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CM 2000/ Q:09

ICES ANNUAL SCIENCE CONFERENCE 2000

Theme Session Q: Trophic dynamics of top predators: Foraging strategies and requirements, and consumption models.

Behavioural switching in North Sea cod: implications for foraging strategy?

D. Righton, K. Turner, and J. D. Metcalfe.

*The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory,
Pakefield Road, Lowestoft, Suffolk, NR33 0HT, UK*

Fax: ++ 44 (0)1502 524511

E-mail: d.righton@CEFAS.co.uk

ABSTRACT

Data Storage Tags (DSTs) which record depth, temperature and light were used to monitor vertical movements and horizontal migrations of adult cod in the North Sea. Fifty-eight cod were tagged off Lowestoft in late March 1999, twenty-two of which were returned by March 2000 after up to 225 days at liberty. Four behavioural phases were discernible from the combined results. Cod were most active as they moved north during April and May, remaining in mid-water and making only brief excursions to the seabed. During June and July, activity fell, and cod spent most of their time on the seabed, exhibiting little vertical movement. During August and September, cod typically left the seabed at nightfall and returned to it before dawn. Throughout October, activity increased as vertical movement patterns returned to those previously exhibited in April. The results suggest that cod may enter into a rest period following their post-spawning migration from the southern North Sea, and increase their activity before their pre-spawning migration. Although we did not measure feeding directly, the lack of activity during summer months indicates that feeding may have taken place only rarely. Such behavioural switching may have implications for fisheries models that assume constancy in feeding behaviour.

Keywords: Data Storage Tags, vertical movement, migration, activity.

INTRODUCTION

The behaviour of free ranging adult cod has been documented by a number of authors (for recent publications see: Lokkeborg et al., 1989; Arnold & Greer-Walker, 1992; Arnold et al., 1994; Lokkeborg, 1998; Lokkeborg & Ferno, 1999; Godø & Michalsen, 2000). Cod is considered a demersal species which spends the majority of its foraging time searching for benthic, or hyperbenthic, prey (Mattson, 1990). However, cod may spend substantial periods swimming in mid-water depending upon the season or availability of food (Zilanov, 1963; Beamish, 1966; Godø & Michalsen, 2000). Furthermore, individuals in most cod stocks undertake long migrations that inevitably carry them through a variety of habitats, in which the motivations to feed, rest or reproduce will differ (McKeown, 1984; Colgan, 1993). One consequence of these varying, and sometimes conflicting, motivations will be changes in activity and vertical positioning on diurnal or seasonal time-scales, which probably relates to the optimal use of a given habitat (McKeown, 1984; Hart, 1993).

Different hypotheses propose that changes in activity and vertical positioning can be motivated by food search, predation risk, energy saving, transport, swim bladder constraints and food digestion (Perry & Neilson, 1988; Hoines & Bergstad, 1994; Arnold et al., 1994; Albert, 1995; Lokkeborg & Ferno, 1999). Patterns of activity can often provide important clues that can be used to distinguish between specific behaviours or behavioural strategies (Noakes, 1992) and, in part, their determinants. For example, Lokkeborg (1998) found that cod in a fjord in northern Norway were more active by day than at night, corroborating evidence from a previous study (Lokkeborg et al., 1989) in which cod were found to increase activity levels at dawn. These results were interpreted as diurnal changes in foraging activity associated with visual feeding. In another example, Arnold et al. (1994) demonstrated patterns of vertical movement in cod that correlated activity with tidal, rather than daylight, periodicity and suggested that cod were using tidal flows to beneficial effect whilst migrating long distances. However, while such studies have been important in advancing the understanding of how cod may modulate their behaviour over short time periods, the activity patterns of cod over longer time-scales have not been described in any detail (Arnold et al., 1994). Such long-term behavioural studies are necessary to reduce or verify the assumptive burden of fisheries management models that incorporate aspects of fish behaviour, such as MSVPA (Magnusson, 1995).

Here we describe the results of a tagging experiment carried out with free ranging adult cod in the southern North Sea between April and November 1999. The tagging was conducted with fish caught off Lowestoft which were assumed to belong to the population that migrates annually between summer feeding grounds in the central North Sea and winter spawning grounds in the Southern Bight and eastern English Channel (Daan, 1978). The aim of the work was to use Data Storage Tags (DSTs) to monitor level and patterns of activity of cod as they move north after spawning in the eastern Channel.

METHODS

Data Storage Tags

The Mark 3 Data Storage Tag (DST) is a small (16g in air, 1g in water) electronic tag capable of storing over 500,000 data samples (Metcalf & Arnold, 1997). The tag records depth ($0\text{--}100\text{m} \pm 0.02\text{m}$) and water temperature (-4 to $23^{\circ}\text{C} \pm 0.03^{\circ}\text{C}$) at ten minute intervals, and light intensity at five minute intervals. Data stored within returned tags are downloaded with dedicated hardware /software and output to PCs for analysis.

