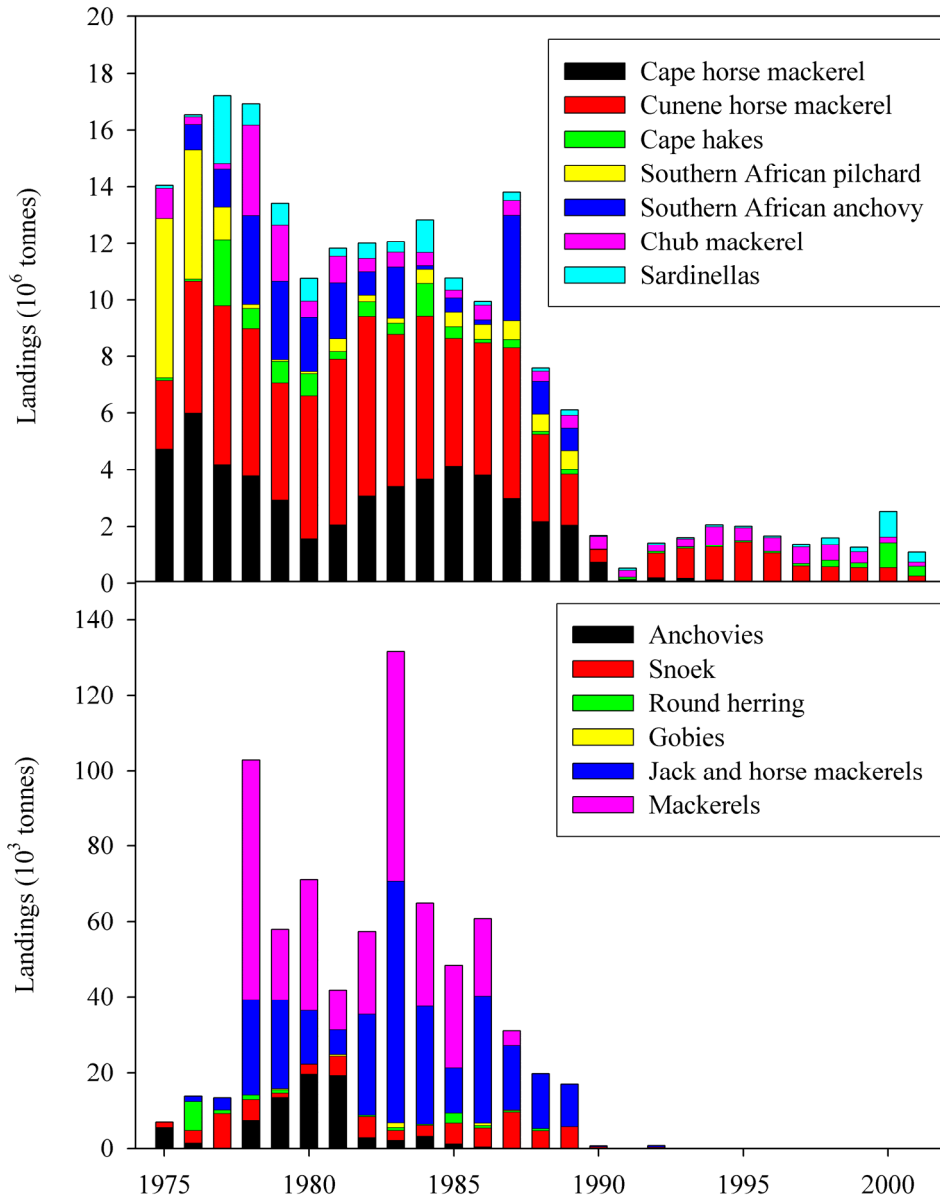


Figure 9.2 Catch of commercial fish species in the Namibian Benguela, data from *FISHSTAT+ Version 2.30* (FAO, 2000) Note that horse mackerel are split in three groups (Cape horse mackerel *Trachurus trachurus capensis*; Cunene horse mackerel *Trachurus trecae*; and the mixed group jack mackerels/horse mackerels *Trachurus* spp.), and that clupeids are likewise split into five groups (Southern African pilchard *Sardinops ocellatus*, Southern African anchovy *Engraulis capensis*, anchovies *Engraulidae*, sardinellas *Sardinops* spp. and round herring *Etrumeus whiteheadi*).

### 9.3. Methods

Recent trawl survey samples, (September 1999, Brierley et al. 2001, and September 2001, Brierley et al. 2004) showed medusae occurring in high densities around 22°S: maximal densities of *Aequorea aequorea* were 168 and 12 individuals per 100 m<sup>3</sup> in 1999 and 2001 respectively and maximal densities of *Chrysaora hysoscella* were 3 and 1 individuals per 100 m<sup>3</sup> in 1999 and 2001 respectively. *Chrysaora hysoscella* were found in largest concentration inshore, while *A. aequorea* were found further offshore (150-200 m bottom depth). However, visual observations carried out during several surveys in the northern Benguela (6 cruises between August 1997 and June 1998, Sparks et al. 2001) have shown that both jellyfish species, in particular *C. hysoscella*, are distributed right through from Conception Point (24°S) to the Namibian–Angolan border, with high density areas in the area immediately south of the Cunene River (near 18°S). In order for this survey to cover the main distribution area, it was decided to cover the entire Namibian coast (from the Cunene River in the north to the Orange River in the south (from 17°15'S to 28°38'S), during the 10 days available, using a coarse zig–zag survey design that would allow continuous acoustic sampling from the coast (25 m depth) to the 350 m depth contour (Figure 9.1). For details of the sampling scheme see Section 8.4.2.

#### *Weighted target strength*

##### Jellyfish

The umbrella diameters, but not the individual masses, of all sampled medusae were measured. So, for each species, the entire mass distribution (in kg) was determined from the measured distributions of umbrella diameters (in cm) (Figure 9.3). The transformation, made using the following equations (Buecher et al. 2001), provides a more accurate description of the mass distribution than measurements of medusa weight alone because complete medusae were rarely caught:

$$\textit{Aequorea aequorea wet weight} = (0.0011 \textit{ inner diameter}^{2.0173}) / 0.44 \quad (16)$$

$$\textit{Chrysaora hysoscella wet weight} = (0.0001 \textit{ diameter}^{2.7057}) \quad (17)$$

As trawled specimens of *A. aequorea* have usually lost the fragile outer umbrella (see Figure 8.24, Section 8.5.2.1) the diameter to mass conversion is based upon inner disk measurements (Buecher et al. 2001).

