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# Fish movement vectors and the temperature gradient: A geometric analysis method for the depth–temperature time series from data storage tags

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The problem of how to extract information about the horizontal movement and estimate the possible location of a fish from a bivariate time series [d(t), c(t)] of depths and temperatures is considered. The ratio $r(t)=[c(t)-c(t-1)]\cdot[d(t)-d(t-1)]^{-1}$ is determined by the movement of the fish in the time interval $[t-1,t]$ and the temperature distribution. Geometric considerations lead to formulae that connect r(t), the average temperature gradient $\overline{\nabla T}$ and the unknown horizontal component of the fish moving in the direction of the horizontal component of $\overline{\nabla T}$. The formulae are tools to study the tag record and CTD data in order to describe the relationship between fish movements and temperature distribution.



Key words: data storage tags, time-series analysis, temperature gradient, temperature distribution, fish movement behaviour.

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## Introduction

In recent years the study of fish behaviour and its links with environmental variables has been aided by the data storage tag. Tags are usually attached to several fish and some are recaptured in the commercial fisheries after surviving long enough to collect interesting time-series data. Several types of tags exist for fish of various size, with different memory capacity and designed to record different types of information. Tags recording ambient light have been used to determine location from sunset and sunrise times, but the latitude accuracy "is at best several degrees" according to a manufacturer. Moreover in the Barents Sea experiment which we refer to later there are many months without sunset or sunrise. Here we concentrate on tags that record only depth and temperature (Godø and Michalsen, 1997).

With pre-programmed time intervals the tag records at time t the temperature c(t) and the pressure, which is converted to depth d(t). In the absence of a direct record of horizontal movements one should look for indirect clues in the bivariate time series of temperature and depth. We consider first a single fish move between two registrations of temperature and depth and relate these observations to the temperature gradient $\nabla T$ and the component of horizontal motion $Fl_x$ along the horizontal component of $\nabla T$. The "tilt" angle between $\nabla T$ and the vertical line is usually very small but it is central in our analysis.

Particular attention is given to the time series of differences $dd(t)=d(t)-d(t-1)$ and $dc(t)=c(t)-c(t-1)$ and their ratios $r(t)=dc(t)/dd(t)$. From the sequence of r(t)-values, together with the depth and temperature series, one may obtain information about the temperature distribution in the waters where the fish has been and its movements in that environment.

## Material

### Background information from oceanographic surveys (CTD data)

CTD data collected in the Barents Sea in August and September 1996 (ICES, 1996) are used as an example of

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the background information on the spatial distribution of temperature in the waters where the fish may have been (Figure 3). For the study of the tag time series it is an advantage to have this background. The figure shows where the vertical component of $\nabla T$ points downwards (at 90 m depth). $\nabla T$ points upwards with a tilt <6° in about 17% of the 59 342 points in a three-dimensional grid; downwards with a similar tilt at about 75% of the points. At the thermocline $|\nabla T|$ is particularly large and the tilt angle particularly small. Besides the temperatures at several depth levels these data also include many other oceanographic parameters e.g. bottom depth, salinity, and current speed and direction.

### Bivariate time series from simulations

Sequences of random fish positions are generated in a cylinder with a vertical axis of radius R=500, 750, or 1000 m and depth 50 m (uniform distribution). Assuming a constant temperature gradient, $\nabla T$, throughout this volume and choosing arbitrarily the temperature at a reference point, a temperature series was calculated from Equation (12). The size $|\nabla T|$ (=0.045 centigrades per m), and four values of the tilt angle $\pi-\theta$ (0.001, 0.005, 0.025, 0.125 radians) were chosen within the typical range of values derived from CTD data mentioned in the previous section. Thus we obtain four simulated series of ratios r(t) defined in Equation (2) below, all based on the same underlying sequence of fish movements. These simulated series mimic that derived from the tag data at the CTD survey time.

## Methods and results

### Notation and geometry

Let d(t) and c(t) denote, respectively, the depth and temperature recorded in the tag at time t; let dd(t) and dc(t) denote the first order differences, i.e. respectively:

$$dd(t)=d(t)-d(t-1) \text{ and } dc(t)=c(t)-c(t-1) \quad (1)$$

Let r(t) be the ratio of temperature change to depth change, i.e.:

$$r(t)=\frac{dc(t)}{dd(t)}=\frac{c(t)-c(t-1)}{d(t)-d(t-1)}, \text{ assuming } dd(t)\neq 0 \quad (2)$$

We do not consider the actual track of the fish in the time interval [t − 1,t], and will, for simplicity, use the average velocity in our calculation: let the fish be at $\vec{p}(u)$ at time u, define the fish move vector $\vec{F}=\vec{p}(t)-\vec{p}(t-1)$, and write $(d/du)\vec{p}(u)=\vec{F}$ for $t-1<u<t$.