Fish tagging

All fish were caught by rod or long-line in an area close to Lowestoft (bounded by the corners $52^{\circ}22.42'\text{N}$, $1^{\circ}45'00\text{E}$ and $52^{\circ}26.39'\text{N}$, $1^{\circ}47.49'\text{E}$) during March when post-spawning cod are present along the East Anglian coast (Arnold et al., 1994). Fifty-eight cod were caught from an area of shallow water where the depth did not exceed 25m. Individuals were brought slowly to the surface to minimise risk of rupture to the swim bladder. None of the caught individuals displayed evidence of swim-bladder rupture such as postural problems or swim bladder eversion through the mouth. Cod greater than 50cm in length were considered suitable for tagging, and were immediately fitted with a Mark 3 Data Storage Tag (Lotek LTD_100 DST). The mean length of tagged cod was 64 cm (range: 50-78cm). Post-tagging, individuals were placed in a shallow tank for 15 minutes to allow them to recover before they were released back into the sea.

Of the fifty-eight tags deployed, 22 (38%) had been returned by March 2000, summing to 1595 days of behavioural data covering the period 24 March to 9 November. Tagged cod had been at liberty between 10 and 224 days (mean = 72 ± 65 days). The number of returned tags that were recording data in any given week of the study period is shown in Figure 1.

Data analysis

Data from the first 24h after release, and any data from the day of capture were not used in the analyses. The difference in depth between successive data-points was calculated to determine vertical distance moved per 10-minute period. When a fish was at rest on the seabed (See Figure 2, Phase II callout), changes in depth (up to 70cm between successive datapoints) occurred due to the rise and fall of the tides. While this enables geolocation (see paragraph below), this apparent movement needed to be taken into account when calculating activity. An active fish was therefore defined as an individual that adjusted its depth at a rate greater than 7cm min^{-1} , or that changed its direction of movement more than 50% of the time in the twenty-minute period either side of the data point under analysis. Mean values of the distance moved by each individual in the vertical plane (hereafter termed vertical movement) and proportion of time spent active were computed per hour for each fish and collapsed to daily and weekly means. Population means and

standard errors were calculated after testing for homogeneity of variance using the Levene test, and appropriate parametric or non-parametric statistical tests were used to investigate the significance of any differences between data populations. All values, unless otherwise stated, are reported as means plus or minus one standard error of the mean.

In the North Sea, the amphidromic system of tides means that geopotential information can be derived from DST depth data if the tagged fish rests on the seafloor long enough (see Figure 2, Phase II callout) that the time of high or low water and tidal range can be extracted (as for Metcalfe & Arnold, 1997). Where possible, these data were extracted from the tracks of individual fish and possible positions were derived using the Tidal Location Method (Hunter et al., in prep). These positions were corroborated with databases on depth (Royal Admiralty Charts) and sea surface temperature (BSH Hamburg and Rostock North Sea SST charts) and spurious positions eliminated. We acknowledge that SST information has limitations because of the variation of temperature at depth. Nonetheless, SST proved useful when differentiating between positions in the Northern North Sea, Eastern North Sea (off the coast of Denmark) and in the English Channel during the first and last few months of the year.

RESULTS

Seasonal activity

As determined by the proportion of time spent active, cod showed four distinct behavioural phases during the period of study (Figure 2). Phase I was characterised by high activity (mean proportion of time active = 0.51 ± 0.01), followed by a rapid decline into Phase II (mean 0.13 ± 0.01) and then rising through Phase III (0.23 ± 0.01) and Phase IV (0.44 ± 0.03). The mean proportion of time spent active differed significantly between phases (Kruskal-Wallis ANOVA $\chi^2_{3}=740$ $p<0.01$).

Vertical movement rates showed a similar pattern to activity (Figure 3). Phase I (April and May) was characterised by directionally erratic vertical movements (mean $142.6\text{m} \pm 2.3$: Figure 2, Phase I callout) unrelated to the diurnal cycle. Visual inspection of the depth profiles suggested that individuals spent most of their time in mid-water although made frequent visits to the seafloor. Toward the end of phase I, vertical movement rates declined sharply (Figure 3) to low levels. Phase II (June through to late August) was characterised by low rates of vertical movement (mean $28.5\text{m} \pm 2$), with fish remaining on the sea floor for most or all of the time (Figure 2, Phase II callout). In Phase III (late August to mid-October), vertical movement rates increased (mean $42.2\text{m} \pm 3$) although not substantially because individuals only left the seabed during darkness hours (Figure 2, Phase III callout). As nights became longer, the mean hourly rate of night-time movement increased as Phase III progressed (Figure 4). The end of Phase III was marked by the sudden return of individuals to Phase I-type behaviour and high vertical movement rates (mean $105\text{m} \pm 10.9$). The vertical movement rates differed significantly between phases (Kruskal-Wallis ANOVA $\chi^2_{3}=798$ $p<0.01$).

