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Predicting fish behaviour in response to abyssal food falls

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Abstract Estimates of fish abundance based on arrival rates and numbers present at baited cameras allow multiple, replicate assessments where data are not available by other means. Unfortunately such estimates are strongly affected by the assumed behaviour of the fish species concerned. Three of the possible foraging strategies of deep-sea fish were modelled and the likely patterns of fish arrival calculated for the same fish density, swimming and current velocities and odour plume properties. Cross-current foraging resulted in the highest numbers of fish at bait, with arrival rates that fitted well to field data. The sit-and-wait strategy produced lower arrival rates with passive drifting animals arriving slowest. Each model produces a distinctive pattern of animal arrivals that may be diagnostic of each foraging strategy. The advantages, disadvantages and likely metabolic and sensory demands of each strategy are discussed.

Introduction

The use of baited camera systems has provided valuable insights into the behaviour and ecology of scavenging deep-sea animals allowing determination of the species attracted to carrion and their rates of arrival at recent food falls (Isaacs and Schwartzlose 1975; Jones et al. 1998; Collins et al. 1999b; Witte 1999). These data allow multiple, replicated, estimates of scavenger abundance not otherwise available due to the difficulty and time required to make quantitative collections of deep-sea animals by trawling or large-scale surveys by submersible or camera sled (Priede and Merrett 1996, 1998; Cailliet et al. 1999).

In conjunction with the use of ingestible acoustic tags autonomous lander platforms have measured fish swimming speeds and allowed the description of behaviour and direction of travel after feeding (Bagley 1992; Collins et al. 1999a; Priede and Bagley 2000). However the biologically important processes by which deep-sea scavengers detect food falls and locate the potential meal cannot be observed in this way. Inferences must therefore be derived from estimates of the sensory abilities of deep-sea animals (Wagner et al. 1998; Warrant 2000), tracking and other studies in shallow water relatives (He 1991; Arnold et al. 1994; Løkkeborg 1998; Løkkeborg et al. 2000) and the behaviour of other scavenging animals (Morton and Yuen 2000).

A variety of potential food acquisition strategies exist, including active foraging across currents (Priede et al. 1991), drifting on the ambient current, sit-and-wait ambush or passive plume detection (Wilson and Smith 1984; Sainte-Marie and Hargrave 1987). Optimal search directions for plumes of different shapes have been calculated by Dusenbury (1989) and show that as plumes become more elongated cross-current foraging should be favoured. Compromises such as active foraging around a "core" area or periodic foraging and torpor have also been documented in Gadids (Løkkeborg 1998; Løkkeborg et al. 2000).

Several factors might affect the number of fish attracted to bait and their rates of arrival and dispersal (Priede et al. 1994b). Current velocity affects the length of the odour plume emanating from the bait; its lateral dispersal and the across-ground swimming speed of fish. The intrinsic, or through-water, swimming speed of foraging fish affects the rate at which animals come into contact with the bait, as does the abundance (density) of the fish. Changes in fish speed in response to odour plumes have been documented in cod, *Gadus morhua* (Løkkeborg 1998), altering their potential rates of

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arrival. The effective length of the plume depends on the bait characteristics and persistence, the olfactory performance and behaviour of the fish. Even the most persistent exposed baits such as marine mammal carcasses do not endlessly accumulate fish with a plateau in numbers being attained (Jones 1999; Witte 1999). The numbers present depend on the staying time of animals as well as their arrival rates (Sainte-Marie and Hargrave 1987).

The complexity of these interacting variables is reflected in the range of relationships between time and fish abundance presented for deep-sea fish (Lampitt et al. 1983; Wilson and Smith 1984; Jones et al. 1998; Collins et al. 1999a; Witte 1999). Unfortunately much of the empirical data required to develop a more complex model to explain these observations does not exist. In the present study, three simple models of fish behaviour around both transient and long-lasting baits are presented. The models demonstrate the importance of our assumptions about the behaviour of foraging fish and which data are required to quantitatively improve our understanding of the ecology of deep-sea fish.

The main model describes the "cross-current" foraging strategy suggested for *Coryphaenoides armatus* (Priede et al. 1991) with "sit-and-wait" and "passive drifting" strategies (Wilson and Smith 1984) considered separately (Fig. 1). The models allow the manipulation of several parameters likely to affect the behaviour of fish around bait or natural food falls in order to develop a priori hypotheses that may be tested by observation.