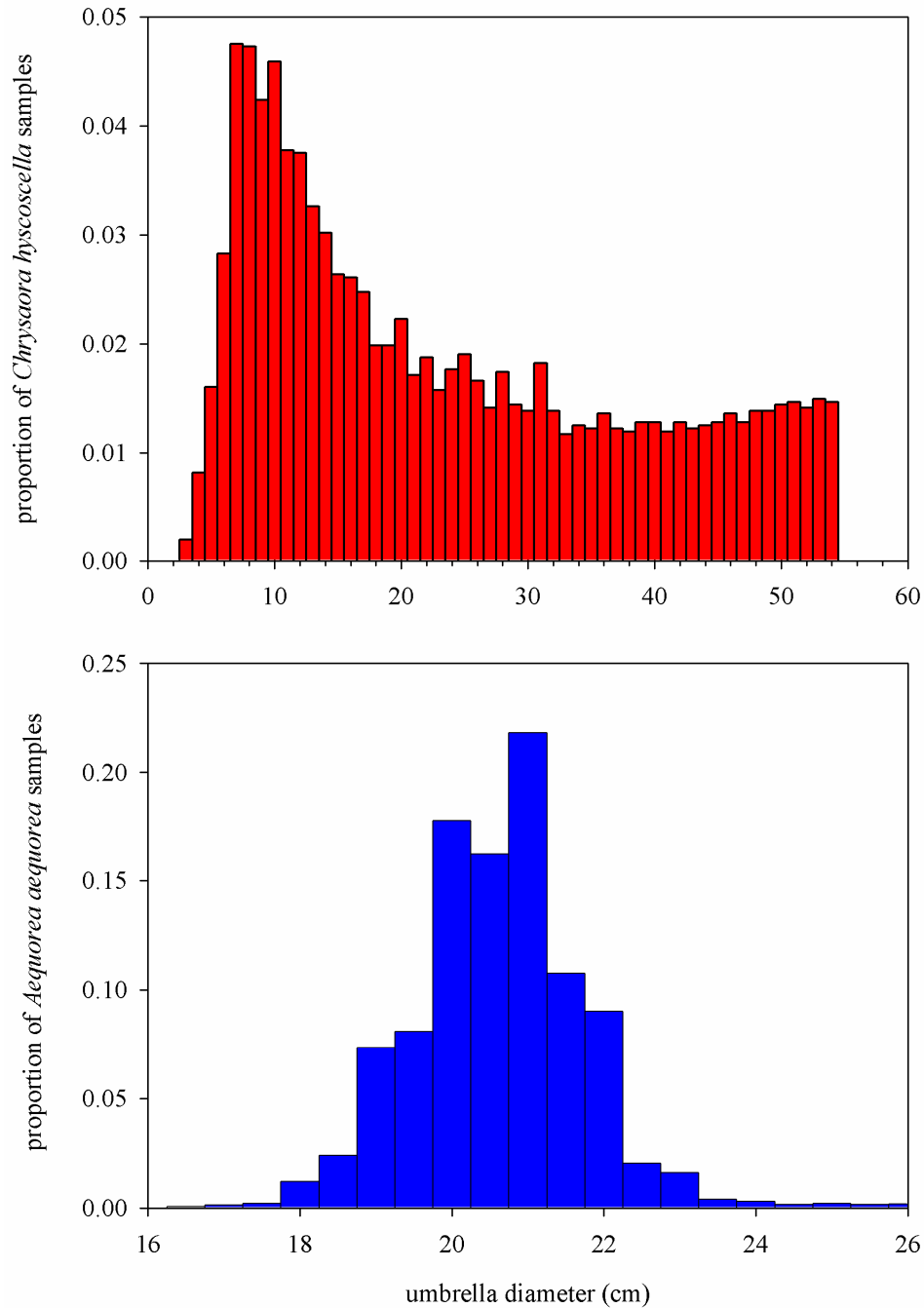


Figure 9.3 Measurements of jellyfish umbrella diameter (cm), note differing scales and that the *Aequorea aequorea* values are converted from inner disk measurements using the equation: umbrella diameter = 0.95 x inner disk measurement + 14 (Buecher et al. 2001).

The TS for each size class was calculated using the wet weight and the relationship determined in Section 8.4.3 (equation 17). The resulting TS distribution was then transformed into a TS per kg distribution using equation 12 (Section 7.5). For each species, weighted TS per kg values were calculated in order to reflect the entire mass distribution as follows:

$$\text{TS per kg}_{\text{weighted}} = 10 \log_{10} \left| \frac{\sum_{i=1}^m n_i 10^{\text{TS per kg}_i / 10}}{\sum_{i=1}^m n_i} \right| \quad (18)$$

where the summation is over each class  $i$  containing  $n_i$  medusae with TS per  $\text{kg}_i$  and  $m$  size classes (shown in Figure 9.3,  $m = 20$  for *A. aequorea* and  $m = 52$  for *C. hysoscella*).

### Clupeids

Total Length TL (in cm) to Target Strength TS relationships were utilised to convert the integrated acoustic data for fish schools to density estimates of the commercially important pelagic species. The most up to date mass–TS relationships for anchovy and pilchard have been determined by *in situ* single target detections of fish in South African waters (Barange et al. 1996) and are beginning to be used for fisheries biomass estimates there.

$$\text{anchovy: } \text{TS}_{\text{dB/kg}} = -12.15 \log_{10} \text{TL} - 21.12 \quad (19)$$

$$\text{pilchard: } \text{TS}_{\text{dB/kg}} = -14.90 \log_{10} \text{TL} - 13.21 \quad (20)$$

No relationship has been determined for round herring, as this is not a heavily fished species (generally caught through bycatch, Boyer and Hampton 2001). Since the  $S_v$ –difference discrimination tool developed in Section 8.5 is unable to distinguish between these three clupeid species, it would be more robust to use a single TL–TS relationship to convert acoustic data into fish densities; rather than making assumptions on the relative abundance of the three species and attempting to use a conversion based on some combined measure. As my interest lies in evaluating the importance of medusae (relative to fish) to the Benguela Ecosystem, I do not want to underestimate the biomass of fish and thus artificially inflate the perceived importance of medusae; therefore I chose to use the anchovy relationship, which would give a greater biomass estimate for fish. The weighted mean total length for clupeids was  $\text{TL} = 10.63$  cm. The distribution of TS per kg values weighted by the mass–frequency distribution was then calculated using equations 12 and 19 (Section 7.5); if equations 12 and



20 were used instead the estimated biomass of clupeids would be 3.3 times lower.

#### Horse mackerel

Barange et al. (1996) also determined the following TS per kg to size relationship for horse mackerel.

$$TS_{\text{dB per kg}} = -15.44 \log_{10} TL - 7.75 \quad (21)$$

The weighted mean total length for horse mackerel was  $TL = 12.41$  cm and the weighted TS per kg was  $-24.64 \text{ dB.kg}^{-1}$ . However, the length–TS relationship currently applied for horse mackerel biomass estimation in Namibia has been based on the North Sea herring relationship (Axelsen et al. 2003):

$$TS_{\text{dB}} = 20 \log_{10} TL - 72 \quad (22)$$

If this herring relationship were implemented here, in combination with a transformation of the horse mackerel length distribution into a mass distribution using the following relationship (equation 23) (Naish et al. 1991), then the subsequent biomass estimates for horse mackerel would be 5.52 times greater.

$$\text{Mass (wet weight) in kg} = 7.8 \times 10^{-9} (10 TL)^{3.11} \quad (23)$$

#### Cape hake

Although no TL–TS relationship has been determined for Cape hake, measurements of TS per kg have been reported (Figure 9.4): for small Cape hake,  $TL = 11.86$  cm, the  $TS \text{ per kg} = -32.07 \text{ dB.kg}^{-1}$  and this was the maximum of all TS per kg values calculated; for large Cape hake,  $TL = 15.60$  cm,  $TS \text{ per kg} = -33.41 \text{ dB.kg}^{-1}$ ; and the minimum  $TS \text{ per kg} = 37.04 \text{ dB.kg}^{-1}$  was found for Cape hake with  $TL = 15.16$  cm (Barange et al. 1994). The weighted mean total length for Cape hake sampled in the Benguela during 2003 was  $TL = 19.22$  cm and therefore outside the range of measurements reported by Barange et al. (1994). I chose to use the mean TS per kg value =  $-32.95 \text{ dB.kg}^{-1}$ . If the extreme published TS values had been used rather than the mean, then the Cape hake biomass estimates produced here would either have increased by 2.56 times (to 4.3 MT) or decreased by 1.20 times (to 1.4 MT).