Daily activity

In addition to the seasonal shifts in behaviour described above, cod demonstrated shifts in diurnal behaviour associated with each phase (Two-way ANOVA $F_{1,3}=80.7$ $p<0.01$). In Phase I, no differences in the proportion of time spent active was discernible between light and dark periods (Figure 5; Student's t-test $p>0.05$, $df=1726$). The same was also true of vertical movement ($p>0.05$, $df=1726$). In contrast, night/ day differences in the proportion of time spent active were manifest in phases II and III ($p<0.01$, $df=1122$ and 1090 for phases II and III respectively). This was also true of vertical movement ($p<0.01$ and $df=1097$ and 1087 for phases II and III respectively). In phase IV, significant night/ day differences existed for the proportion of time spent active only ($p<0.01$, $df=526$).

Geolocation of tags

Of those tags returned, individuals could be geographically located if they were resting on, or close to, the sea floor. The reconstructed tracks of four fish are shown in Figure 6a-d. These data confirm the northeast migration of fish from their release point. Two tagged fish spent the entire summer, i.e. behavioural phases II and III, in the same area (Figure 6c and d). The recapture position of one of those fish (Figure 6c) demonstrates that it had begun a southward migration during behavioural phase IV.

DISCUSSION

The data recovered from the DSTs used in this study have enabled us to identify four distinct phases in the behaviour of those cod recaptured after tagging and release, and demonstrates seasonal changes in activity previously undocumented for free-ranging adult cod. Vertical movement of fishes in the water column is significant because it is linked to migration (Arnold et al., 1994; Godø & Michalsen, 2000), feeding (Sogard & Olla, 1996; Lokkeborg, 1998) and predator avoidance (Sogard & Olla, 1997). Since the cod in this study were 50 cm or over, and therefore unlikely to experience any significant predation risk (Pallson, 1994), and were outside the spawning season, the vertical movement patterns described herein are likely to relate to patterns of migratory and feeding activity.

The period of activity at the start and end of the study period was associated with migratory movement in mid-water. Arnold et al. (1994) observed that cod of the Southern Bight population swam at a constant heading in mid-water and used selective tidal stream transport to migrate to summer feeding grounds. Our results would appear to suggest that cod remain in mid-water as they migrate, rather than using selective tidal stream transport, although individuals did make erratic ascents and descents to the sea floor. It is possible that this may have been to conserve energy in the face of opposing tidal flows, or alternatively to feed on benthic prey. Further analyses will be required.

The end of the period of mid-water swimming corresponded to uptake of seabed residence over alleged feeding grounds in the central North Sea (Daan, 1978) and a switch from a three dimensional to a two dimensional environment. This was followed by an extended

period (Phase II) during which cod exhibited very low levels of vertical movement, which challenges any notion of active foraging. Although descriptions of cod moving from pelagic layers to the benthos have been described (Zilanov, 1963; Beamish, 1966; Godø & Michalsen, 2000), the data presented here suggest a significant behavioural switch from high activity to inactivity that has not previously been recorded for adult cod. Such a rest period, or 'sit and wait' strategy, may be favoured over active feeding in order to conserve energy if prey are not abundant. Summer starvation of wild cod has been noted in cod caught in the Gulf of St Lawrence (Guderley et al., 1996).

Cod exhibited clear nocturnal activity in the third behavioural phase in late August/September, in line with earlier studies that demonstrated that cod in the Norwegian Sea, Barents Sea and north-west Atlantic are more active by night (Zilanov, 1963; Beamish, 1966). Activity increased throughout this phase, a combination of increasing night-length and an increasing range of vertical movement. As the vertical movement at night was not matched to tides and therefore unlikely to relate to a migratory function, the most rational functional explanation of this movement pattern is foraging activity in advance of the pre-spawning migration.

These data demonstrate, for the first time, that cod exhibit clear seasonal shifts in behaviour strongly associated with geographic location. Behavioural information is integral to the development of fisheries management models because the ecological dynamics of populations are directly influenced by the collective decisions of individual fish (Olla et al., 1996). Multispecies models such as MSVPA (Magnusson, 1995) rely on behavioural functions such as prey preferences and food intake embedded within them. Observations on diel and seasonal changes in the behaviour of individuals, such as those we have described here are crucial in assessing the validity of assumptions and approaches used in current multispecies fisheries management models.

ACKNOWLEDGEMENTS

This work was funded by the Ministry of Agriculture, Fisheries and Food under contracts MF0130 and MF0317.