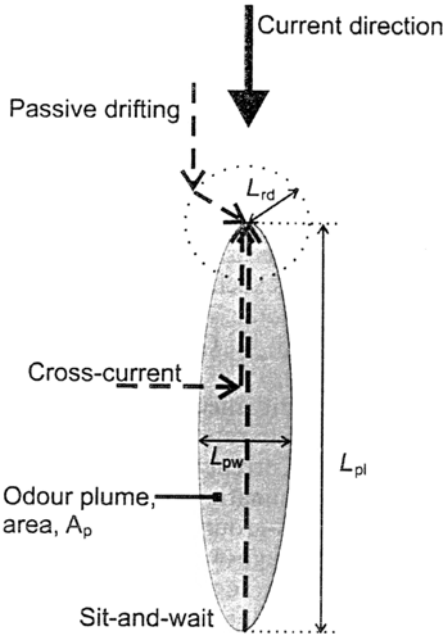

Fig. 1 The types of foraging behaviour proposed for deep-sea fish. The shape of the odour plume with respect to the prevailing current is shown, as are the predicted tracks of fish responding to the bait

Materials and methods

Model development – cross-current foraging

Outline

The plume represents a barrier to fish foraging across the current. On contact with the plume fish turn upstream and swim to the bait then, after a period at the bait, the fish leaves. With small, transient, baits such as single mackerel carcasses, the plume becomes less attractive as it dilutes and eventually falls below the threshold at which the fish can detect the odour. Fish swimming close to the bait continue to be attracted by the sounds, movements, and light emissions of other animals feeding.

Assumptions

Fish swam at an average of 90° to the direction of current movement. This was based on the findings of Priede et al (1991) which showed that the exit direction of *C. armatus* ingesting transponders was biased towards cross-current movement. All fish contacting the plume reacted by turning upstream (rheotaxis) and followed the plume to its source. Approach direction of grenadiers arriving at bait was most often from a downstream direction (Wilson and Smith 1984). The ranges at which fish can detect plumes and react by turning upstream were based on those for cod (Løkkeborg 1998). Fish were evenly distributed across the seafloor. No shoaling behaviour has been demonstrated in tracked fish (Collins et al. 1998) with animals dispersing independently after feeding. Each species or size class was also treated independently with no density dependence affecting fish behaviour. There is some evidence of interspecific competitive exclusion (Armstrong et al. 1992; Jones 1999) but not enough data are available to include this in the models.

Water velocity and direction were constant. While this is reasonable over the first 1–2 h post-deployment during longer-term experiments this may be a significant over-simplification.

Input parameters

The variables that might be manipulated within the model were fish swimming speed (through water as opposed to across ground speed) during foraging. Unless stated the fish swimming speed used was 0.1 m s^{-1}, based on values for *C. armatus* (Priede and Merrett 1996). A different swimming speed could be set for approaching the bait. Cod (*G. morhua*) swim up to 3 times as fast following olfactory contact with bait than during foraging (Løkkeborg 1998).

Staying time, the length of time from arriving at the bait to departing, can be determined from tracking of ingested transponders (Collins et al. 1998) and is set at a fixed value in each model run. Staying times and the time taken to consume the bait used were 60 and 120 min respectively and are based on observations of mackerel bait using photographic or video lander experiments. Observations with marine mammal carcasses demonstrate a turnover of animals with fish leaving before the bait is fully consumed (Jones et al. 1998). Fish densities in individuals per km^2 and current velocity were based on previous trawl and lander data respectively (Priede and Merrett 1998). Fish densities of 1–800 fish km^{-2} were modelled, with a fish density of 100 fish km^{-2} and a current velocity fixed at 0.05 m s^{-1} unless otherwise stated. The inadequacy of trawling as a method of determining *absolute* fish abundances are acknowledged. The radius around the lander within which fish can detect the bait by the sights and sounds of other animals is not known empirically but some estimates based on morphological studies are available (Warrant 2000). The value of 10 m used here is conservative and likely to require adjustment given the high levels of bioluminescence observed by low-light cameras at bait in some deep-sea systems (Herring et al. 2000).