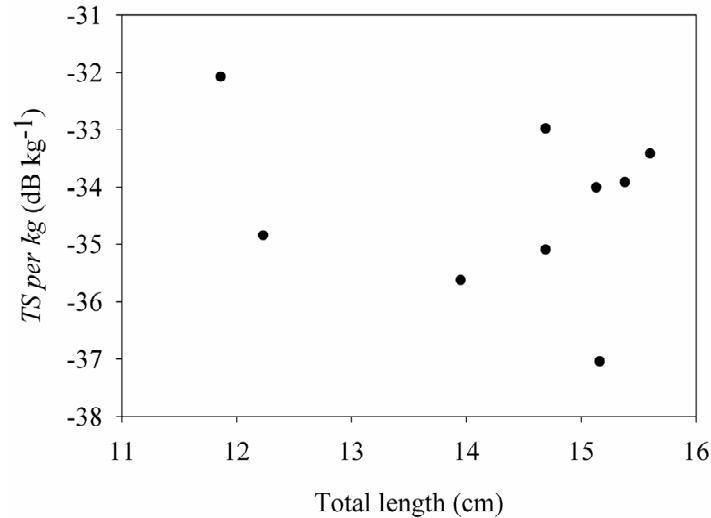


Figure 9.4 TS per kg vs total fish length for Cape hake (Barange et al 1994).

*Acoustic data filtering (species identification)*

Acoustic data were processed in *SonarData Echoview* (Version 3.25.55.14), as described in Section 8.5.2, and echoes due to jellyfish were found through:

1. beam calibration
2. temporal and spatial matching of echoes between beams;
3. noise estimation and removal (including exclusion of acoustic blind zones here considered to consist of the upper 10 m (draft zone plus near field) of the water column and the 5 m immediately above the seabed that may hold seaweeds and sediment in suspension);
4.  $S_v$  data smoothing (i.e. 5 x 5 convolution);
5. construction of  $S_v$ -difference echograms for all possible combinations:  $S_{v18} - S_{v38}$ ;  $S_{v18} - S_{v120}$ ;  $S_{v18} - S_{v200}$ ;  $S_{v38} - S_{v120}$ ;  $S_{v38} - S_{v200}$ ; and  $S_{v120} - S_{v200}$ ;
6. partition of fish schools and dense zooplankton aggregations from weak acoustic scatterers such as jellyfish;
7. allocation of echoes to jellyfish species and finfish groups using binary bitmasks based upon the restricted (67% confidence interval)  $S_v$ -difference data filters (Section 8.5.3).

Strong echoes, due to fish and dense zooplankton swarms (e.g. krill), have the potential to bias greatly any acoustic based estimate of medusa biomass; therefore, dense fish schools and/or zooplankton aggregations were identified

(step 6), prior to integration of echoes due to jellyfish, using the *Schools detection module* in *Echoview* with the settings proposed by Lawson et al. (2001) and detailed in Table 8.5 (Section 8.5.2). At step 7 (above) the two jellyfish species (*A. aequorea* and *C. hysoscella*) are detected in the  $S_v$ -difference data once school detections are removed; the two finfish groups (horse mackerel/Cape hake and clupeids) were identified in the partitioned schools-only data using the appropriate  $S_v$ -difference data filters (Section 8.5.3).

#### *Biomass estimation*

Once  $S_v$ -difference bins had been allocated to species the resulting species-specific binary bitmasks (created in *Echoview*, where a 1 indicates the presence of the species of interest) were overlaid upon the noise corrected 38 kHz data. The resulting species-specific echoes were then integrated along each nautical mile of the cruisetrack to produce along-track density estimates.

#### *Statistical analysis*

At this point, a decision must be made as to the method by which along-track density estimates are scaled up to survey area wide biomass estimates. If transects can be considered independent of each other then the traditional method of Jolly and Hampton (1990) may be used, whereby the mean density over the survey area (*stratum*) is calculated simply as the weighted mean of all transect estimates (weighted by transect length) and the biomass is therefore equal to the weighted mean density multiplied by area surveyed. The common procedure to validate the assumption of independence is to examine the degree of spatial autocorrelation by inspection of the autocorrelation function through plots of correlation against distance between points (Figure 9.5).

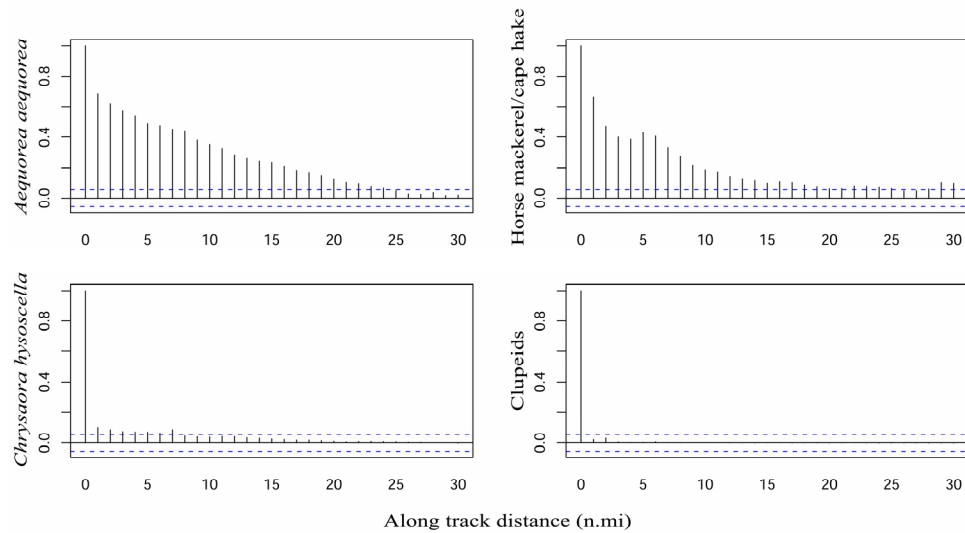


Figure 9.5 Autocorrelation functions for medusae and fish, values that fall within the dashed blue lines are not significantly different to zero.

By this method it is apparent that the jellyfish data and the horse mackerel/Cape hake data contain significant spatial autocorrelation: the autocorrelation distance,  $d$ , for *A. aequorea* was 25 n.mi, for *C. hysoscella*  $d = 8$  n.mi, and for horse mackerel/Cape hake  $d > 30$  n.mi. Therefore to force the transects to be independent, each transect would need to be shortened so that there was at least the autocorrelation distance between transects. In total, >30% of the *A. aequorea* and horse mackerel/Cape hake data would be lost by this process. Therefore a technique that is able to incorporate spatial autocorrelation would be more suitable.

Geostatistical techniques have been applied to some fishery survey acoustic data; however, highly variable distributions such as those characterising jellyfish are not reconstructed successfully by standard linear geostatistics (Rivoirard et al. 2000). The Bayesian method of *MaxEnt* (maximum entropy) image reconstruction has been demonstrated to reproduce successfully the highly skewed distributions of Antarctic krill (*Euphausia superba*) densities from acoustic transect data and the technique is considered suitable for biomass estimation (Brierley et al. 2003). The *MaxEnt* method is used here to reconstruct the most likely distribution of jellyfish species and fish groups in the area of the Benguela surveyed. Analyses were performed using the *MemSys5 Quantified Maximum Entropy* package (Gull and Skilling 1999). *MaxEnt* is founded upon Bayes' theorem:

$$\Pr(h|k) = \frac{\Pr(k|h) \Pr(h)}{\Pr(k)} \quad (24)$$

where  $\Pr(h|k)$  is the posterior probability for the reconstruction of densities  $h$  given the acoustic data estimates  $k$ ,  $\Pr(h)$  is the *prior* probability given to the species/group distribution of densities,  $\Pr(k|h)$  is the *likelihood* (gaussian in this case) of the data given the reconstruction, and  $\Pr(k) = \sum_h \Pr(h,k)$  is the *evidence* term. The aim is, by iteration, to find the image for which the probability of the posterior distribution is maximised. In order to find the most suitable reconstruction the algorithms internal to *MaxEnt* find a balance between under- and over-fitting models. If a given reconstruction is an underfit then the *posterior* probability is penalised through a low *likelihood*  $\Pr(k|h)$ , whereas an overfit is penalised by the low entropy and thus low prior  $\Pr(h) \propto \exp(\alpha S(h))$ , where  $S(h)$  is the *entropy* of the distribution and  $\alpha$  is a monotonic scale constant. The *entropy* is calculated using the initial (chosen) estimates of density,  $m(x_i) = 0.5 \text{ kg n.mi}^2$ , for each  $1 \text{ n.mi}^2$  grid cell of the total  $33,710 \text{ n.mi}^2$  area (Figure 9.6), and the modelled estimates  $h(x_i)$  as follows:

$$S(h) = - \sum_{i=1}^{33,710} \left( h(x_i) - m(x_i) - h(x_i) \log \frac{h(x_i)}{m(x_i)} \right) \quad (25)$$

The final distribution of densities (with the highest *posterior* probability) can be considered to be that which is most consistent with the observations (i.e. has highest *likelihood* given the transect data), but is also as random as possible with regard to all other non-observed points in the survey area (i.e. has the greatest *entropy*) (Sivia 1996). The distribution with the most probable *posterior* probability is formulated directly from the data by *MaxEnt* through the estimation of the single unknown parameter  $\alpha$  (Skilling and Gull 1989). The most probable  $\alpha$  is determined automatically through the iterative modelling procedure that aims to explore the range of possible values of  $\alpha$ :  $h(x_i)$  is adjusted progressively and the associated *entropy* and *likelihood* and thus the *evidence* are computed (Sivia 1996). If the new reconstruction has more *evidence* (greater probability of obtaining the observed data) than the previous then the new  $\alpha$  is kept by the algorithm and perturbed to create a new candidate  $\alpha$ , when no more suitable  $\alpha$  can be found the algorithm is said to have converged and the most probable distribution has been identified. The confidence intervals on the *MaxEnt* reconstructed densities are computed through sampling from the

*posterior* distribution and evaluation of the standard deviation for each inferred density value.

#### 9.4. Results

The weighted TS per kg values were in the order of  $-50 \text{ dB kg}^{-1}$  for medusae and  $-30 \text{ dB kg}^{-1}$  for fish (Table 9.1). Between jellyfish species and also between fish groups the mean along-track densities (determined from acoustic data) were contrasting (Table 9.1); however, due to the great patchiness in animal distributions (Figure 9.6) these average values will not be the most likely densities encountered through random sampling, peaks and troughs are more common for all species with the possible exception of *Chrysaora hysoscella*. The *MaxEnt* modelled distributions (reconstructions) of medusae and fish densities (Figure 9.6) should, and do, agree with the presence/absence of each species/group in the pelagic trawls (Figure 9.7).

| Species                     | TS per kg<br>( $\text{dB kg}^{-1}$ ) | Mean density<br>(tonnes $\text{n.mi}^{-2}$ ) |
|-----------------------------|--------------------------------------|--|
| <i>Aequorea aequorea</i>    | -50.55                               | 1278   |
| <i>Chrysaora hysoscella</i> | -50.35                               | 55   |
| Clupeids                    | -33.60                               | 23   |
| Horse mackerel              | -24.64                               | 33   |
| Cape hake                   | -32.95                               | 133  |

Table 9.1 Values of target strength (TS) per kg used to convert acoustic density estimates to biomass values. Also shown are mean and maximum densities for each species/group calculated from along transect acoustic data (binned into  $N = 1249$  nautical mile transect lengths) before smoothing with *MaxEnt*.

| Species                     | Maximum density <sup>b</sup><br>(kg m <sup>-3</sup> ) |                |              | Mean (SD) density (kg m <sup>-3</sup> ) <sup>b</sup> |                |                 |                 |                           |
|-----------------------------|---|----------------|--------------|--|----------------|-----------------|-----------------|---------------------------|
|                             |   |                |              | on station   |                | whole survey    |                 |                           |
|                             | pel<br>N = 64   | surf<br>N = 27 | dem<br>N = 2 | pel<br>N = 31  | surf<br>N = 11 | pel<br>N = 34   | surf<br>N = 17  | dem <sup>c</sup><br>N = 2 |
| <i>Aequorea aequorea</i>    | 3.73  | 12.93          | 4.33         | 0.87<br>(1.15)                                       | 4.65<br>(4.56) | 0.42<br>(0.88)  | 1.55<br>(3.27)  | 3.32<br>(1.43)            |
| <i>Chrysaora hysoscella</i> | 1.51  | 14.78          | 2.91         | 0.24<br>(0.57)                                       | 0.77<br>(1.14) | 0.02<br>(0.06)  | 2.00<br>(3.94)  | 1.84<br>(1.51)            |
| Clupeids <sup>a</sup>       | 0.26  | 30.94          | None caught  | <0.01<br>(<0.01)                                     | 0.05<br>(0.24) | <0.01<br>(0.03) | 0.63<br>(4.70)  | None caught               |
| Horse mackerel              | 4.34  | 1.05           | 0.66         | 0.24<br>(0.10)                                       | 0.07<br>(0.12) | 0.14<br>(0.74)  | 0.15<br>(0.31)  | 0.33<br>(0.47)            |
| Cape hake                   | 0.42  | 0.04           | 6.04         | 0.31<br>(1.23)                                       | None caught    | 0.03<br>(0.07)  | <0.01<br>(0.31) | 5.06<br>(1.39)            |

Table 9.2 Maximum and mean (on station at for the survey as a whole) and densities of each group calculated from trawled samples for each group (pel = pelagic, surf = surface dem = demersal) and by each gear type. Note: <sup>a</sup>the trawl statistics for clupeids are dominated by high sardine catches; <sup>b</sup>the maximum trawl densities are taken from the maximum of every N trawl fished, but to avoid skewing the mean densities toward the values at each 24-hr station - where repeated trawls were made - the pelagic and surface trawls on-station were averaged prior to calculation of the overall mean densities; <sup>c</sup>trawls were at separate stations.

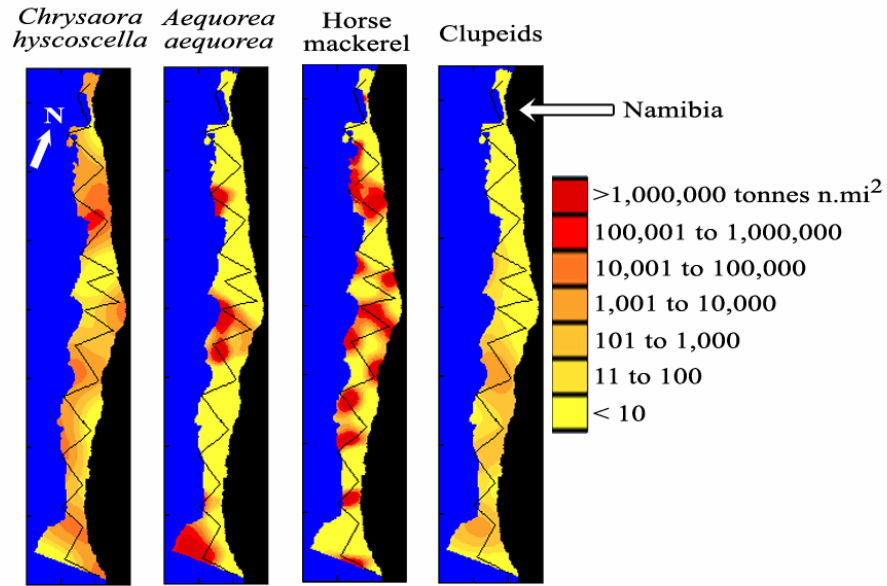


Figure 9.6 Densities (tonnes n.mi<sup>-2</sup>) of medusae (*Chrysaora hysoscella* and *Aequorea aequorea*) and fish (horse mackerel and clupeids: anchovy, sardine and round herring) in the northern Benguela. Note that the distribution of Cape hake is not shown as the map would be similar to that shown for horse mackerel, except the density at each point would be approximately 7 times greater.