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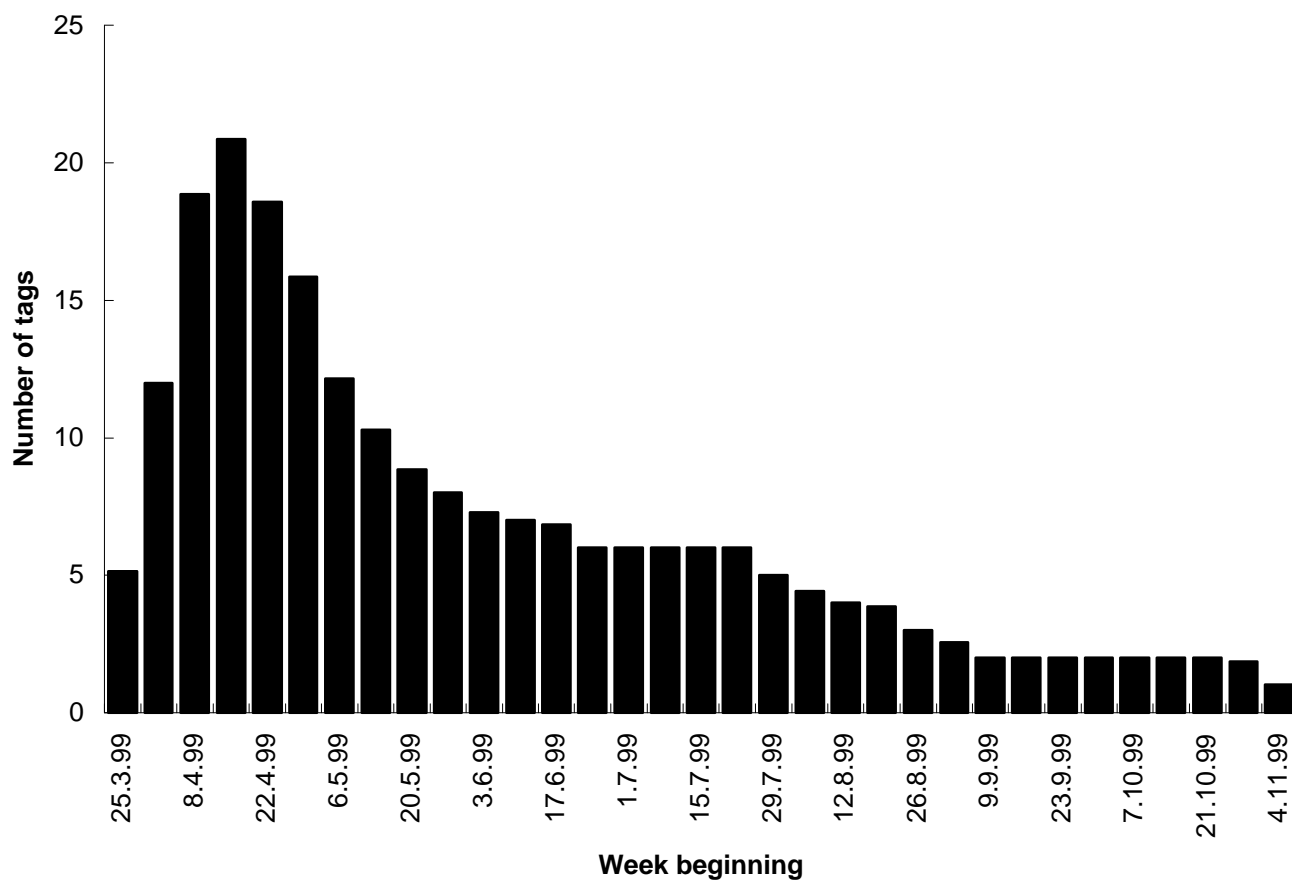


Figure 1. Mean number of returned tags that were recording data for each week of the study period.