Rate of arrival at the plume

Rate of arrival at the plume (R_c, fish s^{-1}) depended on the density of the fish species (n_f, fish m^{-2}), their velocity normal to the current (V_{fc}, m s^{-1}) and the length of the plume (L_{pl}, m). In long-term bait experiments the plume reached a maximum width (L_{pw}max, m) beyond which the plume is too dilute to be detected by the fish species. Within a fixed radius (L_{rd}, m) around the bait the fish were able to detect the food source audio-visually as a result of other animals feeding. Fish density (n_f) was a fixed parameter based upon existing trawl data, plume length (L_{pl}) depended on time (t, s) and the velocity of water flow (V_w, m s^{-1}) across the bait (based on existing current logger data). Fish "over-ground" swimming velocity while moving across the current depended on the fish swimming speed through the water (V_{fs}, m s^{-1}) and the current velocity (V_w).

$$L_{pl} = t \cdot V_w$$

$$V_{fc} = \sqrt{V_{fs}^2 - V_w^2}$$

$$R_c = n_f \cdot V_{fc} \cdot (L_{pl} + L_{rd})$$

An effect of this is that the fish is orientated at an angle to its direction of movement, a fact of potential significance to any use of sight and hearing during foraging. The angle, ϕ, depends on the relative velocities of the current and fish.

$$\phi = \text{ArcSin}\frac{V_w}{V_{fs}}$$

Time to arrive at the bait

A delay existed between the fish contacting the plume and arriving at the bait. This delay depended on the distance between the fish and the bait, its swimming speed and the velocity of the current. Assuming uniform fish distribution the mean distance between the bait and the fish was taken as half the plume length. Mean time to bait (t_{mb}, s) was then mean distance between the fish and the bait divided by the approach speed of the fish (V_{fa}, m s^{-1}) where V_{fsa} is the through-water speed of the fish during the approach up the plume. Mean time to bait was added to elapsed time to create an elongated timescale over which fish arrive (t_{arr}, s).

$$t_{mb} = \frac{L_{pl}}{2(V_{fsa} - V_w)}$$

The rate of fish contact with the plume depended on plume length and therefore increased with time. Cumulative fish arrival at time t (n_{arr}) was calculated from the sum of the individual second-by-second arrival rates in fish s^{-1} until t.

$$n_{arr} = \sum R_c$$

Staying time

In all the models, fish left at an identical rate to that at which they arrived with a delay corresponding to the staying time (t_{stay}). Unless stated a staying time of 60 min is used throughout. Deduction of leaving rate from arrival rate gave the net rate of change in numbers from which the cumulative number of fish present was calculated. At time t, numbers present (n_{pres}) depended on the number accumulated by time t and the number accumulated by t-t_{stay}, as these fish leave by time t (Fig. 2).

Numbers of fish present continued to rise while the plume lengthened. As the plume diluted, a threshold dilution after which fish were not attracted to the plume was crossed. This fixed the plume at a maximum length. Olfactory foraging deep-sea fish were assumed to be able to detect plumes at up to 700 m, the maximum range from bait at which cod were observed turning to follow odour plumes (Løkkeborg 1998). When the plume was at a fixed length, time to arrive (t_{mb}) was also fixed. Arrival and departure rates were equal so fish numbers stabilised.

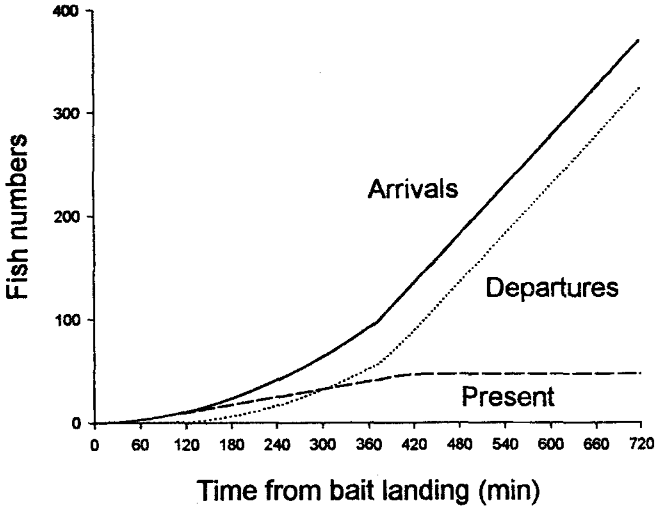

Fig. 2 Cross-current foraging model, persistent bait. Predicted fish arrivals, departures, and number of fish present with time from the arrival of the bait on the seafloor. The bait does not deteriorate and is not consumed during the model run. A continuous plume is produced. See text for model parameters

Modelling transient baits Fish were attracted to, and left from, transient baits such as single fish carcasses, according to the same "rules" as for persistent baits. With such small baits the odour plume did not increase up to a fixed width as described above. As the plume area increased the proportion of the plume which was concentrated enough to attract fish, or coherent enough to provide a useful cue, was likely to reduce.