At each point in the water mass we consider two gradient vectors. The gradient of the temperature, $\nabla T$, points in the direction of fastest temperature increase and its length $|\nabla T|$ is proportional to this rate of increase. The gradient of the depth, D, is a unit vector (|D|=1) pointing vertically downwards.

Generally $\nabla T$ depends on the position $\vec{p}(u)$, $t-1\leq u\leq t$. The temperature difference is:

$$dc(t)=\int_{t-1}^{t}\vec{p}'(u)\cdot\nabla T[\vec{p}(u)]du=\vec{F}\cdot\overline{\nabla T} \quad (3)$$

Here · means scalar (inner) product, and:

$$\overline{\nabla T}=\int_{t-1}^{t}\nabla T[\vec{p}(u)]du \quad (4)$$

is the average gradient between $\vec{p}(t-1)$ and $\vec{p}(t)$. Let β and φ be the angles between $\vec{F}$ and, respectively, $\overline{\nabla T}$ and D. Then:

$$dc(t)=|\vec{F}|\cdot|\overline{\nabla T}|\cdot\cos\beta,$$
$$dd(t)=|\vec{F}|\cdot|D|\cdot\cos\varphi=|\vec{F}|\cdot\cos\varphi$$

and provided $\cos\beta\neq 0$:

$$|\overline{\nabla T}|=\frac{dc(t)}{dd(t)}\cdot\frac{dd(t)}{|\vec{F}|\cdot\cos\beta}=r(t)\cdot\frac{\cos\varphi}{\cos\beta} \quad (5)$$

It will be convenient to describe the move in Cartesian coordinates. We choose the origin at the departure point $\vec{p}(t-1)$, let the z-axis (the depth axis) point vertically downwards and choose the two horizontal axes for x and y so that $\overline{\nabla T}$ lies in the xz-plane with a non-negative x-coordinate (Figure 1). Clearly:

$$D=(0\ 0\ 1) \quad (6)$$

Let θ be the angle between $\overline{\nabla T}$ and D. Then:

$$\overline{\nabla T}=|\overline{\nabla T}|\cdot(\sin\theta\ 0\ \cos\theta) \text{ with } \theta\in[0,\pi]. \quad (7)$$

In most cases $\overline{\nabla T}$ is approximately vertical so sinθ will be close to 0. The smallest of θ and π − θ we call the "tilt angle"; it shows how much the temperature gradient deviates from the vertical line (z-axis).

For short let the fish move length be called F:

$$\vec{F}=F\cdot(l_x l_y l_z) \text{ with } l_x^2+l_y^2+l_z^2=1 \quad (8)$$

We take inner products between the unit vector $(l_x l_y l_z)$ in (8) and the unit vectors in (7) and (6) and get:

$$\cos\beta=l_x\cdot\sin\theta+l_z\cdot\cos\theta \text{ and } \cos\varphi=l_z \quad (9)$$

The vertical component of the fish move is the depth

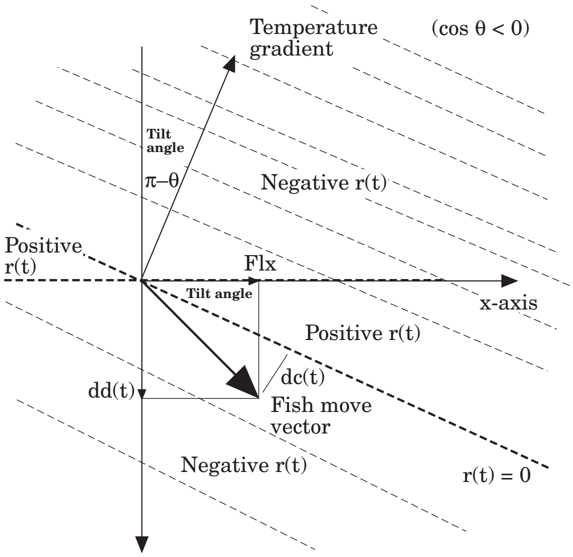


Figure 1. A fish move vector between two observations projected into a vertical plane through the temperature gradient $\overline{\nabla T}$ (the xz-plane). The figure illustrates Equations (12) and (20).