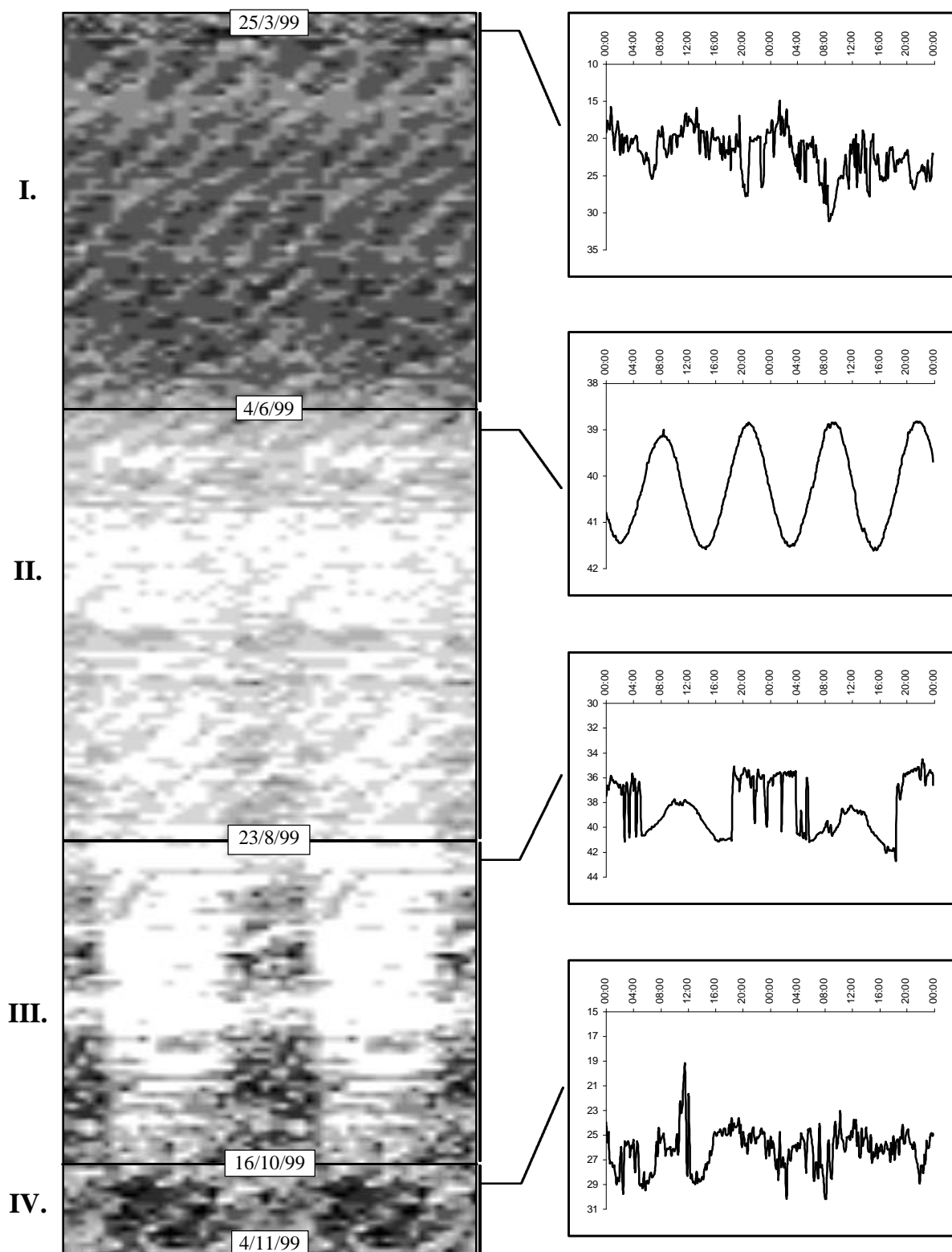


Figure 2. Double plot actogram (left) of cod activity (consolidated data from 22 individuals) based on activity level and typical depth profiles (call-outs to right) associated with each identified behavioural phase. Activity levels are coded by shade: darker shades represent greater proportions of time spent active.