Odour plumes are not evenly diluted and consist of "strands" (Finelli et al. 2000) of more concentrated odour interwoven with odour-free water. Chemosensory rules were assumed to operate allowing the animal to determine whether the energetic costs of moving upstream to the bait will be outweighed by the value of the meal (Zimmer-Faust 1989).

Plume spread was calculated according to the equations of (Stanley et al. 1985; Sainte-Marie and Hargrave 1987) and gives the plume width (L_{pw}, m). The distance versus concentration relationship for a diluting plume with a weakening source is not simple and given our poor knowledge of the thresholds of detection this level of complexity is not justified at this point. At a fixed time the plume stopped due to bait consumption and only the radius of direct detection (L_{rd}) remained (Warrant 2000).

$$L_{pw} = 2a \cdot L_{pl}^b \left(\frac{(b+d)}{b}\right)^{0.5} \cdot e^{0.5}$$

$$a = \frac{B_y}{V_w}$$

$$A_p = \pi\left(\frac{L_{pl} \cdot L_{pw}}{4}\right)$$

Values of all constants are as for Sainte-Marie and Hargrave (1987). B_y = diffusivity constant, or spreading velocity, estimated at 10^{-3}m s^{-1} in deep waters. The constants b and d were assumed to equal 1. Vertical spread was estimated at 10^{-5}m s^{-1} using the above formula.

As no data for the odour detection thresholds of deep-sea fish exist data for other modid species was used as a model. The odour detection threshold of wild cod was estimated here from Løkkeborg's (1990, 1998) data for alanine release from mackerel and response range of tagged cod together with Sainte-Marie and

Hargrave's (1987) model of plume dispersal. The calculated value of 1.96×10^{-10} mol l^{-1} is similar to experimentally obtained (Løkkeborg et al. 1995) values for sablefish starved for 1 day (1.83×10^{-10} mol l^{-1}).

Løkkeborg et al's (1995) data for the effects of satiation on the threshold concentration of amino acids required to elicit a feeding response in sablefish allows the calculation of the power law relationship between time since feeding (just fed to 4 days) and threshold level ($F_{10} = 60.21$, $P < 0.001$, $R^2 = 0.86$). If we assume that wild fish vary between these values of satiation according to a binomial distribution, the cumulative distributions of threshold concentrations of individuals within the fish population can be calculated. From Løkkeborg et al.'s (1995) data for sablefish a mean odour threshold (*ι*) of 1.57×10^{-8} mol l^{-1} with a standard deviation (*ó*) of 2.51×10^{-8} mol l^{-1} was calculated.

For any value of plume length the mean plume concentation (*x*) can be estimated from the amino acid emission rate of mackerel and the plume volume. The proportion of fish for which this is the odour plume threshold (*p*) can be determined using the formula below. The cumulative probability of response was computed numerically in Mathematica (Wolfram) and gives the proportion of fish responding to odour plume strengths up to, and including, the calculated mean value.

$$p = \frac{1}{\sigma\sqrt{2\pi}} \cdot e^{\frac{-x \cdot \mu^2}{2 \cdot \sigma^2}}$$

Animal arrival rates, and thus their rates of accumulation and departure, were then the product of the number of animals encountering the plume and the proportion which were responsive to a plume of that strength.

Modelling of other foraging strategies – sit and wait

Animals remained stationary on the sea floor until the bait plume reached them. On contact with the plume all animals were assumed to move upstream to the source, remain there for a set staying time, then depart. Number contacted (*n*) was calculated from the density of the fish (n_f) and plume area (A_p) assuming an elliptical plume shape from the equations of Sainte-Marie and Hargrave (1987) as above. A time delay was added between contact with the plume and arrival of the animal at the bait according to the length of the plume, the approach swimming speed of the animal and the water velocity.

$$n = n_f \cdot A_p$$

$$t_{mb} = \frac{L_{pl}}{V_{fsa}}$$

Passive drifting

The final modelled strategy was passive drifting. The neutrally buoyant animal floated down-current. Rate of arrival of passive drifters (R_{pass}) depended on the current velocity (V_w), fish density (n_f) and the range at which the foragers detect the bait (L_{rd}). Cumulative arrivals were calculated from arrival rate.

$$R_{pass} = n_f \cdot V_w \cdot L_{rd}$$

$$t_{mb} = \frac{L_{rd}}{V_{fsa}}$$

Mean time to bait is also a fixed value as the range at which fish detect the bait is fixed. This resulted in a simple linear increase in fish numbers with time until fish began to leave, after which numbers remained stable.