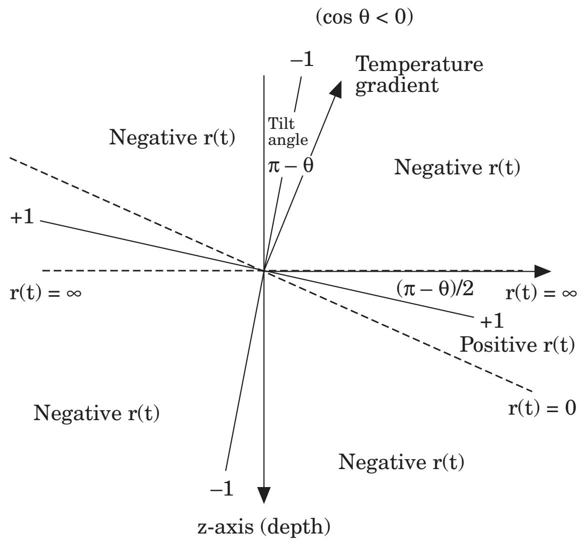


Figure 2. Fish moves along the bisecting lines labelled +1 and − 1 make $r(t) = \pm |\nabla T|$.

difference dd(t), so we have (if $l_z \neq 0$):

$$\frac{\cos\beta}{\cos\varphi} = \cos\theta + \frac{l_x}{l_z}\cdot\sin\theta = \cos\theta + \frac{F\cdot l_x}{F\cdot l_z}\cdot\sin\theta$$

$$= \cos\theta + \frac{F\cdot l_x}{dd(t)}\cdot\sin\theta \tag{10}$$

## Some basic formulae

It is convenient to rewrite (5) as:

$$r(t) = \frac{dc(t)}{dd(t)} = |\overline{\nabla T}|\cdot\frac{\cos\beta}{\cos\varphi} \tag{11}$$

Inserting (10) into (11) and multiplying with dd(t) we find:

$$dc(t) = |\overline{\nabla T}|\cdot[\cos\theta\cdot dd(t) + \sin\theta\cdot F\cdot l_x] \tag{12}$$

This links together the observed differences of temperature and depth, dc(t) and dd(t), the horizontal move component $F \cdot l_x$ along the x-axis, the size of the temperature gradient $|\overline{\nabla T}|$, and the parameter θ. If $dd(t) \neq 0$, we introduce the ratio between horizontal movement in the x-direction and the vertical movement within one period:

$$q = \frac{F\cdot l_x}{F\cdot l_z} = \frac{F\cdot l_x}{dd(t)} \tag{13}$$

and rewrite r(t), using (11)–(13), as:

$$r(t) = |\overline{\nabla T}|\cdot(\cos\theta + \sin\theta\cdot q) \tag{14}$$

An immediate consequence of (14) is that the sign of r(t) is determined by θ and q; the gradient size $|\overline{\nabla T}|$ will only influence the size $|r(t)|$ of the ratio.

## The tilt angle and the size of r(t)

With vertical $\overline{\nabla T}$ we have sinθ=0, and by (6), (7), and (14):

$$\overline{\nabla T} = (|\overline{\nabla T}|\cdot\cos\theta)\cdot D = r(t)\cdot D \quad \text{(where } \sin\theta = 0\text{)} \tag{15}$$

Thus r(t) tells the size and direction of the (vertical) temperature gradient.

We now consider non-vertical $\overline{\nabla T}$; then sinθ>0. Figure 1 shows the orthogonal projection of the fish move vector $\vec{F}$ in the time interval [t − 1,t] into the xz-plane in a situation with cosθ<0. The dotted bold lines are the orthogonal projections of two planes. One is a plane perpendicular to $\overline{\nabla T}$ through the origin; we treat it as an isotherm plane even though it is an approximation to the actual isotherm surface. The other is the horizontal xy-plane. (The dotted plain lines show other isotherm planes.) These two planes divide the water volume in four parts which appear as sectors in the xz-plane (Figure 1). It is convenient to draw both gradients from the origin, even though $\overline{\nabla T}$ depends on $\vec{F}$.

We consider the orthogonal projection of the fish move vector $\vec{F}$ into the xz-plane, and make some observations from (11)–(14) and Figures 1 and 2.

- The ratio r(t) is not defined if the projected move is along the x-axis [when dd(t)=0].