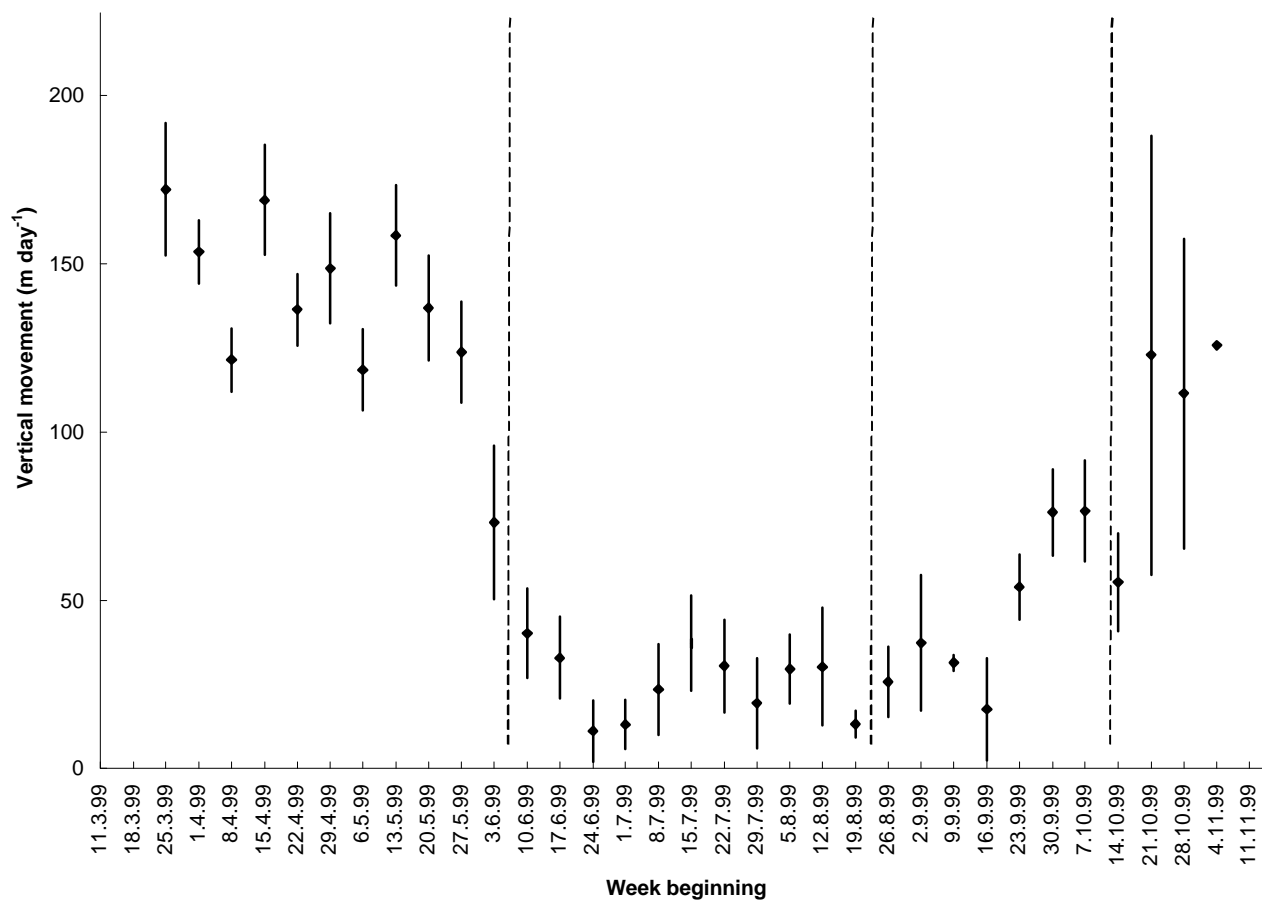


Figure 3. Mean daily rate (error bars show plus/minus one standard error) of cod vertical movement for all weeks during the study period. Data were consolidated from all individuals still at liberty.

