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International Council for Exploration of the Seas

Use of data storage tags to reveal aspects of fish behaviour CM2006/Q:04

"All men have need of the cods (sic)" (Homer, the Odyssey)

or

"An overview of the results of the EU-CODYSSEY project"

The CODYSSEY research team*†

Cod stocks in European waters are in serious decline, prompting the adoption of Recovery Plans in some areas e.g. North Sea, and similarly serious management measures elsewhere e.g. Barents Sea, Baltic Sea. CODYSSEY (Cod spatial dynamics and vertical movements in European waters and implications for fishery management) is an EU-funded R&D project that involves nine European research institutions in eight different countries. The aim of the project is to improve understanding of the behaviour and distribution of cod in the NE Atlantic in support of stock assessments and Recovery Plans. Over the last four years, members of the CODYSSEY research team have tagged over 2500 cod with electronic tags in four different regions (North Sea, Barents Sea, Baltic Sea and Icelandic plateau). To date, over 450 tags have been returned, yielding tens of thousands of days of data. The results challenge previously held assumptions regarding migratory behaviour, feeding behaviour and the tolerance of cod for extreme environmental conditions. We have been able to derive rates of migration, stock mixing and availability to fisheries from the tag data. The results of the CODYSSEY project are of value to fish biologists and fisheries managers at national and international level.

Keywords: Data storage tags, migration, behaviour, tagging

**full listing in Appendix*

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INTRODUCTION AND METHODS

Fisheries managers face a number of management problems for European cod stocks, some of them generic, some of them specific. Most seriously, stock decline in the NE Atlantic has alarmed fisheries managers everywhere (Walters & Maquire, 1996; EU, 2001) The development of Recovery Plans for North Sea and Irish Sea cod stocks (EU, 2000, 2001) and the introduction of Regional Advisory Councils as part of the CFP have highlighted the absence of high quality basic biological information on which to build robust multi-annual technical measures to conserve and rebuild stocks. Such information is particularly important for evaluating the utility of the closed areas that have already been applied to protect cod in the North Sea and to the west of Scotland.) Similar problems are likely to be experienced in the Baltic Sea and Barents Sea. Secondly, assessment of stocks has become increasingly difficult as the quality of commercial catch statistics declines (Pennington & Stromme, 1998. Korsbrekke *et al.*, 2001; Godø & Wespestad, 1993). Attention is now shifting towards fisheries independent stock assessments, and greater emphasis needs to be placed upon understanding the causes of variation in these assessments (Hjellvik *et al.*, 2001. Beamish, 1966; Harden-Jones & Scholes, 1985; Arnold & Greer-Walker, 1992; Aglen et al, 1999; Righton *et al.*, 2001a;Ottersen *et al.*, 2001). Thirdly, the effect of climate change on stock distribution and spatial dynamics of cod may be considerable (O'Brien *et al.*, 1999; Brander, 1993, 1994; Dickson, *et al.*, 1994; Drinkwater, 2006). In each of these problems, a lack of basic biological knowledge hampers the development of conservation policy (EU, 2001). Behaviour is one of the crucial aspects to consider because behavioural decisions underlie habitat selection and therefore influence the distribution, abundance and survival of populations (Sutherland, 1996). In 2002, researchers from 7 European states and from 9 different marine biological institutes started working together on a project called CODYSSEY (**COD** spatial d**Y**namic**S** and vertical movement**S** in **E**uropean waters and implications for fisher**Y** management) to improve our understanding of the horizontal and vertical movements of cod and the influence of environmental and biological factors on these movements. The aim was to provide management relevant information as to the *availability, accessibility* and *vulnerability* of cod to fishing activities.

The CODYSSEY project was designed to take advantage of recent advances in electronic data storage tags (DSTs) to record and store the behaviour and environmental experience of large (>45cm) cod over periods of 9-12 months. Normally, direct observations of fish behaviour at sea are costly to undertake (Green & Wroblowski, 2000; Arnold & Dewar, 2001) because individuals may not be easily followed, particularly for long periods of time. In consequence, surprisingly little is known about the natural behaviours of cod (Righton *et al.*, 2001b). However, DSTs combine the advantages of conventional tags with those of acoustic tags by providing information on the minute-by-minute behaviour of the fish, and its experience of the immediate physical environment, and therefore provide a very powerful tool with which to describe patterns of behaviour in natural populations. Information of great utility as regards the interpretation of fishery and survey data can be readily collected. Although DSTs typically record two or three environmental parameters, such as pressure (depth), temperature, light, or salinity, the behaviour of the tagged fish can be reconstructed in remarkable detail (Arnold *et al.*, 1992; Righton *et al.*, 2001; Hunter *et al.*, 2004a). For example, depth data from DSTs used in the North

Sea can be compared to hydrographic data on tidal patterns to reconstruct migration paths (Metcalfe & Arnold, 1997; Hunter *et al.*, 2003). Migration paths can also be reconstructed by using the rates of change in depth and temperature (Stensholt,2001). The application of this approach has been demonstrated successfully for plaice in the North Sea. For example, investigations into the vertical movements of plaice in the North Sea have demonstrated that plaice availability to trawl gears changes dramatically during periods of migration (Hunter *et al.*, 2004b). More recently, information from electronic tagging data has revealed regional complexities in stock structure (Hunter *et al.*, 2004a) that will enable regionally based management scenarios to be tested. A similar application of DSTs on cod at a larger scale was therefore an ideal approach and a cost-effective research tool for studying the behaviour of individuals and populations.

The fundamental basis and innovation of the CODYSSEY project was in its application of the comparative approach. The project was designed to operate on a modular basis in several different ecosystems: the North Sea and Skagerrak, the Barents Sea, the Baltic Sea, and the Icelandic shelf (including the Faroe Islands). A key benefit of using a multi-ecosystem comparative approach is that a greater range of behaviour and environmental conditions will be observed than by looking at one ecosystem only, thus permitting the formulation of quantitative relationships between specific behavioural traits and ecological variables. In doing so, these relationships can then be used to formulate and test specific management hypotheses or scenarios. The adoption of this approach was prompted by findings that suggest cod behaviour is rather more variable than has been assumed (Godo & Michalsen, 2000; Righton *et al.*, 2001; Righton & Metcalfe, 2002). It was thought that such differences may be linked to genetic or environmental factors (Righton *et al.*, 2001), and by simultaneously comparing the behaviour of geographically, and apparently genetically (Hutchinson *et al.* 2001; Neilsen *et al.*, 2001), separate stocks, the role of environment and stock identity could be separated.

Within each ecosystem module, five core tasks were carried out: (1) a comprehensive tagging programme; (2) implementation of novel geolocation methods; (3) analysis of horizontal and vertical movements of individual cod; (4) analysis of environmental experience (temperature/ salinity/ food) of cod and (5) development of models to interpret and predict cod behaviour. A schematic of the data flow from the tagging programme is shown in Figure 1. The CODYSSEY project was, therefore, an ambitious attempt to bring the benefits of behavioural data to fisheries management at an unprecedented scale. This paper is intended as an overview of the main achievements of the data collection and analysis modules of the project over the last four years, with reference to the original sources of more detailed results published to date, and pointers to results that are soon to be published.

RESULTS

Tagging programme

At the intitiation of the CODYSSEY project, experiments were conducted to assess the relative merits of external attachment or surgical insertion into the peritoneal cavity (Figure 2a&b). Growth rates relative to controls were not affected by either attachment method, although the growth rates of internally tagged fish were the closest match to control fish (Figure 2c &d). Comparison of the growth of cod returned from the North Sea tagging programme showed that growth rates of internally or externally tagged fish were not different to growth rates expected of wild cod. Full details and results of the experiments can be found in Righton *et al.* (2006).