- The ratio r(t) becomes positive if and only if this projected vector is in one of the two tilt angle sectors bounded by the x-axis and the isotherm through the origin.
- Inside a ball with the origin for centre, the fraction of the volume that gives positive r(t) is $(\pi-\theta)/\pi$, i.e. proportional to the tilt angle.
- Large $|r(t)|$-values come with large values of $|q|$, i.e. when the projection of $\vec{F}$ makes a very small angle with the positive or negative x-axis.
- $r(t)=0$ for a fish move along the temperature isotherm plane (undefined along the y-axis).
- A small change in the move $\vec{F}$ will not lead to significant change in $\overline{\nabla T}$ and it can lead to a sign change in r(t) in two different ways. See Figure 2 and Equations (11)–(14). Either (A) q passes $-\cot\theta$ and $|r(t)|$ is very small (the move is almost along the isotherm plane through the origin), or (B) q changes sign "by passing infinity" [i.e. dd(t) changes sign by passing 0] and $|r(t)|$ may be very large.
- If we know $\overline{\nabla T}$, i.e. both $|\overline{\nabla T}|$ and $\theta$, the tag data determine $F\cdot l_x$ by (12).
- Changes in the y-component $F\cdot l_y$ will not change r(t).
- The ratio r(t) decreases from $+\infty$ to $-\infty$ when the projection of $\vec{F}$ is rotated clockwise from the positive or negative x-axis until it meets the x-axis again.

The line marked "+1" in Figure 2 corresponds to $\beta=\varphi=\theta/2$ or $\beta=\varphi=\pi-\theta/2$; it bisects the sectors of positive r(t). Along this line $r(t)=|\overline{\nabla T}|$. The line marked "$-1$" is perpendicular to the "+1"-line and bisects the tilt angle. It corresponds to $\beta=(\pi-\theta)/2$, $\varphi=(3\pi-\theta)/2$. Along this line $r(t)=-|\overline{\nabla T}|$.

From these considerations we get some useful "rules of thumb". They assume the temperature gradient points upwards (i.e. $\theta$ is near $\pi$), and are modified by one sign change if it points downwards:

- Large positive r(t) come with a slightly downward [upward] move with a large positive [negative] x-component.
- Small positive r(t) come with a move slightly above [below] the isotherm plane through the origin with a positive [negative] x-component.
- Large negative r(t) come with a slightly upward [downward] move with a large positive [negative] x-component.
- Small negative r(t) come with a move slightly below [above] the isotherm plane through the origin with a positive [negative] x-component.

## Changes in the tilt angle

We now consider in more detail how the ratio size $|r(t)|$ depends on the tilt angle. Consider two fish moves $\vec{F}_1$ and $\vec{F}_2$ with the same q-value but with two different angles, $\theta_1$ and $\theta_2$, between the temperature and depth gradients, and let the corresponding ratios be $r(t)_1$ and $r(t)_2$. Assuming temperature gradients of the same size, we have by (14):

$$\frac{r(t)_2}{r(t)_1}=\frac{\cos\theta_2+q\cdot\sin\theta_2}{\cos\theta_1+q\cdot\sin\theta_1}=\frac{q^{-1}\cdot\cos\theta_2+\sin\theta_2}{q^{-1}\cdot\cos\theta_1+\sin\theta_1} \tag{16}$$

By inspecting (16) we see how the change of tilt angle from $\theta_1$ to $\theta_2$ affects the ratio r(t). For very small [large] $|q|$ the sines [cosines] may be ignored.

Usually we expect the tilt angles to be close to 0; then the cosines in (16) are approximately $\pm 1$ while the sines are very small, and $|\sin\theta_2\cdot(\sin\theta_1)^{-1}|$ is approximately the ratio between the tilt angles.

Consider a set of fish moves in a depth interval where $\nabla T$ may be sufficiently well represented by the same average $\overline{\nabla T}$ for all moves. By Equation (14):

$$r(t_i)=|\overline{\nabla T}|\cdot[\cos\theta+\sin\theta\cdot q(t_i)],\ i=1,2,\ldots,n. \tag{17}$$

Assume the q-values are negative and positive about equally often; this seems reasonable if the fish is operating in the same environment for some time. The median of the r(t)-values corresponds to the median of the q-values, which is likely to make the term $\sin\theta\cdot q$ negligible. *The median r(t) is therefore a reasonable estimator for* $|\overline{\nabla T}|\cdot\cos\theta$.