Statistical analyses

Where possible, model predictions were compared with existing data. First arrival times predicted by the models for a range of fish density and swimming velocity parameters were compared to arrival times for *C. armatus* observed by Priede and Merrett (1996) where arrival times were correlated to fish densities estimated by trawling. The proportion of the variance in observational data accounted for by the model was calculated and R^2 values generated (Zar 1996).

Results

Arrival, departure and numbers of fish present

Cross-current foraging

Rate of fish attraction increased with time as the length of the plume increased and then remained stable once the maximum plume width was reached. After a delay fish began to leave at the same rate as they arrived. Rate of arrival decreased and numbers of fish stabilised with the same number arriving as leaving (Fig. 2).

Small transient baits such as fish carcasses present the most complex scenario modelled here (Fig. 3). The plume became less attractive due to dilution and deterioration in the bait's odour emissions (Løkkeborg 1990). Upon bait consumption plume emission ceased and only animals which passed within the range in which they could detect other fish by sight or sound appeared at the bait site.

Sit and wait

Rate of fish attraction increased as the plume area increased but fell to zero when the maximum plume width had been reached and all the animals enclosed in the

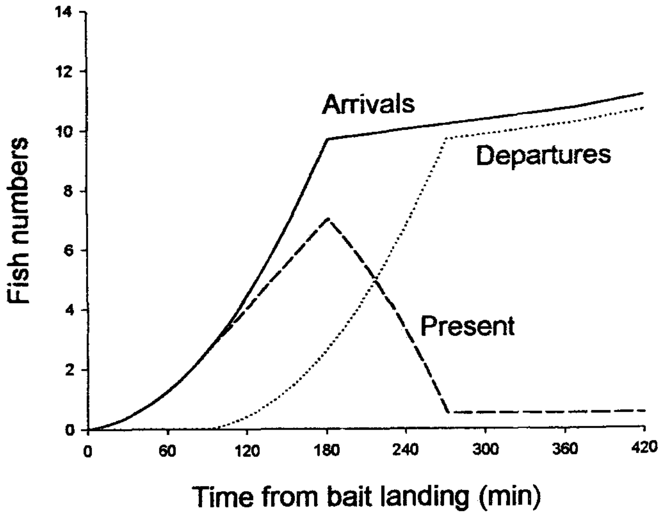

Fig. 3 Cross-current foraging model, transient bait. Predicted fish arrivals, departures, and number of fish present with time from the arrival of the bait on the seafloor. Plume elongates then reduces in effective length due to bait deterioration. Rate of attraction rises, falls and eventually drops to zero upon eventual bait consumption. A small residual population is maintained by animals that come within 10 m of the bait by chance and are attracted by non-olfactory means. See text for full model parameters

plume had arrived at the bait. No further animals were attracted and after animals began to leave, numbers at the bait decreased rapidly. Each change in current direction may result in repeated attraction events until the entire area surrounding the bait has been "swept" by the plume (Fig. 4).

Drift

Rate of fish attraction was proportional to the range at which the fish could detect the bait. This remained the same throughout and was not affected by the plume characteristics. Fish numbers increased linearly until fish began to leave, after which fish numbers stabilised. For each fish species and given density the rate of arrival would on average be proportional to current velocity around the bait (Fig. 5).

The short-term relationship between current velocity and arrival rate distinguishes drifting from the other two model strategies. Once a plume has been established a reduction in current will decrease arrival rate of drifters but result in a short-term increase in arrival rate of cross-current and sit-and-wait foragers as their cross-ground swimming speed as they move across and up the current would be increased.

Effect of foraging strategy and current velocity on initial fish arrival rate

The strategy adopted by the foraging fish greatly affects the numbers arriving at the bait. The alternative odour plume models give very different results with cross-current foraging animals appearing in greater numbers than sit-and-wait animals. With a current velocity of 0.05 m s^{-1} and fish swimming speed of 0.1 m s^{-1}, predicted first arrival times differ substantially with 108 min for sit and wait and 35 min for cross-current foraging (Fig. 6 A). Drifting animals arrive in the lowest numbers as their arrival rate does not continue to rise with time.