Despite historically low cod stock biomass in most regions, and with sweeping cuts in EU cod fishing fleets, the tagging programme was completed successfully within 2 and a half years. Since October 2002, 2676 DSTs have been deployed on cod in EU waters (Table 1). Approximately 80% of tags were tags were surgically inserted into cod to minimise drag and irritation that might be caused by external attachment. Due to salinity sensor configuration, the DSTs deployed in the Baltic Sea required external attachment. To date, over 450 tags (>17%) have been returned, and this figure is likely to increase to 20% by the end of the project. The low return rate may reflect the poor state of cod stocks, reduced fishing effort due to the introduction of revised management measures, lack of co-operation from the fishing community resulting from animosity towards and mistrust of fisheries scientists/managers or unintentional discarding of internal tags. It is also possible that mortality occurred due to tagging, although the results of field and laboratory experiments suggest that the procedures used were not likely to incur significant mortality, if at all (Righton *et al.*, 2006). Future reductions in tag size may permit subcutaneous or the reintroduction of external tagging, and will almost certainly lead to increases in tag recovery (Righton, unpubl. data). However, the return rate compares favourably to the return rate for flatfish and roundfish tagged with conventional tags in the North Sea (Burt *et al.*, 2006), and typical of electronic tagging programmes (Block *et al.*, 2003).

Region	***Total***	***Recaptures***	***Proportion***
North Sea	709	115	0.16
Barents Sea	558	31	0.06
Baltic Sea	446	166	0.37
Icelandic shelf	963	25	0.23
	2676	439	0.17

Table 1 DST tags deployed and recaptured by region

The behavioural effects of tagging appear to be limited to a brief period of equilibration behaviour immediately after release (Heffernan *et al.*, 2004; Nichol & Chilton, 2006; van der Kooij *et al.*, 2006). Surprisingly, the response of cod to the ‘barotrauma’ (Nichol & Chilton, 2006) of capture was similar in all ecosystems except the Baltic Sea, with the gradual restoration of neutral buoyancy over hours and days. Cod typically undertook a series of vertical movements between the seabed and a progressively decreasing depth as the individual’s swimbladder re-equilibrates to neutral or negative buoyancy at the seabed (Figure 3). van der Kooij et al (2006) describe full details of this behaviour, which can also occur naturally as cod move between locations with differing seabed depth. The ubiquity of this behaviour indicates that cod exhibit similar preferences for neutral or slightly negative buoyancy irrespective of their residence depth, and suggests that their re-adaptation to residence depth has a common basis, perhaps that of energy minimisation (van der Kooij *et al.*, 2006).

Geolocation of tagged fish

Geolocation is a technique that can relate the measurements of environmental parameters (such as light, temperature and depth) recorded by animals fitted with electronic tags to specific geographic locations (Arnold & Dewar, 2001). Inevitably, it proved impossible to develop a standardised geolocation query system for all four ecosystems, for several reasons. First, environmental databases for each ecosystem are not always available in the same formats, with the same resolution, and with the same precision. Second, each ecosystem is very different in terms of the dynamic range of data, and therefore the discriminatory power of a standardised geolocation query system would vary considerably. It was therefore the case that applying a standard method was neither appropriate nor necessary, and geolocation methods for each ecosystem were refined to optimise results in those ecosystems.

A critical element of the methods that were developed is that, rather than attempting to pinpoint an individual to an exact location, they provide a probability that an individual is at each particular location within the geographic domain of the environmental databases used. This kind of estimate of uncertainty of the technique, transforming the data from infrequent point estimates of geographic positions to areas of more or less certain position. Neuenfeldt *et al.* (2006) described a technique that determined geographic locations by comparing the temperatures and salinity measurements from a DST with the environmental variables as obtained from the highly temporally and spatially resolved hydrodynamic model output fields. Weighting factors are necessary in order to make parameters of incommensurable units comparable, which means that information obtained from each parameter is of identical quality. The accuracy of the geographic positions along the migratory route of a tagged cod has been improved where ever possible through the use of other datasets where appropriate (e.g. bottom topography, oxygen concentrations). Geolocation algorithms in other regions have followed suit. For example, Righton *et al.* (in prep) describe an advancement of the tidal location method (TLM; Hunter *et al.*, 2003) that uses depth and seabed temperature data to reconstruct the most plausible migration path of a tagged cod, as well as the computation of the likelihood that the individual was in any given location (Figure 4a). Adlandsvik *et al.* (2006), developed the ‘Spaghetti method’ of geolocation which defines with 100% certainty where the tagged cod could not have been. The method then uses a movement algorithm to create possible migration paths (Figure 4b). Andersen *et al.* (2006) has formally described a particle filter method that refines these techniques. The motivation for this work came from three sources: 1) the need for a common algorithm that in principle can be applied to all the different systems in CODYSSEY; 2) the need to move away from ad hoc algorithms and into territory which is statistically better founded and 3) the need to calculate confidence intervals on the geolocation. The basis for the particle filter is 1) a movement model and 2) an error model. The particle filter is a simulation method. Many (up to 1 million) particles, each representing a possible path of the fish, are moving around randomly, according to the movement model. At each time step the probability of each particle is assessed using the information from the DST, and particles with low probability may be discarded, and replaced with a new random particle. The advantage of the particle filter model is that the measurement errors associated with each parameter used in the geolocation (e.g. accuracy of pressure sensor, accuracy of bathymetry) are all used to quantify the probability that the position of a particle matches the position that the tagged cod occupied. An example of use of the method is shown in Figure 4c.

Horizontal migration

As a result of the development of geolocation algorithms, it has been possible to describe cod migrations in detail. Cod can exhibit a range of migratory strategies within ecosystems, and estimates of migratory speed can vary. Broadly, cod can be classified as residents or migrators (after Robichaud & Rose, 2004). Resident cod occupy a limited home range throughout the year. Examples of resident cod were found in the North Sea (Figure 5a) and Skagerrak (Neat *et al.*, 2006; Righton *et al.*, 2006b; Wright *et al.*, 2006; Svedang *et al.*, 2006), the Barents Sea (Michalsen, unpubl. data) and the Icelandic shelf (Palsson & Thorsteinsson, 2004). Resident cod have not been documented in the Baltic Sea as yet. Migratory cod are those cod that make significant seasonal movements and that occupy considerably different areas throughout the year. Within this group, cod can be further subdivided into those that migrate continuously throughout the year, as found in the Faroe Islands, Barents Sea and Baltic Sea (Figure 5b), and those that ‘switch’ relatively quickly between spawning grounds and feeding grounds, as for cod of the Icelandic Shelf and some cod populations in the North Sea (Figure 5c & d).

The different migratory strategies have considerable implications for the management of stocks. Firstly, resident cod may be particularly vulnerable to fishing activity because they are vulnerable to exploitation all year round. Their recovery from exploitation may be slower than for other populations because population size is unlikely to be increased through immigration, and average growth rates may be slow due to seasonal fluctuations in food availability (Green & Wrobleowski, 2000; Robichaud & Rose, 2004). Second, because migration in most species has evolved and been maintained in response to food shortages, stock residency may be an indication that individuals no longer need to migrate. The documentation of resident cod stocks has increased in recent years, and may be an indication of low population size and lead to the loss of migratory capacity (Robichaud & Rose, 2004). Thirdly, migratory cod cross management boundaries and are vulnerable to different sectors of the fishing industry. The rate at which they migrate, and the duration and period of the year that they migrate will determine the extent of this vulnerability. ‘Switch’ migrators move rapidly between management areas and are therefore likely to be vulnerable to fewer fleets than ‘continuous’ migrators. For example, cod that leave the Skagerrak to spawn in aggregations in the eastern North Sea in spring (Svedang *et al.*, 2006) are likely to face high fishing effort for a limited period of time.