The median should be preferred to the average, since the latter is more affected by a few very large $|r(t)|$-values. If the study of fish behaviour should lead to a modification of the assumption on the distribution of q-values one may modify the estimator accordingly to be another fractile of the observed r(t)-values.

Environmental data show that in most situations $\sin\theta$ is so small that $\cos\theta=\pm 1$ is an acceptable approximation. Then, by the above rule, we determine $|\overline{\nabla T}|$ and $\cos\theta=\pm 1$ from tag data when the tilt angle is small, without actually determining the tilt angle first.

Thus it is natural to consider the deviation of the ratio from $|\overline{\nabla T}|\cdot\cos\theta$:

$$q\cdot\sin\theta=r(t)-|\overline{\nabla T}|\cdot\cos\theta \tag{18}$$

Comparing two tilt angles, we then have:

$$\frac{r(t)_2-|\overline{\nabla T}|\cdot\cos\theta_2}{r(t)_1-|\overline{\nabla T}|\cdot\cos\theta_1}=\frac{\sin\theta_2}{\sin\theta_1}\approx\frac{\pi-\theta_2}{\pi-\theta_1}\ \text{or}\ \frac{\theta_2}{\theta_1} \tag{19}$$

Increasing the tilt angle from $\theta_1$ to $\theta_2$ means that the differences $r(t)_1-|\overline{\nabla T}|\cdot\cos\theta_1$ get multiplied by a constant factor about $\sin\theta_2\cdot(\sin\theta_1)^{-1}$. This simple connection is important in the study of the time-series plot of r(t). The plots of the simulated r(t)-series below with different tilt angles show it clearly since they have the same underlying move sequence.

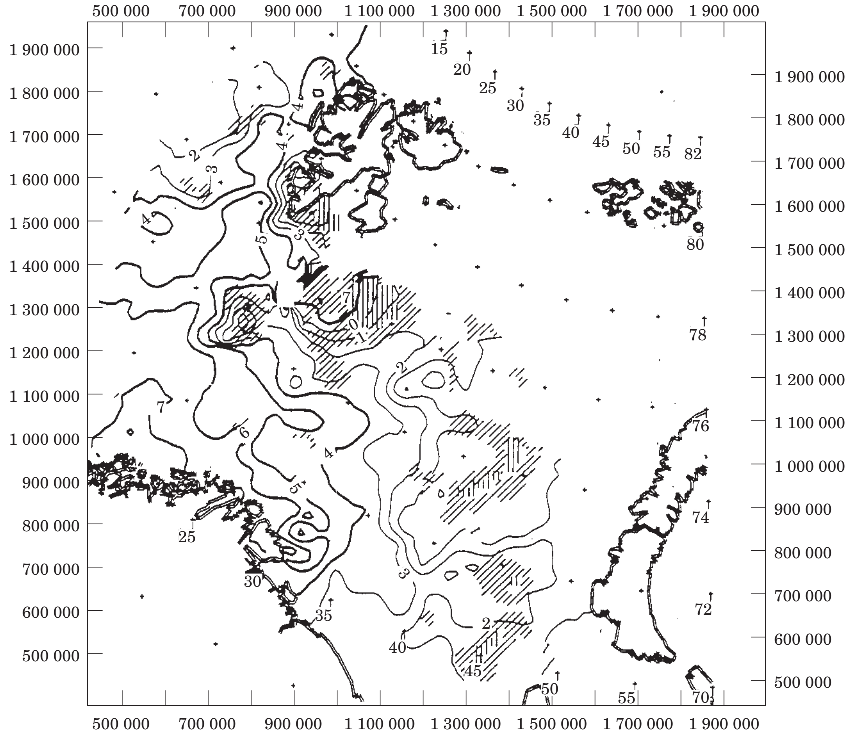


Figure 3. The map indicates areas with θ<0.1 (vertically hatched) and 0.1<θ<π/2 (diagonally hatched) at 90 m depth. These are the areas where the vertical component of ∇T points downwards. These conditions arise where a warm water mass (Atlantic) has higher density than a cold water mass (Polar or from estuaries) due to higher salinity. Notice also the isotherms of the Atlantic waters. The small marks (↑) indicate longitude 15, 20, . . ., 55°E and latitudes 72, 74, . . ., 82°N. The xy-coordinates show distance in meters (polar stereographic projection).

## Simulations

Bivariate time series of depth and temperature are generated as described previously. To simulate a stationary bivariate temperature–depth series, we generate a series of fish move vectors within a short time window.