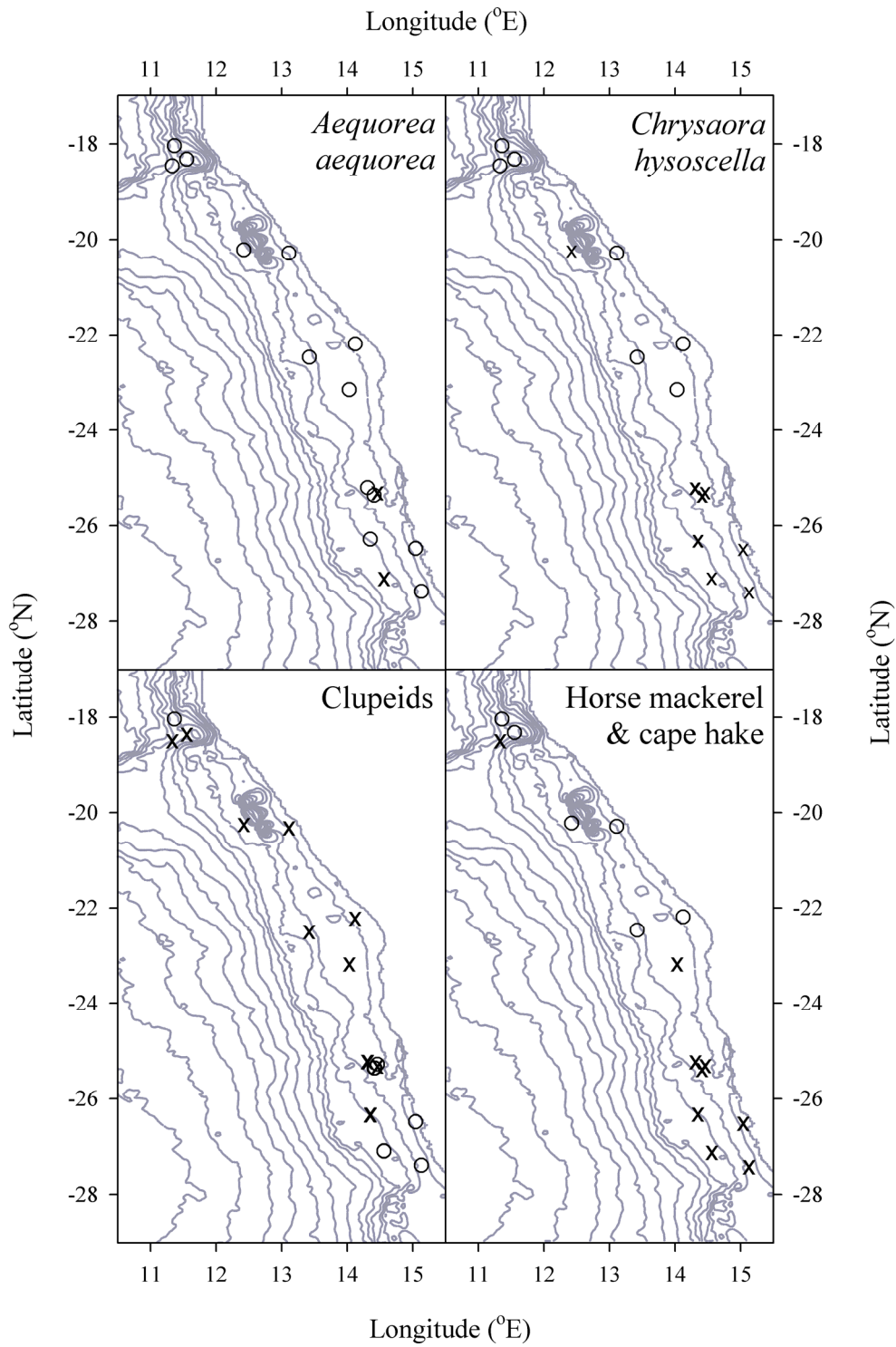


Figure 9.7 Presence (circles) and absence (crosses) by location in trawled samples of medusae (*Chrysaora hysoscella* and *Aequorea aequorea*) and fish (horse mackerel/Cape hake and clupeids: anchovy, sardine and round herring) in the northern Benguela. Note that either 2 or 3 samples were taken using the pelagic trawl at each location. Details of bathymetry in Figure 9.1.

The total biomass of medusae in the 33,710 n.mi<sup>2</sup> surveyed was estimated at 12.2 million tonnes, and was found to be greater than the estimated biomass of either fish (Table 9.3). Given that Cape hake are generally a demersal species and were found in high density ( $>5 \text{ g m}^{-2}$ ) in the demersal trawl only (Table 9.2) then the majority of detections by the horse mackerel/Cape hake acoustic data filter are most likely to be from horse mackerel. If we assume that the proportion of horse mackerel to Cape hake in the pelagic trawl (4.67:1 by mass) are representative of the entire survey area the most likely total biomass of each species is: horse mackerel ( $1.35 \times 82.36\% = 1.12 \times 10^6$  tonnes) and Cape hake ( $1.66 \times 17.64\% = 1.67 \times 10^6$  tonnes). These biomass values are consistent with current knowledge of the Namibian stocks (B. Axelsen, Institute of Marine Research, Bergen, personal communication, 2006). Although clupeids were found in low densities in the trawl samples, the total biomass estimate of ~1 thousand tonnes is so low that it sheds doubt upon the multifrequency discrimination technique for this group, which is perhaps not surprising given the lack of data for these species and the use of limited multifrequency data (Section 8.5.1). If we consider all schools that were isolated by the schools detection module to be either Cape hake, horse mackerel or clupeids then we may further consider all schools that were not identified as Cape hake or horse mackerel to be most likely clupeids. Analysis of these data suggest that the total biomass of clupeids could in fact be 0.77 million tonnes, which would agree well with current knowledge of the Namibian stock (B. Axelsen, Institute of Marine Research, Bergen, personal communication, 2006).

| Species                     | Total biomass<br>(10 <sup>6</sup> tonnes) | CV<br>(%) | Mean density<br>(tonnes n.m <sup>-2</sup> ) |
|-----------------------------|---|-----------|---|
| <i>A. aequorea</i>          | 12.133                                    | 518       | 413   |
| <i>C. hysoscella</i>        | 0.026                                     | 611       | 0.792                                       |
| Clupeids <sup>a</sup>       | 0.001                                     | 806       | 0.008                                       |
| Clupeids <sup>b</sup>       | 0.77                                      | 466       | 22.9  |
| Horse mackerel <sup>c</sup> | 1.36                                      | 497       | 33.2  |
| Cape hake <sup>c</sup>      | 9.46                                      | 499       | 49.6  |