Vertical movements

Cod occupy water depths between 5m and 600m and their capacity for changing depth permits them a great deal of behaviour flexibility. The rate at which depth is measured has a critical effect upon the estimates of the magnitude and frequency of vertical movements, which in turn has a large influence on the interpretation of vertical movement patterns. Heffernan *et al.* (2004) showed that estimates of vertical movement rate were inversely proportional to sampling interval, whether the data were recorded in the North or Barents Sea (Figure 6a). In consequence, all deployments of DSTs in the CODYSSEY project were standardised to a recording rate of once every 10 minutes as a minimum. Some DSTs were programmed to record more frequently than this. 10 second sampling intervals proved useful in estimating tilt angles of cod in the North Sea, and showed that the angle of tilt is greater at night than day (Figure 6b; Heffernan *et al.*, 2004). This rapid rate of sampling can also provide more information about which portion of the water column the individual is using (Neuenfledt, pers. comm.).

Cod in the Barents Sea exhibit the greatest range of vertical habitat use (Godo & Michalsen, 2000), and can frequently exhibit rates of vertical movement well in excess of 175 m per hour, and occasionally over 300 m per hour (Heffernan *et al.*, 2004; Figure 7a). Total vertical swimming activity can, in consequence, be very high, presumably as individuals move away from the seabed to forage for capelin. In contrast, cod in the North and Irish Seas, much shallower in comparison, move over correspondingly smaller distances, sometimes amounting to only a few metres in total per day (Righton & Metcalfe, 2002; Figure 7b). In the Baltic, cod often appear to occupy a mid-water position cross the halocline for brief periods to chase herring and sprat (Figure 7c). On the Icelandic shelf, cod exhibit seasonal changes in depth as they migrate between off-shore and in-shore areas (Figure 6d; Palsson & Thorsteinsson, 2004). Overall, the results show that cod tended to reside in shallower water in the spawning seasons. This is likely to be an adaptive trait that has evolved in order to maximise spawning success, either through gaining successful spawnings in suitable habitat (Rowe & Hutchings, 2003), or because the survival of eggs and larvae are likely to be greater in shallow, productive waters, or where surface currents will disperse the eggs & larvae over a wider distance. In the feeding seasons, cod depth distribution would be more heavily influenced by the availability of prey, and it was during this season that the biggest differences between ecosystems. Cod with access to cold, deep water (Barents Sea and Icelandic Shelf) were able to utilise these habitats, and exhibited frequent short and medium-term changes in depth that greatly exceeded those of cod in other ecosystems, and were probably related to prey searching activity. Cod in the North and Baltic Seas exhibited less frequent, smaller scale vertical movement, and vertical activity may instead have been directed more at prey capture.

High sampling rates have permitted the evaluation of periodicity and rhythm in the vertical movements of cod. Cod were usually more active in hours of darkness, and at slack water, times when prey capture success was likely to be higher. During the migratory phase (if present), periodicities were more difficult to detect, a consequence of more variable vertical movement and a lower dominance of the foraging modalities. Neat *et al.* (2006) showed that resident cod in the northern North Sea exhibit a range of periodicities in their movements that appear to be related to seasonal changes in food availability, and also to tidal patterns (Figure 8a). Righton *et al.* (in prep) used fast fourier transformations to analyse periodicities in vertical movements of cod in the North Sea. Dominant rhythms were based on tidal and diel modalities of 6.2h, 12.4h 24h and 15 days (Figure 8b). Thus, despite the differences between regions, the timing and periodicity of vertical movements had similar modalities in the feeding season, being based around the strong cues of tidal strength and the day night cycle.

Environmental experience

Although individuals can adapt to changes in temperatures, they are thought to behave in a way that reduces thermal stress and to be unable to tolerate large, abrupt changes in temperature. Consequently, it is believed that thermoclines of only a few degrees can constitute fairly impenetrable boundaries and that this may contribute to the segregation of cod populations in nature. Our studies of the movements and temperature experience of adult cod in the North Sea and further north indicate that the movements and distribution of individual animals is much less restricted by environmental temperature than laboratory studies suggest. Some individuals occupy shallow habitats in the southern North Sea where summer temperatures are consistently above 17°C for several months (Figure 9) while others tagged at the same time move to deeper, cooler waters. Cod in the northern North Sea also seem to tolerate temperatures within the upper seasonal limits, although these are much closer to laboratory derived temperatures that are optimal for growth (Neat & Righton, in submission). In the short-term, cod appear capable of tolerating temperature changes that are much greater than expected. This is in direct contrdiction of recent laboratory studies that have suggested that this reported intolerance of temperatures above 17°C will result in a general northward movement of North Sea cod and their extirpation in the southern reaches. Our results suggest that cod may be more tolerant of high temperatures than previously thought (Neat & Righton, 2006).

In other areas, where average water temperatures are much cooler, cod can repeatedly experience abrupt temperature changes of up to 8°C while moving through steep temperature gradients. For instance, cod in the Barents Sea and Icelandic Shelf regularly move into and out of cold frontal water masses for periods of a few hours or days (Figure 10a & b). Similarly, in the Baltic Sea, cod experience large fluctuations in water temperature as they migrate through different water masses (Figure 10c), and as they move through the thermocline. these movements were sometimes accompanied by movements through the halocline and into poorly oxygenated water. In most of these cases, the vertical movements observed at times of large temperature change are indicative of short-term foraging behaviour. The results highlight how high-resolution behavioural data collected from the field can challenge assumptions regarding physiological and behavioural limits. In addition, such results may help to refine laboratory experiments to re-test and redefine these assumptions.

DISCUSSION

CODYSSEY has provided new knowledge of migration paths and the spatial dynamics of stocks. The fact that cod undertake long migrations between nursery, feeding and spawning grounds is well established (Daan, 1978; Brander, 1994b) and such migrations often cause individuals to cross the boundaries between ICES divisions and other quota areas. Evidence from the CODYSSEY project has provided firm evidence that the scales of cod movement can vary considerably through the year, with individuals in some locations displaying little, if any, signs of large-scale movement. Scales of movement differ considerably between stocks and movements of individuals appear to vary in response to important environmental drivers, although perhaps in some unexpected ways. Such data are useful to fisheries stock assessment and management, for several reasons. Firstly, fisheries-independent stock assessment methods require knowledge of stock distribution in order to *plan* effective surveys (Pennington & Stromme, 1996) and also to interpret them (Righton *et al.*, 2001; Strand *et al.*, 2005). Secondly, fisheries management measures can only be designed to protect individuals at vulnerable stages if it is known when and where these vulnerable individuals are (EU 2001, 2002). Collecting data on fish migrations is nothing if the results do not shed light on the processes of migration. To date, the CODYSSEY project has identified a variety of migration mechanisms that cod use and shown how, by using these mechanisms as a basis for simple population movement models, how cod movements might be influenced by the environment. For instance, Mills *et al.* (2006) have shown how cod in the Baltic Sea are able to locate and reside in areas that maximise the probable survival of offspring. Similar simulations are underway to investigate how cod distribution in the North Sea would be affected by temperature.

Data from CODYSSEY can also be used to understand the vertical distribution of cod, which is important in defining ‘catchability’. Catchability indices can be used to tune or design fisheries independent stock assessment methods (Godo & Wespestad, 1993; Aglen, 1999), or evaluate the potential effectiveness of proposed technical measures that prohibit the use of certain fishing gear types (ICES, 2001). While the vertical dynamics of small cod are well documented (Bromley & Kell, 1999), vertical positioning in adult cod is less well understood. Strand *et al.* (2005) constructed a model of cod buoyancy control to determine the optimal swimming speeds, depth and buoyancy status of cod in the Barents Sea. These predictions were then tested successfully against data collected from cod tagged in the Barents Sea (Godo & Michalsen, 2000). The observations from CODYSSEY suggest that cod are usually under-buoyant, thus aiding the development of tools to improve the accuracy and precision of acoustic survey methods. The model is also being used to investigate the energetic consequences of re-equilibration behaviour (van der Kooij *et al.*, 2006). A refinement of the model is the inclusion of foraging behaviour to predict how vertical positioning and buoyancy are likely to be affected by prey availability and location.