Plots of the corresponding r(t) series are shown in Figure 4, a–d. For the smaller tilt angles the term $|\nabla T| \cdot \sin\theta \cdot q$ in (14) may be ignored (unless $|q|$ is exceptionally large). The r(t)-values are distributed symmetrically around $|\nabla T| \cdot \cos\theta \approx -|\nabla T|$.

As the underlying motion sequence is the same, the plots a–d illustrate the effect of changing the tilt angle, which is discussed above after Equation (19). Assuming the approximations $r(t)_i - |\overline{\nabla T}| \cdot \cos\theta_i \approx r(t)_i + |\overline{\nabla T}|$ are acceptable in the left hand side of Equation (19), the differences $r(t) - (-0.045)$, will get multiplied by a factor $\approx 5$ from one plot to the next.

The number of positive r(t)-values depends on θ and the distribution of q-values. To illustrate this, we generated five series of 1001 fish positions for each of three different radii R (1000, 750, and 500 m) of the cylinder described earlier and height 50 m. The numbers of positive r(t) are given in Table 1.

Table 2 shows the distributions of $|F \cdot l_x|$, from 10 simulations of 1000 moves each.

# Discussion

## The importance of background knowledge

From the CTD data we obtain knowledge of the spatial distribution of ∇T. The CTD data are spatially correlated (Journel and Huijbregts, 1978; Cressie, 1991). The spatial correlation property is important also for the analysis of tag data. Values located at points close together are generally highly correlated and in particular the temperature gradient ∇T does not change abruptly in length or direction. When the time window is small it will be an acceptable approximation to regard ∇T as a function of depth alone and assume the same average $\overline{\nabla T}$ for all fish movement vectors over the same depth interval. From the CTD data and the locations of release and recapture the angle θ may be known at the beginning and the end of the time series.

The bivariate time series recorded in a tag reflects two components: the fish behaviour i.e. its sequence of move