For the same through-water fish swimming speed, higher current velocities affect the relative arrival rates of foragers with different strategies (Fig. 6B, C). At a current velocity of 0.07 m s^{-1} drifting animals arrive in greater numbers than sit-and-wait foragers (Fig. 6B). At 0.09 m s^{-1} the order of arrival rates is reversed compared to the 0.05 m s^{-1} current situation, with drifting animals arriving in the greatest numbers, followed by sit-and-wait animals, with active, cross-current, foragers arriving in the lowest numbers (Fig. 6B).

Evaluation of the cross-current model of behaviour

Time to first arrival

Predicted mean first fish arrival was calculated for fish densities from 10 to 800 fish km^{-2}. The effect of foraging swimming speeds (through water) of 0.1, 0.2 and 0.3 m s^{-1} were modelled (Fig. 7A) as were increases in swimming speed from 0.1 to 0.2 and 0.3 m s^{-1} upon contact with the bait plume (Fig. 7B).

The importance of the assumptions made about fish swimming speed is demonstrated by Fig. 6A. A fish arrival time of 2,000 s (33 min) would predict fish densities of 330, 120 or 80 fish per km^{-2} depending on

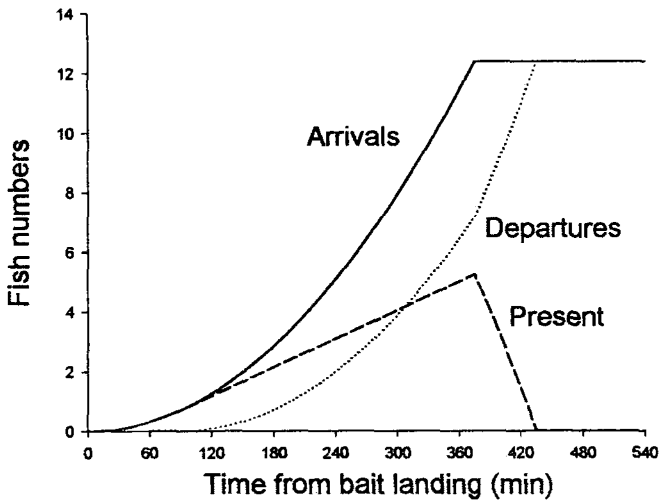

Fig. 4 Sit-and-wait model, persistent bait. Predicted fish arrivals, departures, and number of fish present with time from the arrival of the bait on the seafloor. Rate of fish attraction rises as the plume area increases until it reaches the maximum width at which it ceases to be attractive to waiting foragers. Once plume area is frozen no more animals are attracted and numbers begin to fall

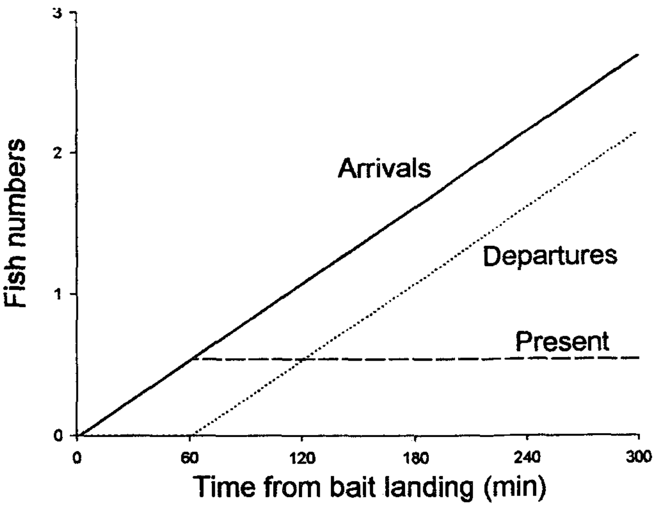

Fig. 5 Passive drifting model, persistent bait. Predicted fish arrivals, departures, and number of fish present with time from the arrival of the bait on the seafloor. Fish arrivals are linearly related to the time the bait spends on the bottom as the range at which foragers detect the bait is fixed throughout. As fish begin to leave arrival and leaving rates equalise and a plateau is reached. In this case an average density of less than one fish results. See text for model parameters