Conclusion

A fundamental part of CODYSSEY was the cross-ecosystem approach. A key benefit of using this approach is that the relationships discovered between environment, hydrography and behaviour can be used to formulate and test specific management hypotheses or scenarios. The research undertaken so far in CODYSSEY, has improved our understanding of cod behaviour and the environment. As the project draws to a close, it is critical we remember that conservation of cod stocks was the primary motivation for the proposal of the research and the EUs funding of it. We intend to use our knowledge to propose improvements to assessment survey methods and to evaluate technical conservation measures that will help to safeguard stocks. Peter Dass (*Trumpet of Nordland*, Norway, 1739) makes the point most saliently:

> *"If codfish forsake us, what then would we hold?*
> *What Carry to Bergen to barter for gold?"*

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FIGURES

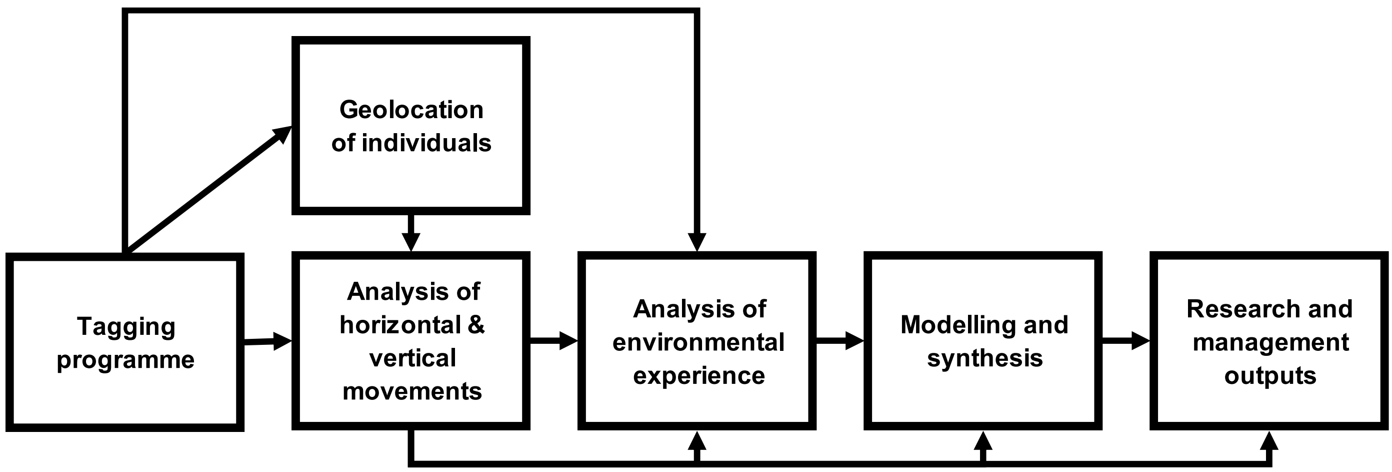

Figure 1. Schematic of the main work areas in the CODYSSEY project.

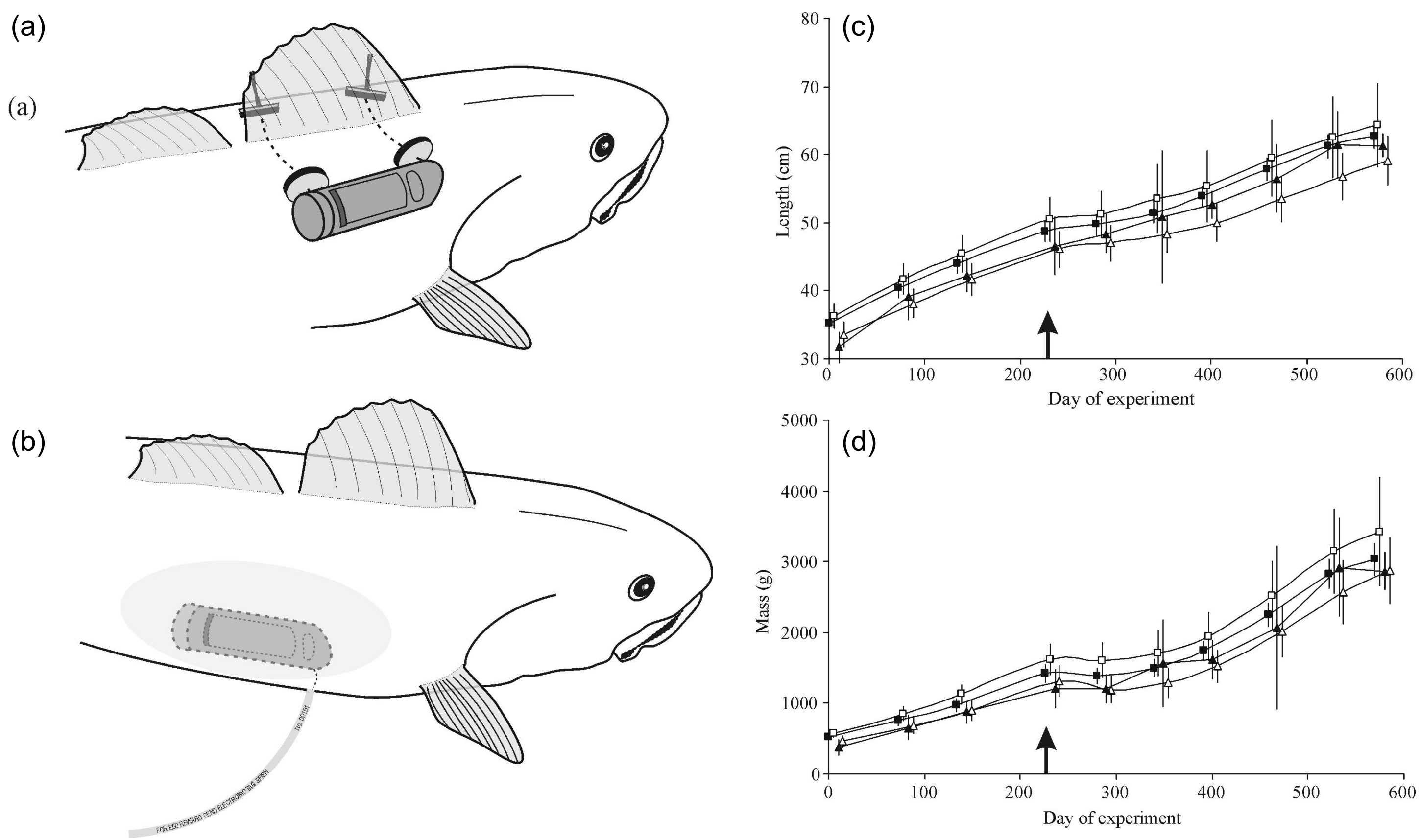

Figure 2. Tagging techniques and their effect on Atlantic cod. Methodology for (a) external tagging; (b) internal tagging. The effect of tagging on cod growth is negligible, either in terms of (c) length or (d) weight. Values for tagged cod are shown by hollow symbols.