Table 9.3 Bayesian *MaxEnt* estimates of total biomass and associated coefficient of variation (CV), and mean densities for: *Aequorea aequorea*; *Chrysaora hysoscella*; horse mackerel (*Trachurus trachurus capensis*); Cape hake (*Merluccius capensis*); and clupeids (consisting of round herring *Etrumeus whiteheadi*, anchovy *Engraulis capensis*, and sardine *Sardinops ocellatus*). Notes: <sup>a</sup> estimates arise from detections distinguished using Sv-difference data; <sup>b</sup> these estimates result from an integration of all schools that were not distinguished as either horse mackerel or Cape hake; <sup>c</sup> these estimates for horse mackerel and Cape hake consider all detections by the Cape hake/horse mackerel filter to be due completely to one of either species

## 9.5. Discussion

Previously, the biomass of jellyfish in the northern Benguela has been assessed using bycatch from paired BONGO net catches (57 cm mouth openings) of the upper 50 m of the water column during the South West African Pelagic Egg and Larvae Surveys (Fearon et al. 1991). The biomass estimates of Fearon et al. (1991) refer to a survey area of 47,793 n.mi<sup>2</sup> (1.42 x the area considered here), from 0 to 70 miles offshore, but with the same northern and southern bounds (17 °15'S – 28°38'S), during January–March 1982-1989 (late summer/early autumn, all months/years combined), and are therefore not directly comparable to those estimates calculated here for water column integrated data during August (late winter/early spring) 2003 and to a lesser extent offshore (from 0 to approximately 50 miles offshore). If the estimates of Fearon et al. (1991) are reduced, to account for the areal mismatch with my survey area, then the estimates are: for *Chrysaora hysoscella* 19.0 x 10<sup>6</sup> tonnes and for *Aequorea aequorea* 6.9 x 10<sup>6</sup> tonnes, giving a total biomass of 25.9 x 10<sup>6</sup> tonnes. I have

found only 46.8% of this total, with a much lesser biomass of *C. hysoscella* and a greater biomass of *A. aequorea*: 0.1% and 176% of the Fearon et al. (2001) values respectively. Although these values are quite different, the total is of the same order of magnitude, suggesting that the biomass estimates calculated here are not infeasible. Indeed, when either my estimates or those of Fearon et al. (2001) are compared to recent calculations for the Black Sea both appear possibly conservative: the total surface area of the Black Sea is 123,500 n.mi<sup>2</sup> and was estimated to contain up to 270–450 x 10<sup>6</sup> tonnes of *Aurelia aurita* during the late 1980s, in addition to other gelatinous species such as *Rhizostoma pulmo* (Mills 2001), which equates to densities between 4 (Fearon's biomass estimate per n.mi<sup>2</sup> divided by the minimum Black Sea biomass estimate per n.mi<sup>2</sup>) and 15 (my biomass estimate per n.mi<sup>2</sup> divided by the maximum Black Sea biomass estimate per n.mi<sup>2</sup>) times the estimates for the Benguela.

Some of the difference between the jellyfish biomass estimates found in this study and those calculated by Fearon et al. (2001) may be explained by the difference in depth of sampling, particularly so for *C. hysoscella*; aggregations of this medusa were found through surface trawling to be 100 times greater in the surface (0–20 m) layer that the echosounder is unfortunately blind to (Tables 9.1 and 9.2). The remaining difference may be simply explained by the great inter- and intra-annual variability found in jellyfish abundance (Venter 1988). The estimates of fish biomass calculated here (Section 9.3, Table 9.3) are consistent with present knowledge of the state of the Benguela Sea stocks (Boyer et al. 2001; Boyer and Hampton 2001; Cury et al. 2005): in deeper waters, >500 m, horse mackerel and Cape hake form the greatest biomass in fisheries landings at approximately 0.5 x 10<sup>6</sup> tonnes per annum anchovy are commercially extinct, while round herring and sardine catches are fluctuating between 1000 and 25000 tonnes per annum.

The high coefficient of variation associated with each total biomass estimate calculated using *MaxEnt* indicates the great uncertainty in the estimates due to the relatively large proportion of cells within the survey area that are off transect and thus non-sampled (Table 9.3). While this suggests that the Bayesian estimate is highly uncertain, the traditional Jolly and Hampton (1990) technique does not explicitly include this variation and as such produces lower

estimates of variance. A greater sampling intensity over the survey area would improve biomass estimates via the *MaxEnt* technique.

The distribution of *A. aequorea* and *C. hysoscella* has also been assessed by surface observations (Sparks et al. 2001) and BONGO samples (50 cm mouth openings) (Pagès and Gili 1991; Pagès 1992) (Section 1.11.2). Significant ( $P < 0.05$ ) latitudinal and longitudinal gradients were evident in the medusa abundance data reported by Sparks et al. (2001), which supports our decision to use *MaxEnt* in order to accommodate the autocorrelation expected in the data. Sparks et al. (2001) found that, during August/September 1999, the mean abundance in the surface layer of *A. aequorea* was greatest offshore (>150 m depth), while *C. hysoscella* abundance was greatest inshore (< 150 m depth). Pagès (1992) also considered a spatial segregation between jellyfish species with *A. aequorea* a shelf edge species and *C. hysoscella* a coastal–shelf species. It has been suggested that young *C. hysoscella* are released from polyp beds in the north during the winter and are then advected southward by coastal currents (Sparks et al. 2001 and references therein). These observations are consistent with the distribution maps produced here, which show higher *A. aequorea* abundance in patches at the most offshore limit of the survey area and a general peak in *C. hysoscella* abundance in the north and in some inshore areas (e.g. Walvis Bay and in the far south of the survey area); those peaks in *C. hysoscella* abundance off Lüderitz (27°S) may also be explained by advection of medusae away from the upwelling zone.

The distribution maps (Figure 9.6) rely fully on the validity of the *in situ* discrimination tool, which allocated echoes to species based upon reference acoustic data and corresponding pelagic trawl samples (Section 8.5). The remotely controlled multisampler system that operated the trawl enabled discrete samples from the scattering layers in the water column (Section 8.5.2). Jellyfish acoustic–reference samples at each station were selected to avoid fish contributions. The acoustic measurements used for filter construction are therefore not likely to have been biased by fish echoes. Although the medusae often feed within relatively dense aggregations of zooplankton, the target strengths of these groups are several orders of magnitudes weaker than the target strengths of both jellyfish species (possible bias to jellyfish TS <1 dB, Brierley et al. 2005), and their contribution to the acoustic estimate of medusa

biomass is small, particularly so relative to the variability in the biomass estimate due to TS calculations: for an average *A. aequorea* and *C. hysoscella* medusa variability in TS estimates are  $\pm 4.4$  dB and  $\pm 6.7$  dB, and therefore a factor of  $10^{0.44}$  and  $10^{0.67}$  respectively in the biomass estimate (Section 8.4.4). The reliability of the jellyfish biomass estimates produced here would be greatly improved if the variability in the TS estimates could be reduced; further research is required in this area.

Given the above caveats on the great variability in the jellyfish and finfish biomass estimates we can make the following important observation on the state of the Benguela ecosystem: the biomass of jellyfish in the coastal and shelf area of the northern Benguela Sea, an important nursery area for commercially fished clupeids, Cape hake, and horse mackerel, appears to be greater than the total biomass of these stocks in the area. These stocks have been overexploited in the past and may now be suppressed by the high abundance of predatory medusae. Medusae are opportunistic feeders, consuming fish larvae and their zooplankton prey, so the possible impact on the Benguela pelagic fish stocks is great (Fearon et al. 1991). The potential for top-down control does exist and should be considered as part of any further work on the state of the Benguela ecosystem and its fisheries.