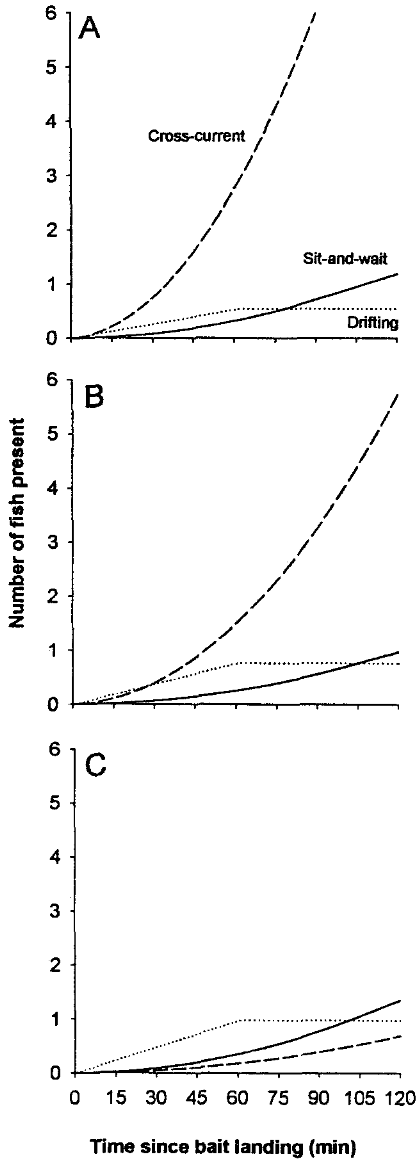

Fig. 6A–C Effect of current velocity on the predicted build-up in fish numbers at bait for three differing foraging strategies. In all cases fish density was 300 fish km^{-2}, and fish swimming speed (through water) was 0.1 m s^{-1}. Fish remained at the bait for 60 min before departing and drifting animals detected the bait from 10 m. As current velocity is increased from 0.05 m s^{-1} (**A**), to 0.07 m s^{-1} (**B**) or 0.09 m s^{-1} (**C**) the relative rates of arrival change, so that the order of increasing arrival rate is reversed. As current increases drifters are increasingly favoured as their movement speed, and therefore rate of arrival at the bait is increased. Rates of arrival of cross-current foragers fall as, although the plume is longer, their movement across the current and up the plume is increasingly slowed. This reduces rates of encounter with the plume and the time taken to move to the bait

assumed fish swimming speeds of 0.1, 0.2 or 0.3 m s^{-1}. Changes in fish swimming speed on contact with the plume were less important in changing arrival time. With the same fish arrival time of 2,000 s predicted fish densities were 330, 190 or 170 fish per km^{-2} depending on whether the fish remained at 0.1 m s^{-1} or accelerated to 0.2 or 0.3 m s^{-1} respectively (Fig. 7B).