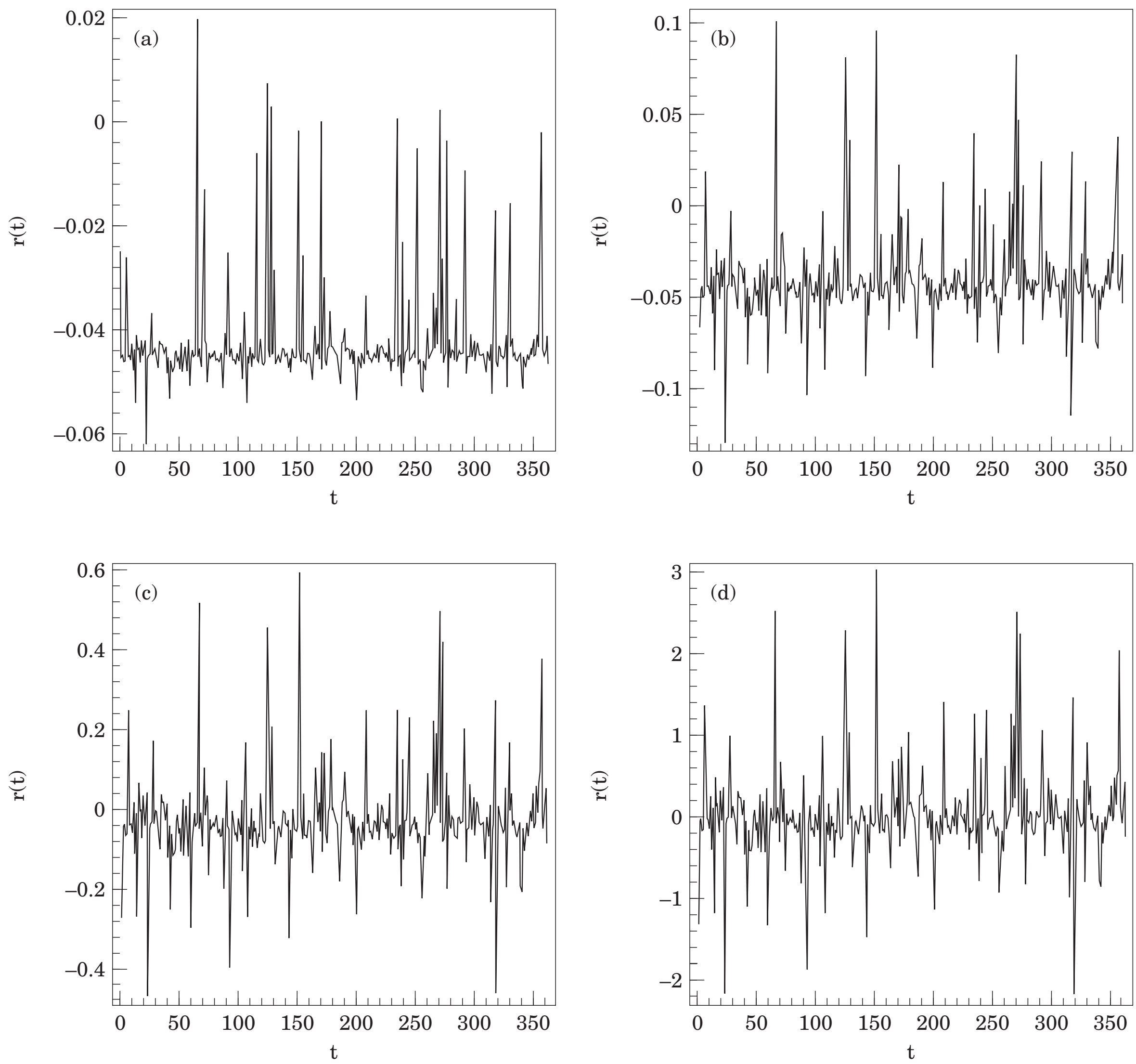


Figure 4. Tilt angle (a) 0.001, (b) 0.005, (c) 0.025, and (d) 0.125. Three hundred and sixty periods, R = 1000 m, height = 50 m.

vectors $\vec{F}$, and the distributions of the temperature T, $|\nabla T|$ and θ. The analysis of the bivariate time series should make use of available background information on either of these two components from CTD data or observed fish behaviour. The more we know about one of them the more the analysis can tell about the other.

Perhaps other environmental information than the temperature distribution, like, for example, current patterns, may give a useful background to be combined with the tag data in order to understand the horizontal migration. Arnold and Holford (1995) have modelled the moves of fish from several species with known tidal current patterns in the North Sea. However, we make no attempt to include such information in the present discussion.

A time-series analyst may also have to consider the significance of the difference in scale. The CTD data come from line transect stations which are much further apart than the length F of one fish move. Even so the spatial dependence between data from different stations makes it reasonable to assume that in most locations there is no important small-scale structure in the temperature distribution which does not fit with the large-scale picture. A notable exception, however, is when the fish is in turbulent waters near a front.

It should also be remembered that the study of the r(t)-series must be accompanied by standard time-series techniques on the series {d(t), c(t)}. In particular we mention spectral techniques (Priestley, 1981) for the detection of time stretches with cyclical behaviour, e.g.

Table 1. The number of positive r(t) in simulations of 1000 fish moves.

| Radius | $\pi-\theta=0.001$ | $\pi-\theta=0.005$ | $\pi-\theta=0.025$ | $\pi-\theta=0.125$ |
|---|---|---|---|---|
| 1000 | 19 | 62 | 220 | 435 |
| 1000 | 10 | 44 | 239 | 431 |
| 1000 | 08 | 48 | 224 | 424 |
| 1000 | 08 | 57 | 245 | 455 |
| 1000 | 12 | 57 | 239 | 420 |
| 750 | 07 | 37 | 175 | 401 |
| 750 | 10 | 45 | 200 | 412 |
| 750 | 10 | 41 | 208 | 398 |
| 750 | 04 | 34 | 183 | 416 |
| 750 | 08 | 51 | 200 | 423 |
| 500 | 02 | 25 | 114 | 351 |
| 500 | 05 | 39 | 150 | 373 |
| 500 | 06 | 31 | 125 | 384 |
| 500 | 15 | 32 | 143 | 367 |
| 500 | 09 | 31 | 146 | 381 |

Table 2. The distribution of $F \cdot l_x$ in simulations of 1000 fish moves.