## **Chapter 10**

### **General discussion and summary**

## 10. General discussion

At the outset of my research, very few studies had been able to statistically quantify the proposed impacts by medusae upon fish populations (Purcell and Arai 2001, and references therein), and no work had yet shown a clear link at the scale of a regional sea. Regular outbreaks in biomass of medusae in the Mediterranean had been suggested to arise from climatic fluctuations (Goy et al. 1989); however, no study had shown a clear correlation between jellyfish abundance and a regional atmospheric weather pattern, such as the North Atlantic Oscillation, and no mechanism had been proposed to link jellyfish abundance to climatic change. Much of the lack of progress in gelatinous zooplankton ecology can be explained by the particular problems encountered when traditional (crustacean focused) zooplankton sampling methods are applied to fragile, jelly-like creatures. Zooplanktonologists are in dire need of a tool that will allow rapid surveying of gelatinous zooplankton over wide-ranging areas. In this dissertation, I have attempted to address the theories outlined above (concerning climatic effects on jellyfish abundance, Chapters 2–4, and possible impacts by medusae upon the ecosystem, Chapters 5–6) and develop a multifrequency acoustic technique to estimate the biomass of medusae *in situ* (Chapters 8–9).

### *Summary of results*

Through regression analyses, I have related the abundance of medusae in the North Sea to climatic fluctuations, as encapsulated by the North Atlantic Oscillation Index (NAOI) (Chapter 2). I proposed that the relationship between NAOI fluctuations and jellyfish abundance is modulated by hydrographic conditions that vary across the North Sea (Chapter 3). Thus, the strength of the mechanisms (proposed in Chapter 2 and refined in Chapter 3) linking jellyfish abundance to the climate may also vary regionally. I attempted to evaluate the likely importance of the various mechanisms using a modelling approach, and found that much of the difference between regions may stem from oceanographic changes that can alter the distribution of particular zooplankton species (Chapter 4). This research has led the field regarding jellyfish population responses to climatic fluctuations and has been followed by studies showing similar links throughout the northern hemisphere (see section below).



The possible impacts of medusae on the pelagic ecosystem are explored in Chapters 5 and 6, where contrasting relationships are reported between medusae and herring and between medusae and whiting. The 0-group recruitment of North Sea herring may be detrimentally impacted by medusae through competition for prey or by direct predation upon larvae; however, other explanations, such as environmental forcing of both herring recruitment and jellyfish abundance, remain possible (Chapter 5 and see following section). In Chapter 6, a commensal relationship, whereby whiting shelter under the umbrella and among the tentacles of jellyfish, is shown to improve the survival of 0-group whiting through the provision of refugia from predation.

The automated acoustic identification of species, regarded by many as the ‘holy grail’ of marine acoustic science (Horne 2000), would solve the sampling problem facing gelatinous zooplanktonologists. In progress towards this goal, I have measured the density and speed of sound within jellyfish tissues, which may be used to parameterise acoustic models of sound scattering by jellyfish (Section 8.2); I have improved *Target Strength* estimates for jellyfish and determined a species-independent *Target Strength*–mass relationship (Sections 8.3 and 8.4), and developed an *in situ* multifrequency discrimination tool that can separate echoes due to medusae from those from fish (Section 8.5). In Chapter 9, I have demonstrated how these acoustic techniques can be applied to estimate the biomass of jellyfish and I have produced the world’s first acoustic-based estimate of jellyfish biomass in the Namibian Benguela Sea.

*Recent studies relating jellyfish populations to climatic changes and a life-stage analysis of North Sea herring survival*

Chesapeake Bay (North Atlantic Oscillation) (Purcell 2005).

During the 1960s, *Chrysaora quinquecirrha* medusae were so abundant in Chesapeake Bay that a U.S. congressional act was passed to provide funding in the period 1968–1972 for research on their ecology. Numbers of medusae, from visual counts, in summer have been significantly negatively correlated ( $R^2 = 0.576$   $P < 0.01$ ) with discharge from the Susquehanna River in the 6 month period between January and June from 1960 to 1986 (Cargo and King 1990). Production of ephyrae is greatest at salinities between 9 and 25 ppt, therefore in years of low precipitation, when river discharge is reduced and salinities rise,

large populations of medusae develop on the Bay (Purcell et al. 1999). The North Atlantic Oscillation Index was significantly inversely correlated with medusa numbers in summer from 1960 to 1995, at three deep stations in the central region of Bay (Purcell and Decker 2005). The 1960s were in a cool, dry, regime, which shifted with Hurricane Agnes in 1972 to a warm, wet regime. Medusae were extremely abundant in the 1960s, when NAOI was generally negative, and in low abundance after 1972, when the NAOI was generally positive. .

Ligurian Sea, Mediterranean (North Atlantic Oscillation) (Molinero et al. 2005). Through principal component analysis, the interacting climate patterns of the North Atlantic Ocean (as characterised by the indices of the North Atlantic Oscillation, East Atlantic Pattern, Gulf Stream, East Atlantic Western, Russian Pattern) have been linked to changes in the abundance of jellyfish (Hydrozoa *Liriope tetraphylla*, *Solmundella bitentaculata*, and *Rhopalonema velatum*; Scyphozoa *Pelagia noctiluca*; Siphonophora, *Abylopsis tetragona* and *Chelophyes appendiculata*; and Ctenophora *Pleurobrachia rhodopis*) and copepods (*Centropages typicus*, *Temora stylifera*, *Acartia clausi*, *Oithona* spp., and *Oncaea* spp.) in Villefranche Bay (Ligurian Sea) between November 1966 and December 1993 (identified in weakly vertically hauled samples from 80 m depth to the surface of the Bay). The 1<sup>st</sup> principle component of the North Atlantic climate was shown to change in synchrony with regional changes in the climate of the Ligurian Sea (mean monthly values of: air and sea surface temperature; atmospheric pressure; and precipitation) and local changes at Villefranche Bay (mean monthly values of: air and sea temperature; atmospheric pressure; irradiance; and precipitation). An increase in jellyfish outbreaks during the 1980s coincided with high positive anomalies observed in climate at each spatial scale analysed. Long-term water temperature anomalies (during December to March at 1, 20, 50, and 75 m depths) appeared to play a key role in the relationship between copepods and jellyfish: warm water temperature, dry and calmer conditions were proposed to effect jellyfish abundance directly through water column stability, while copepod abundance was suggested to response indirectly to warm temperatures through increased predation pressure by jellyfish. Copepods form the main prey item for small

pelagic fish (sardines and anchovies) in the Mediterranean, thus an abundance of jellyfish could have a cascading effect on the trophic structure of the ecosystem and further research should be directed at this possibility.

#### Tropical western Pacific (El Niño)

The strong 1997-98 El Niño event may have caused the collapse in *Mastigias* sp. (Scyphozoa) biomass in Jellyfish Lake, Palau (7°N 134°E) (Dawson et al. 2001). Jellyfish in the lake were estimated to number 1.8 million in 1996. A dramatic decline was noticed in autumn, 1998, and medusae had virtually disappeared by March 1999. The unusually warm temperatures (reaching 35.2 °C) appear to have caused a great mortality of young medusae and a loss of zooxanthellae (bleaching) from the polyps, preventing strobilation. The density of *Mastigias* medusae (>2 cm umbrella diameter) has been negatively correlated with temperature anomalies in the mixolimnion layer (mixed water between 0–12 m deep) ( $R = -0.88$   $P \leq 0.02$   $N = 55$ ) and positively associated with El Niño Southern Oscillation (ENSO) anomalies three months later ( $R = -0.89$   $P \leq 0.05$   $N = 55$ ). So the tightly coupled relationship between temperature in jellyfish lake and ENSO fluctuations, the zooxanthellae–*Mastigias* photosymbiosis, combined with the temperature dependent survival of the medusae creates a rapid feedback mechanism by which jellyfish may be sensitive indicators of ENSO fluctuations in the tropical western Pacific (Martin et al. 2005).