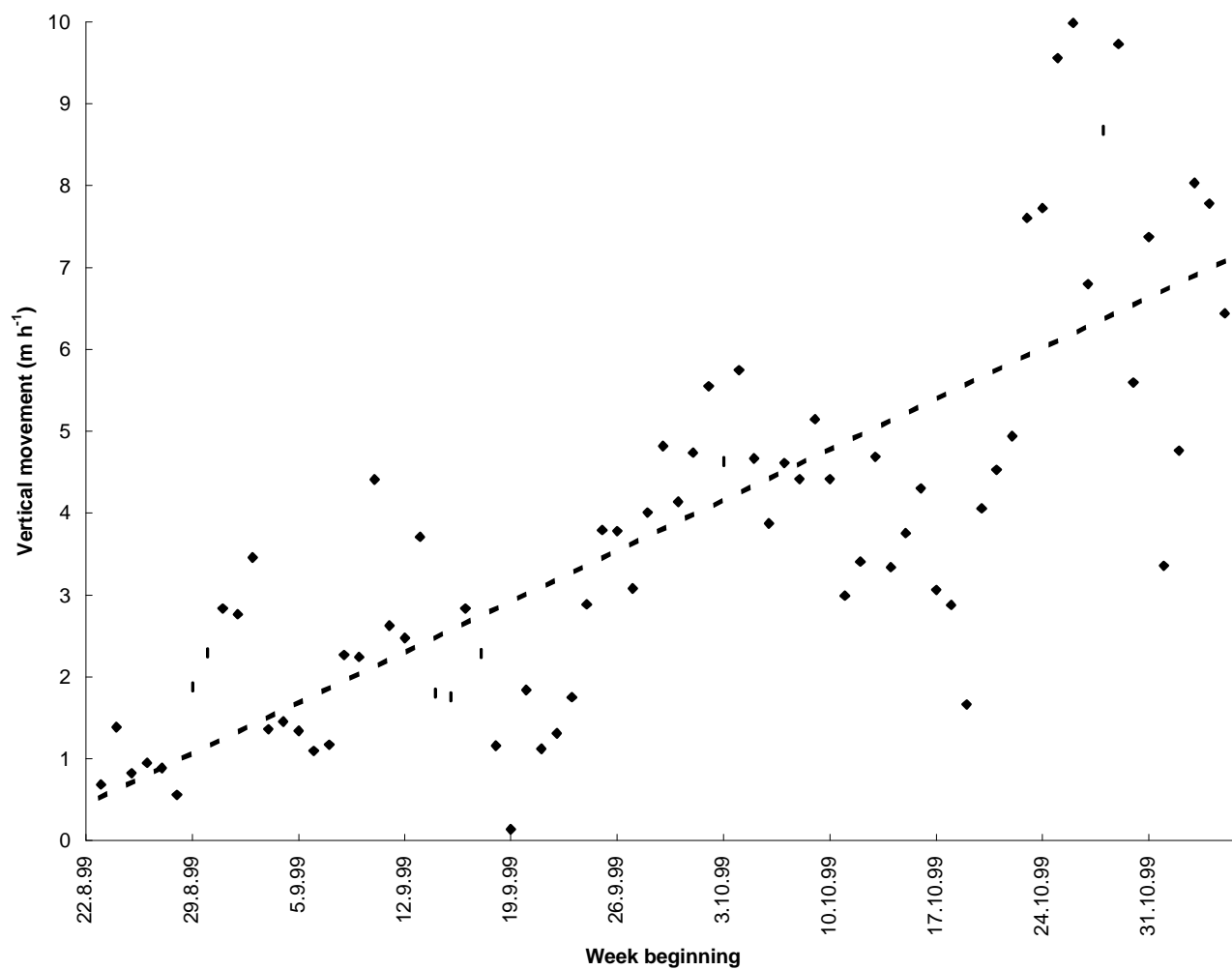


Figure 4. Mean rate of vertical movement (m h^{-1}) of cod during darkness hours in phases III and IV. The fitted line has an R^2 value of 0.62 ($p < 0.01$).

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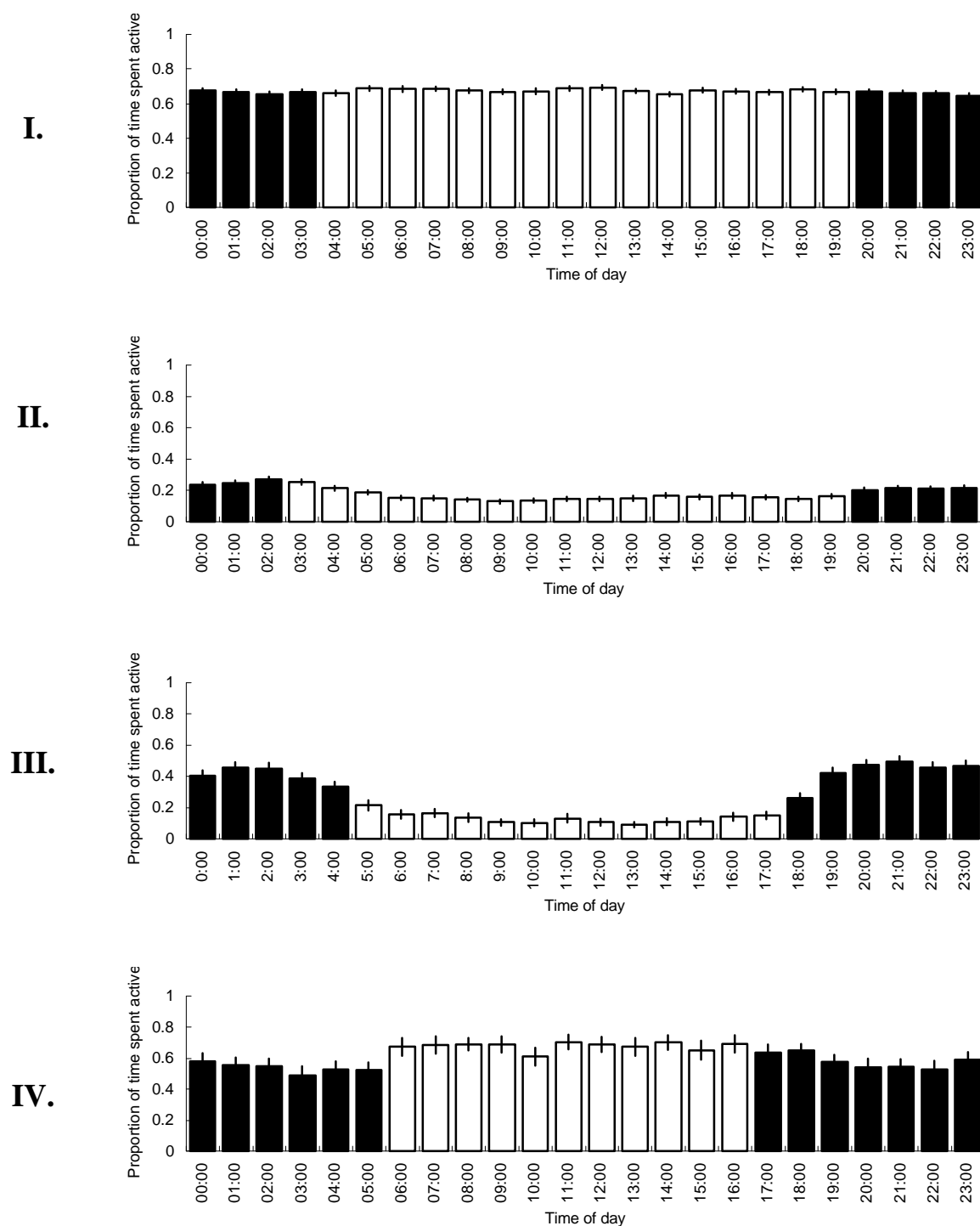


Figure 5. Mean proportion of time spent active (error bars show plus/ minus one standard error) during phases I-IV of the study period. Shaded bars denote darkness hours. Data were consolidated from all tags still at liberty.