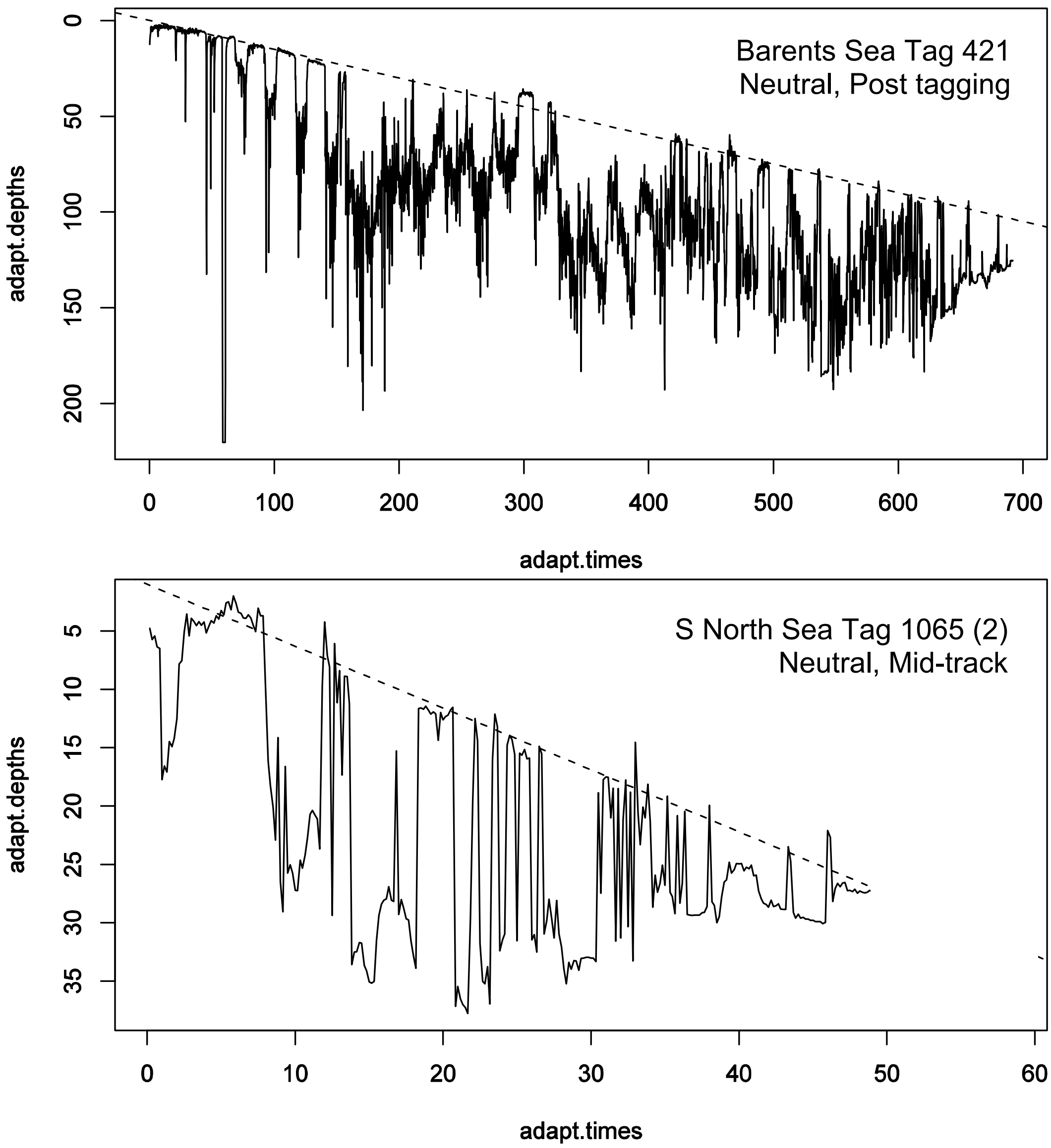

Figure 3. Re-equilibration behaviour of cod following (a) tagging and re-release and (b) during a transistion from shallow to deeper water. Depths are shown in metres and time in hours. The dotted line shows the estimated rate of adaptation.

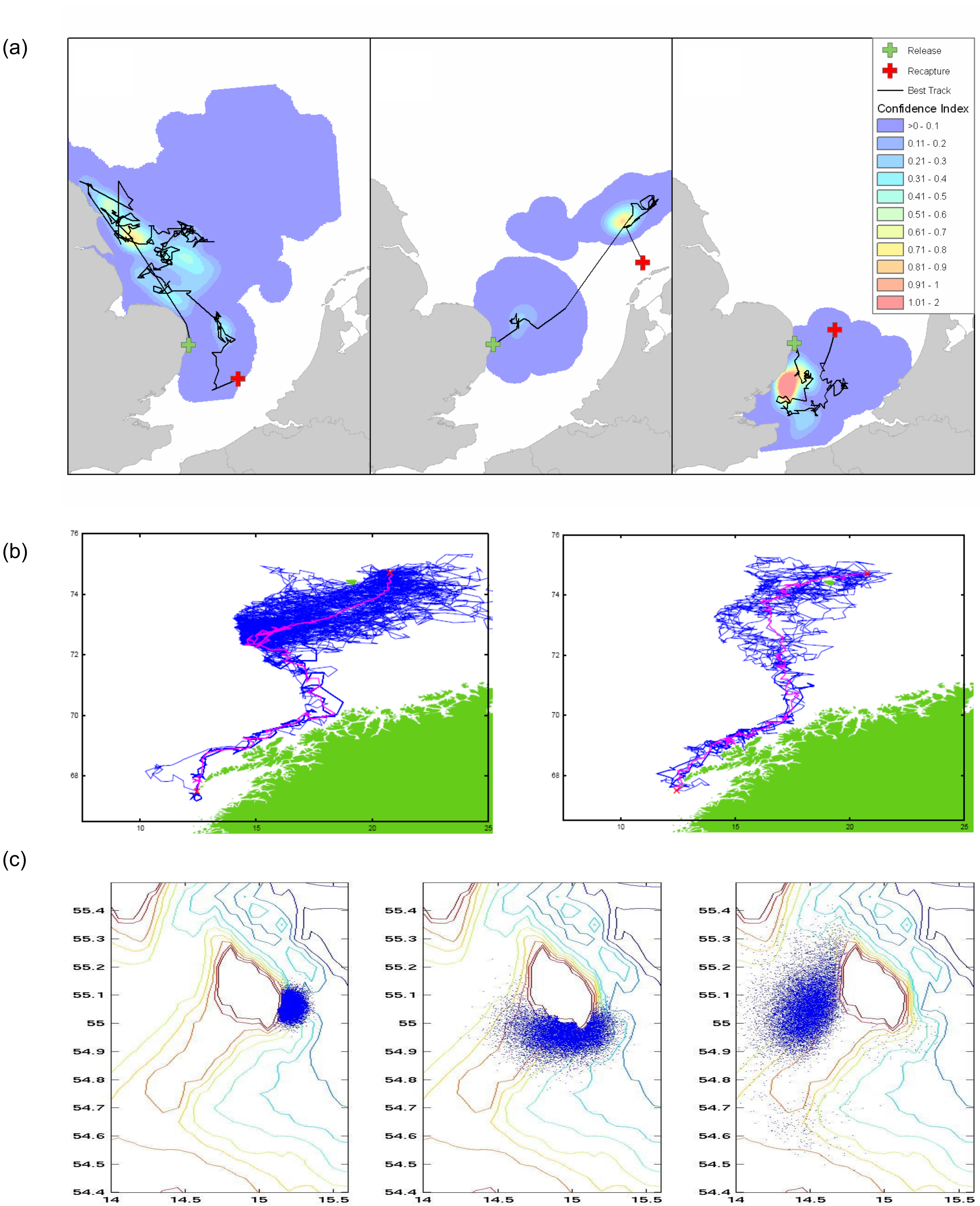

Figure 4. Example outputs from geolocation methods in the (a) North Sea. Lines show the best estimate of migratory path for three cod, while shading shows the likelihood of location of cod in the occupied area. (b) Barents Sea. Blue lines show possible migration paths of a single cod, while the pink line shows the most likely path. The right-hand panel shows the effect of increasing the stringency of geolocation conditions. (c) The Baltic Sea. The blue points show the possible locations that an individual could have occupied at three separate points in time as the individual migrated from east to west around Bornholm Island.