#### The Bering Sea (North Pacific Decadal Oscillation)

Between 1990-2000, the combined biomass of *Aequorea aequorea*, *Cyanea capillata*, and *Chrysaora melanaster* increased ten-fold, in the area of an important fishery, concurrent with changes in atmospheric pressure patterns reflected in the North Pacific Decadal Oscillation Index (Brodeur et al. 1999). Brodeur et al. (2002) proposed that the increase in jellyfish might be due to a release from competition with planktivorous forage fishes. Since 2001 the population has crashed and as, as yet, there is no explanation; however, the last published biomass estimate (for the year 2003) was circa  $60 \times 10^9$  tonnes and greater than any estimate between 1975 and 1990 (no sampling between 1976 and 1978) (Hunt and Drinkwater 2005).

North Sea herring survival

A detailed study of the interannual variability in North Sea herring year class strength split the population into six stages: spawning stock biomass; egg production; larvae; fish with 0– 1– and 2–winter rings in the otolith (0–wr, 1–wr and 2–wr) (Nash and Dickey-Collas 2005). The authors concluded that the strength of anomalous year classes during 1976–2000 was determined by mortality inflicted between the pelagic larval and juvenile stages, which is the period proposed in Chapter 5 in which an impact by jellyfish on herring survival may be imposed. They suggested that the survival of young herring could be limited by *Calanus finmarchicus* abundance however, no negative effect on the survival of herring was observed during 1996–2000 when *C. finmarchicus* abundance was low. Winter (January–March) sea bottom temperatures (SBTs) were correlated with herring life stage abundance: a positive correlation between SBT and larval abundance was found (<10 mm length in the northern North Sea between September and October and <11 mm in the southern North Sea between December and January) ( $R = 0.68$ ,  $P < 0.01$ ); no significant relationship was found with 0–wr abundance ( $R = -0.47$ ,  $P = 0.67$ ); and a significant negative correlation was found with 1–wr abundance ( $R = -0.54$ ,  $P < 0.01$ ). So cold years may result in lower abundance of larvae, have no effect on 0–group abundance (upon which I have suggested jellyfish may impact, Chapter 5), but increase the number of 1–group recruits. No link between the NAOI and the abundance of any herring life stage, or between the NAOI and either *C. finmarchicus* abundance or SBT, was found.

Although no direct link has been found between jellyfish abundance and SBT, jellyfish were found in highest abundances during 1977–1979 when the North Sea was in a cold biological period (Section 2.5). The modelled probability of capture of jellyfish has been significantly correlated with SBT (Chapter 4), suggesting that in cold years jellyfish (*Aurelia aurita*, *Cyanea lamarckii* and *C. capillata*) are more widely distributed in most areas of the North Sea (north and east of Scotland, east of Shetland, and west of northern Denmark), with the exception of *C. capillata* pr(capture) west of northern Denmark which was positively correlated with SBT.

The results of the study of Nash and Dickey-Collas (2005) imply that of, the mechanisms suggested in Chapter 5, mechanism 2 (*Correlations describe*

*coupled trends that are a result of NAO-driven environmental change*) is unlikely given that no significant correlation was found between the NAOI and any life stage of herring. The lack of significant correlation between *C. finmarchicus* and the abundances of each herring life stage also lends doubt to mechanism 4 (*The association between herring and jellyfish is the result of more widespread changes in the North Sea ecosystem, e.g. plankton community change or the 'Gadoid outburst', possibly due to the 'Great Salinity Anomaly'*); however, the significant correlations between SBT and abundance of either herring larvae or 1-wr may support this mechanism since the incursion of the Great Salinity Anomaly resulted in a cooling of the North Sea. Mechanisms 1 (*The abundances of A. aurita and C. capillata are high during the period of lowest herring SSB due to the release of jellyfish from competition with herring. Herring residual survival is thus lower than expected because at low herring stock and high jellyfish abundances the possible competition and predation impacts of jellyfish are greatest.*) and 3 (*NAO-mediated possible impact by jellyfish on herring survival*) are entirely possible given the new study. Given the possible importance of SBT to herring and its link to the distribution of jellyfish mechanism 3 may be the most likely explanation for the correlations found between jellyfish abundance and larval herring survival.

#### *Implications of my research and recommendations for future research*

Jellyfish may serve as sensitive indicators of ecosystem-wide responses to climatic fluctuations. My work linking jellyfish abundance to fluctuations in the North Atlantic Oscillation Index (NAOI) (Chapters 2–4) has been supported by scientists studying jellyfish abundance in American coastal waters (Purcell and Decker 2005) and the Mediterranean Sea (Molinero et al. 2005), indicating that jellyfish populations across the Atlantic are influenced by NAOI-driven environmental change. I have demonstrated the importance of jellyfish in the pelagic ecosystem and their ability to impact both positively and negatively on the survival of commercially important fish stocks (Chapters 5 and 6). This information should be of interest to fisheries managers, particularly given the present drive towards ecosystem-based management (Cury et al. 2005). A forecast of the NAOI for the coming winter (2005/06), by the UK Meteorological Office ([www.met-office.gov.uk/research](http://www.met-office.gov.uk/research)), has suggested that

the index will be at its lowest level for a decade (-1.1, standard deviation 1.0). A low index would result in jellyfish abundance in 2006 being: high west of Denmark, east of Scotland, and in Chesapeake Bay; and low in the Ligurian Sea and north of Scotland, and may favour the survival of whiting over herring in the North Sea.

The multifrequency acoustic technique developed in Section 8.5 presents a real possibility for surveying jellyfish biomass rapidly over extensive areas. This method can be incorporated into the current routine acoustic surveys carried out to assess fish biomass in many locations worldwide (e.g. the herring larval surveys of the North Sea) and offers a cost-effective approach to monitor jellyfish biomass. Outbreaks of jellyfish often occur without forewarning, simply because jellyfish samples are not collected frequently enough (CIESM 2001); these outbreaks should be easily identifiable from routine acoustic surveys, and may even be predictable from preceding climatic fluctuations.

Further research should be conducted in order to determine whether the mechanisms proposed in this thesis linking jellyfish abundance to climatic fluctuations are correct (Chapters 2–4). The multifrequency acoustic technique should be developed further to reduce variability in the biomass estimate, particularly with regard to Target Strength (TS) and the characteristic frequency response ( $S_v$ -difference) (Chapter 8). A greater range of frequencies would improve the discriminatory power of this method and more species should be studied to verify the species-independent relationship for TS determined in Section 8.4. The biomass of jellyfish should be monitored using data from routine acoustic surveys; for the North Sea, data arising from the current and historic ICES herring larvae surveys could be used to test the relationships described in this dissertation between jellyfish abundance, NAOI fluctuations, and herring and whiting 0-group survival (Chapters 2–6).

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### 13. Appendix A

Reproduced in this appendix are copies of the published papers, of which I am first author, that refer to the research described in this thesis. The papers are reproduced in chronological order, as follows:

Lynam, C. P., S. J. Hay, A. S. Brierley (2004). Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. *Limnol. Oceanogr.* 49(3): 637-643.

Lynam, C. P., A. S. Brierley, B. E. Axelsen (2004). Pinging down the food web: multi-frequency acoustic discrimination of jellyfish and fish. ICES report CM2004/R:06.

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Lynam, C. P., M. R. Heath, S. J. Hay, A. S. Brierley (2005). Evidence for impacts by jellyfish on North Sea herring recruitment. *Marine Ecology Progress Series* 298: 157-167.