| 0.0–0.2 | 0.2–0.4 | 0.4–0.6 | 0.6–0.8 | 0.8–1.0 | 1.0–1.2 | 1.2–1.4 | 1.4–1.6 | 1.6–1.8 | 1.8–2.0 |
|---|---|---|---|---|---|---|---|---|---|
| 207 | 202 | 178 | 131 | 111 | 79 | 55 | 24 | 12 | 1 |
| 236 | 188 | 173 | 123 | 113 | 76 | 54 | 24 | 11 | 2 |
| 224 | 178 | 170 | 133 | 96 | 98 | 55 | 26 | 17 | 3 |
| 217 | 181 | 168 | 136 | 115 | 87 | 55 | 23 | 14 | 4 |
| 209 | 188 | 169 | 160 | 111 | 67 | 50 | 36 | 9 | 1 |
| 211 | 195 | 170 | 125 | 106 | 92 | 60 | 28 | 13 | 0 |
| 240 | 203 | 150 | 149 | 108 | 79 | 43 | 18 | 8 | 2 |
| 213 | 187 | 173 | 138 | 110 | 80 | 58 | 25 | 15 | 1 |
| 211 | 199 | 174 | 144 | 108 | 69 | 56 | 24 | 14 | 1 |
| 230 | 189 | 178 | 119 | 110 | 86 | 51 | 23 | 12 | 2 |

The upper left 207 means there were 207 cases with $0 < F \cdot l_x \leq 2/10 \cdot R$ in the first simulation, etc.

diurnal or tidal cycles (Stensholt, 1998). With the techniques from the Methods and results section one may describe the temperature distribution where such cyclical behaviour occurs.

## The interplay between background knowledge and the tag data

Two vectors, $\overline{\nabla T}$ and $\vec{F}$ determine the scalar r(t). Obviously r(t), and even the four observed scalars $d(t-1)$, $d(t)$ and $c(t-1)$, $c(t)$, are insufficient information to recover two vectors. In particular, as pointed out earlier, the tag information does not allow us to recover any move component $F \cdot l_y$ along the y-axis. However, the time-series data may well allow us to draw some conclusions about the two unknown vectors $\overline{\nabla T}$ and $\vec{F}$.

It is convenient to rewrite (12) as:

$$\sin\theta \cdot F \cdot l_x = [dc(t)/|\overline{\nabla T}|] - \cos\theta \cdot dd(t) \tag{20}$$

Equation (20) exhibits the mentioned interplay by bringing together $\overline{\nabla T}$ and $\vec{F}$. Assuming the approximation $\cos\theta = \pm 1$ is acceptable, we may estimate $|\overline{\nabla T}|$ from a set of moves as explained in the section on "Changes in the tilt angle". We then obtain by (20) a set of products $\sin\theta \cdot F \cdot l_x$ from the tag data. The better we know θ, the better we can determine the move component $F \cdot l_x$. Conversely, empirical knowledge about how the $F \cdot l_x$ may be distributed may indicate a reasonable interval estimate for θ.

In order to get information about the angle θ from the tag data, consider the whole set of $F \cdot l_x$-values for a time stretch where we may assume that $\nabla T$ has not changed.

- The sizes $|F \cdot l_x|$ are bounded upwards by the swimming speed (for some species about one fish length per second), and this puts a lower bound on our estimate of $\sin\theta$.
- Let m be the (unknown) median of the $|F \cdot l_x|$, and M the median of the $\sin\theta \cdot |F \cdot l_x|$. M is calculated from tag data by (20), using the approximation $\cos\theta = \pm 1$.

If experience indicates that $m \in [\alpha,\beta]$ with a certain probability, the equivalent formulations:

$$m \in [\alpha,\beta] \Leftrightarrow M \in [\sin\theta \cdot \alpha, \sin\theta \cdot \beta] \Leftrightarrow \sin\theta \in [M/\beta, M/\alpha]$$

give an interval estimate for $\sin\theta$.

Moreover, it may be useful to combine various items of information to discover special patterns in the fish's movement behaviour. We mention a few examples:

- If a move sequence is characterized by large dd(t)-values together with small r(t)-values, and the tilt angle is not unusually large, then the fish has made several moves with large $|F \cdot l_x|$ close to the isotherm plane.
- Large $|r(t)|$ may be explained in different ways. At the thermocline $|\nabla T|$ is particularly large, while the tilt angle is very small. The r(t)-values are all close to $-|\overline{\nabla T}|$. In front areas the tilt angle is often large. Both positive and negative r(t) with very large $|r(t)|$ occur.
- The distribution of $F \cdot l_x$-values may be calculated from (20) (based on some $\theta$-value, which itself is not important in this context). What restrictions does the calculated distribution impose on the joint distribution of the vectors $(F \cdot l_x, F \cdot l_y)$? Is there reason to suspect that the latter is not rotationally symmetric, i.e. that the fish prefers some move directions to others? Tracking experiments may perhaps be worthwhile.

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