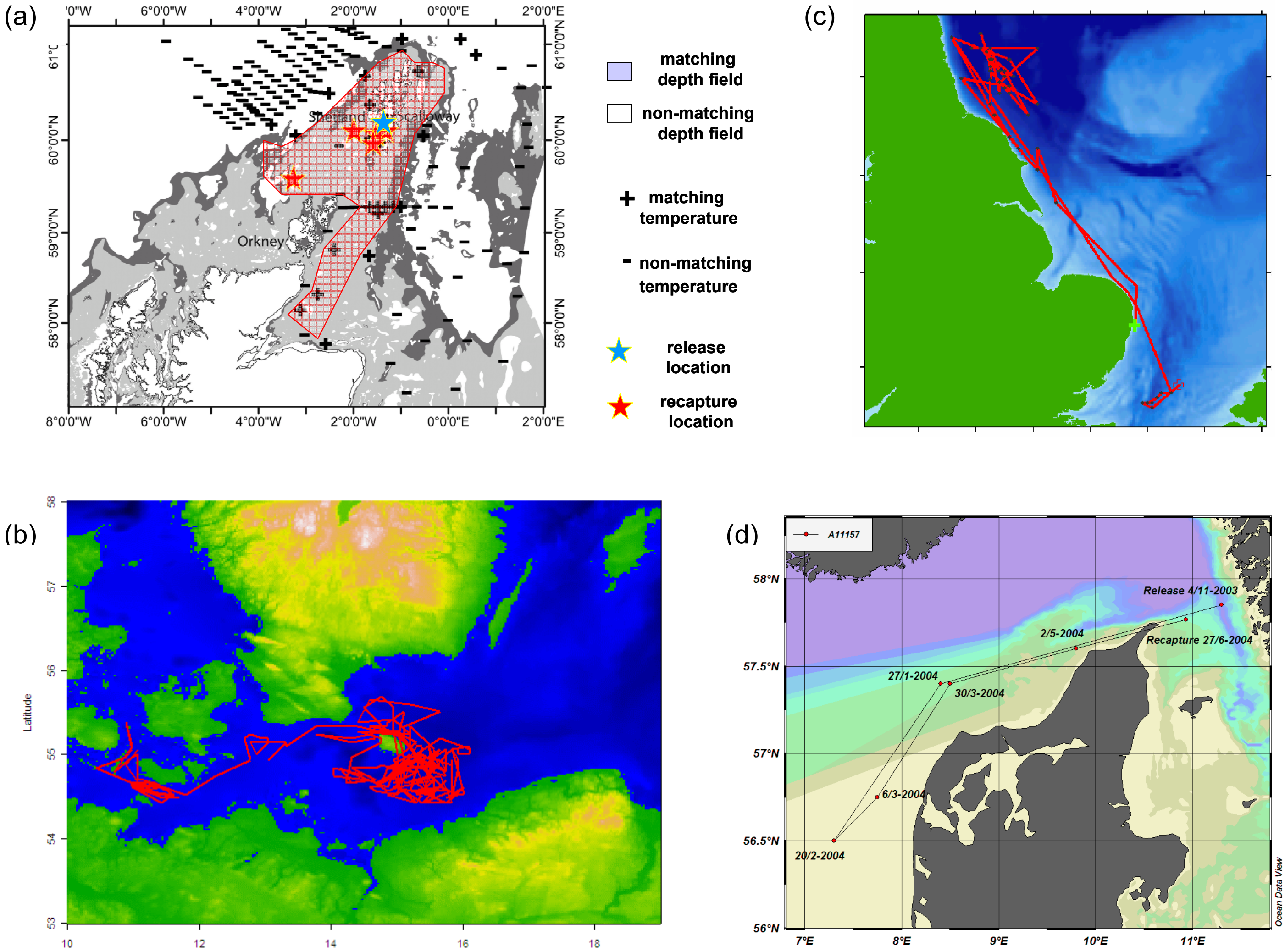

Figure 5. Example migrations of cod in (a) the northern North Sea, showing the limited area of dispersal (red hatching) of cod from releases off Shetland (blue star). (b) the Baltic Sea, showing a migration into the west Baltic/ Kattegat after tagging east of Bornholm Island. (c) the North Sea, showing a feeding migration to the north of the Dogger Bank and a return spawning migration to the southern North Sea. (d) a spawning migration from the Skagerrak into the North Sea and the subsequent return migration. Shading indicates depth.

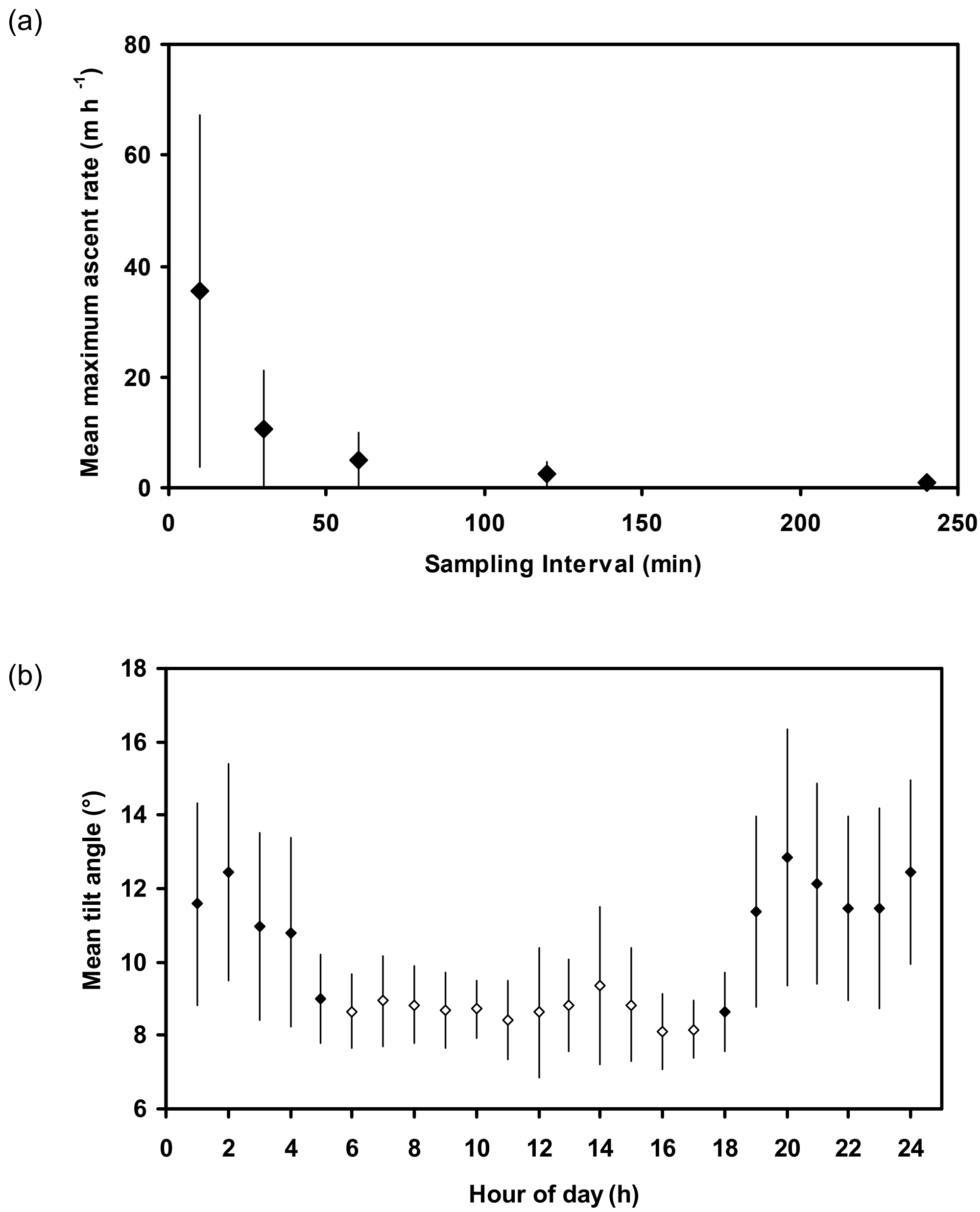

Figure 6. The use of different sampling rates to derive estimates of cod movement. (a) the effect of sampling rate on estimates of vertical movement rate of cod in the North Sea. (b) estimates of tilt angle derived from high frequency sampling (10 s).