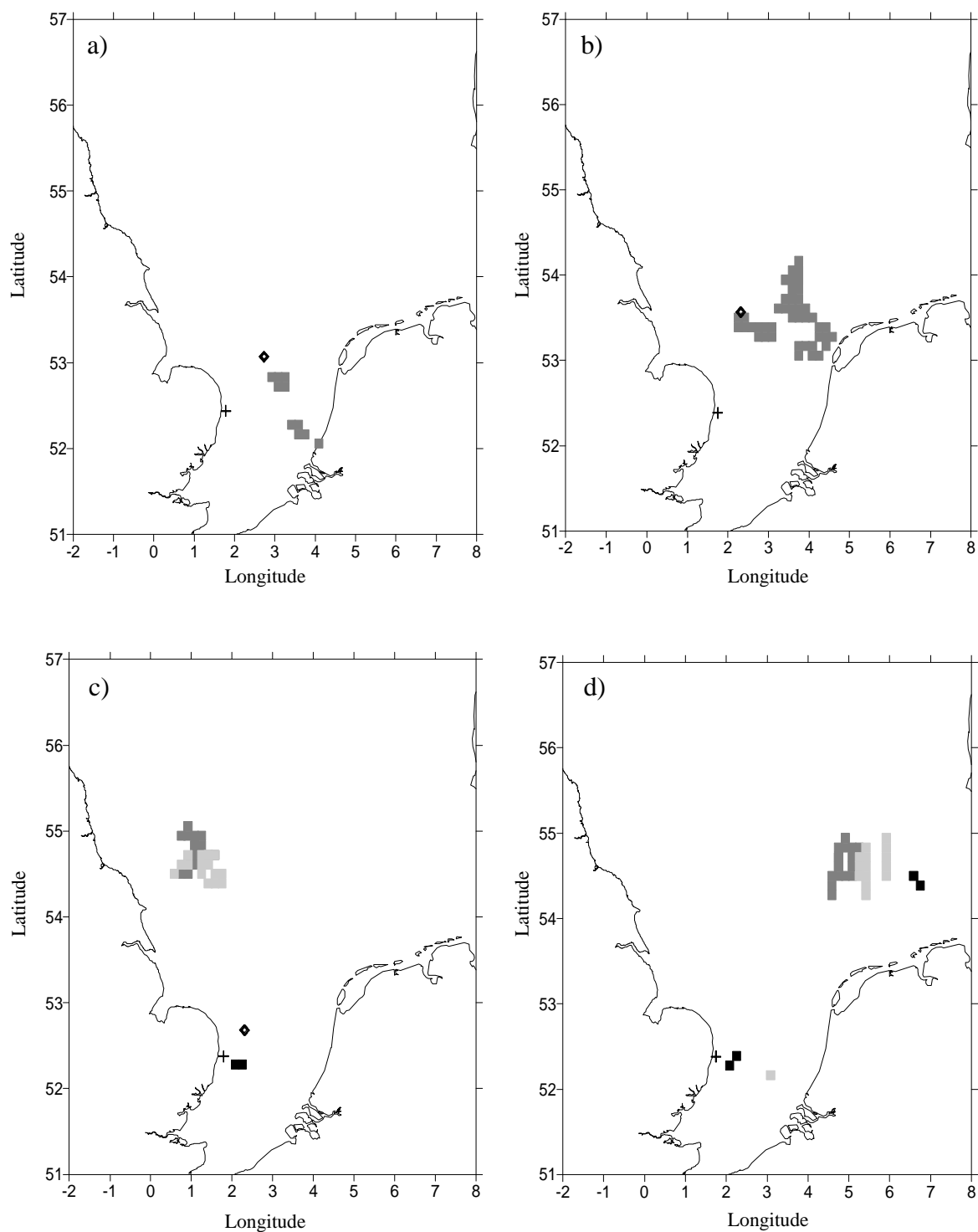


Figure 6. Reconstructed tracks of four fish showing the release position off Lowestoft and most probable geographic locations during each behavioural phase (+ = Release position, ■ = Phase I, ■ = Phase II, ■ = Phase III and ♦ = Recapture position)