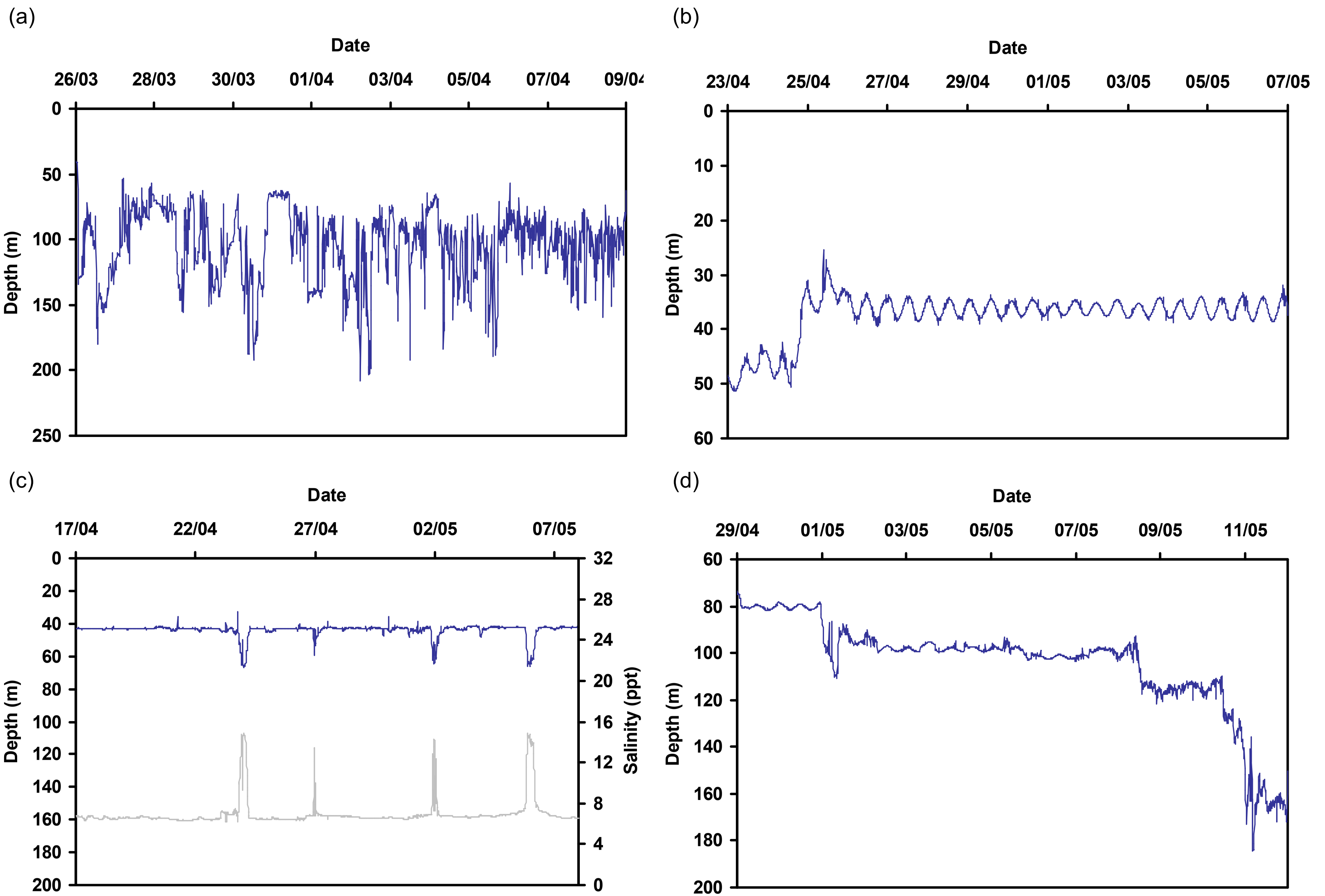

Figure 7. Vertical movements and depth change of cod in the (a) Barents Sea. (b) North Sea. (c) Baltic Sea. (d) Icelandic shelf. Blue lines show depth, grey lines show salinity, where measured.

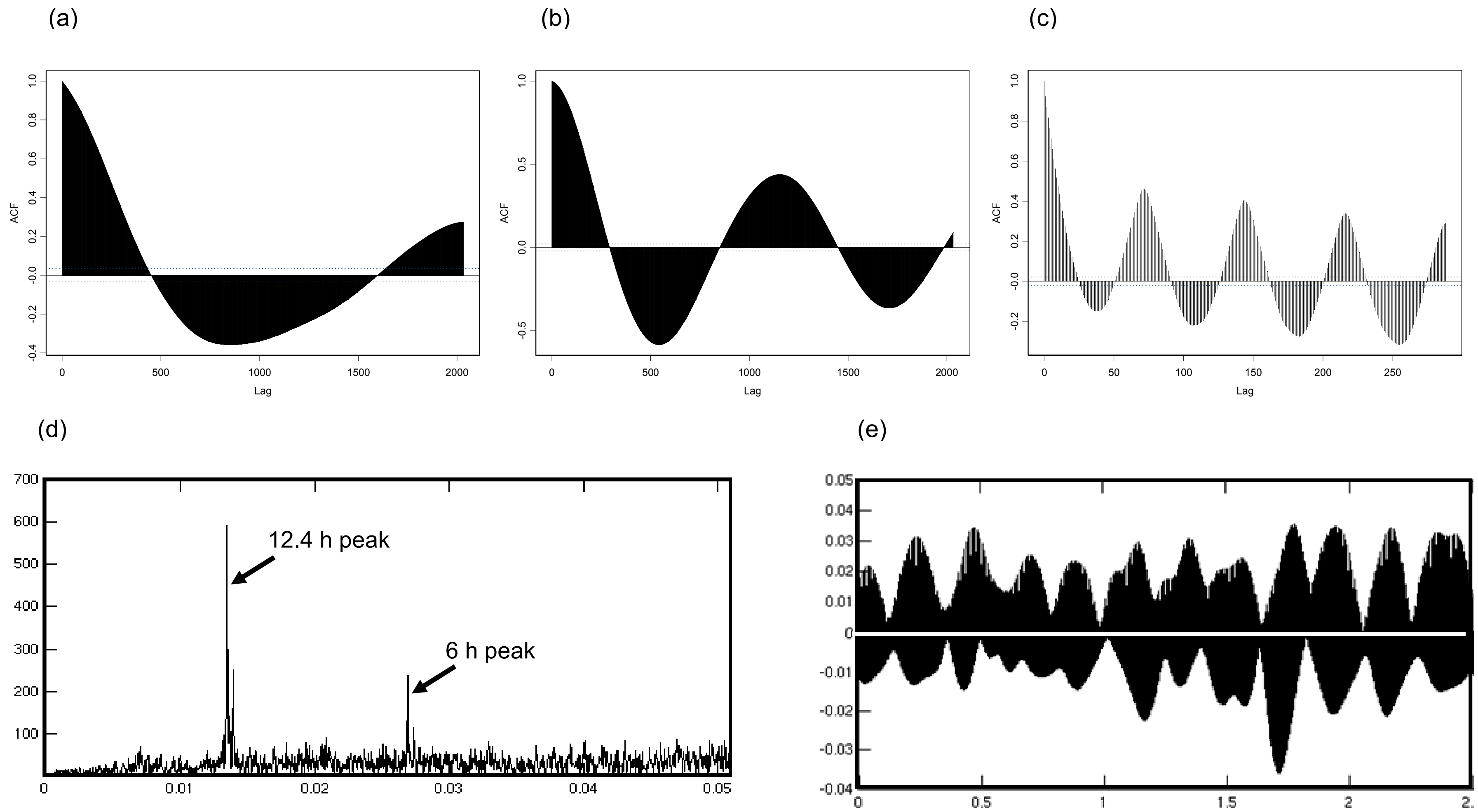

Figure 8. Analysis of periodicity in the depth changes of cod in the northern North Sea (top panels) and the southern North Sea (lower panels). (a) autocorrelation showing 4-week pattern to depth changes. (b) autocorrelation showing 2 week pattern to depth changes. (c) autocorrelation showing daily pattern of depth changes. (d) Spectral analysis that indicates a significant 12.4 hr and 6 h periodicity in depth changes. (e) the amplitude of the depth changes over time for the periodicity at 6h (above white line) and 12.4 hr (below white line)

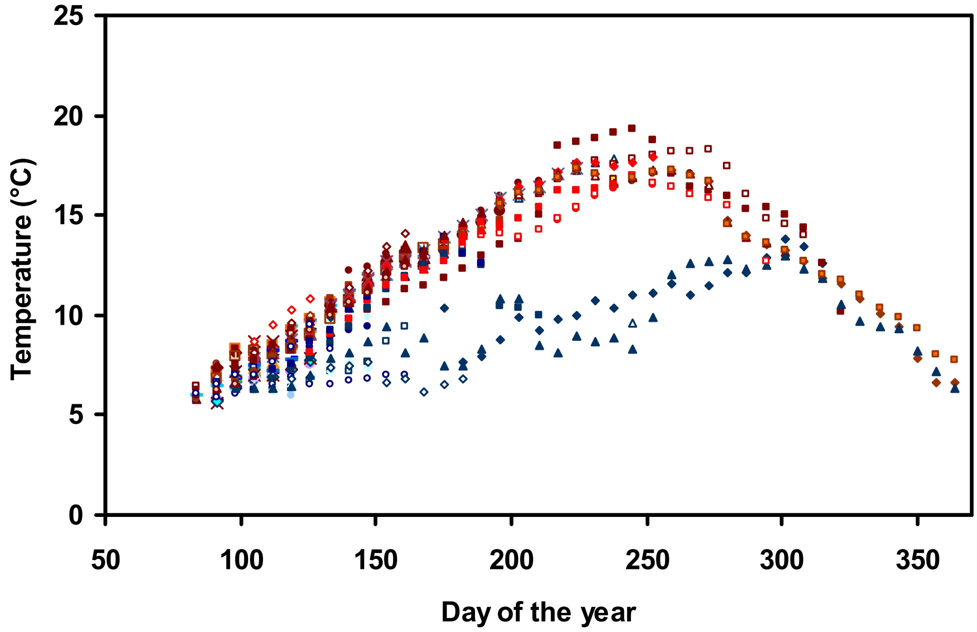

Figure 9. Weekly mean temperature experience of cod in the southern North Sea. Red symbols show individuals that followed a 'warm water' strategy, blue shows those that followed a 'cool water' strategy.

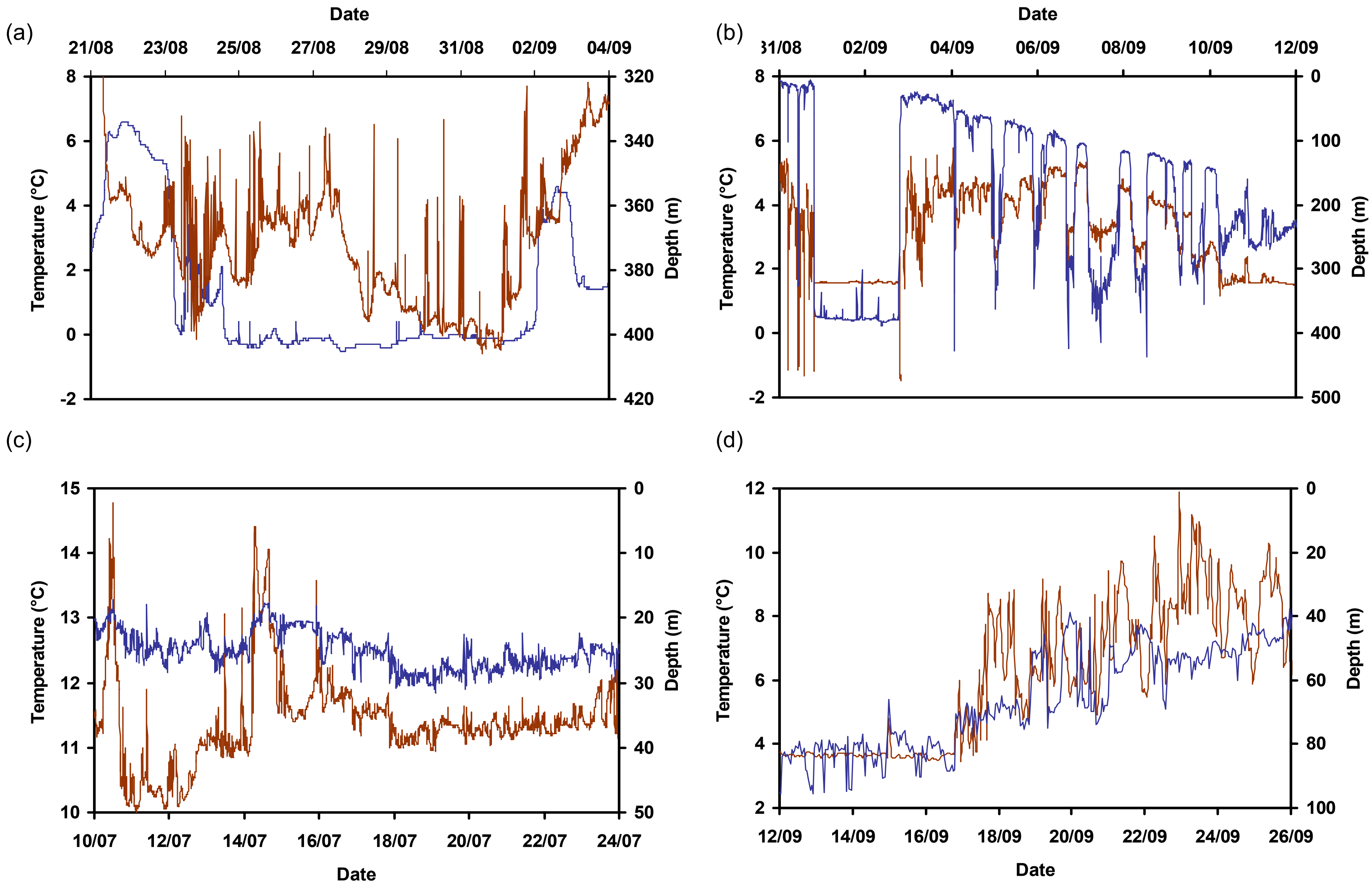

Figure 10. Temperature (red) and depth experience of individual cod as they move between water masses in (a) the Icelandic shelf. (b) the Barents Sea. (c & d) the Baltic Sea.

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