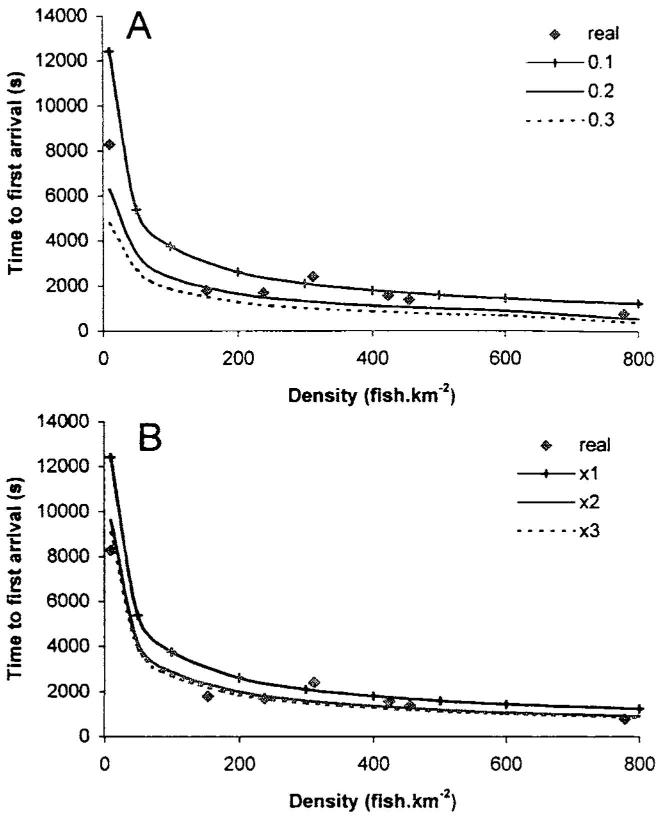

Fig. 7A, B Cross-current model, predicted first arrival times. First arrivals were calculated for a range of fish densities and through-water swimming speeds. These predicted data are compared to arrival times for stations where the fish abundance was determined by trawling (Priede and Merrett 1998). **A** The effect of different through-water swimming speeds is presented. **B** The effect of the fish increasing its through-water swimming speed upon contact with the plume. In each case the proportion of the variance in the real data accounted for by the model was determined and the R^2 values calculated. See Table 1 for details

These data are presented with field observational data obtained by Priede and Merrett (1996) on the same axis. As these experiments used mackerel to attract scavengers the data obtained are comparable to those of the models presented here, where the odour plume produced by this bait is modelled. The field data are *C. armatus* from three N. Atlantic locations, at depths of 2,500–5,000 m. A high proportion of the variance in the real data could be accounted for by the model results, especially where approach speed was elevated above foraging speed (Table 1). At low fish density, predicted arrival times were high, with small absolute changes in estimated fish density causing large differences in arrival time.

At present, swimming speed in deep-sea fish outside the field of view of cameras is determined using ingested acoustic transponders (Priede et al. 1994b; Bagley and Priede 1997a, b). These transponders are attached to small amounts of bait in order to avoid satiating the animal. They allow the accurate measurement of foraging activity but are not able to measure speed on approach to bait. New applications of technology such as

Table 1 Fits of fish density–first arrival time relationships predicted by the cross-current foraging model to those observed in the field

Swimming speed (m s^{-1})	0.1	0.2	0.3
R^2	0.48	0.93	0.74
Increase in swimming speed	×1	×2	×3
R^2	0.48	0.92	0.95

active sonar is required in order to determine fish behaviour prior to feeding. Foraging swim speed and, to a lesser extent, any change in swimming speed on contact with the plume, make a big difference to estimates of fish abundance.

Initial arrival rates

Fish arrival rate during deployment is a potentially more reliable measure of fish abundance as it usually uses the time to arrive of several fish. Assuming uniform fish distribution bait might by chance land closer than average to one fish but would therefore land further away than average from another. First hour arrival rate was used in order to minimise the assumptions necessary about the properties of the plume and current direction, fish odour thresholds etc. It is assumed that no fish leave within the first hour so cumulative numbers equal the number present.

An abundance of at least 100 fish km^{-2} was required in order for first arrival to occur, on average, within an hour (Fig. 7A) at all the swim velocities modelled (attain fish arrival rates of > 1 fish hr^{-1} or 0.00028 fish s^{-1}). At 0.1 m s^{-1} swim speed a density of at least 300 fish km^{-2} was required in order for 2 fish to arrive at the bait, the minimum requirement in order for arrival rate to be a better measure of abundance than first arrival alone.

Relatively high abundances are required before the advantages of first hour arrival can be utilised at the swim speeds estimated for deep-sea fish. In sparsely spread animals the options are (1) many replicate short deployments in order to determine first arrival time, or (2) estimates derived from longer deployments accepting that plume characteristics may differ from those predicted.

Discussion

Alternative foraging strategies

The models presented allow for a matrix of animals moving down and across currents with stationary animals on, or above, the seabed. The differences in arrival rates and the form of the build up in numbers may be diagnostic of the different foraging strategies and allow predictions of the characteristics of the fish to be made.

Actively searching for odour plumes dramatically increases the rate of arrival of animals at bait. Calculations of fish density based on arrival rates and models that assume that animals are stationary on the bottom until contacted by the plume (the sit-and-wait strategy) will seriously overestimate the numbers of fish present. Drifting on ambient currents and detecting bait by the sounds of other animals feeding may result in surprisingly large numbers of fish at the source of the sound. A range of detection of at least 19.7 m is required in order for one animal to arrive on average within 1 h. Experiments to determine the volume of sounds emitted and the hearing thresholds of deep-sea fish will be required to evaluate this further.

The different strategies carry different risks to the forager. Sit-and-wait minimises any acoustic or visual "signature" but the animal emits its own odour plume. Drifting releases a reduced odour plume, also with minimal acoustic signature. Cross-current swimming, as well as being energetically expensive is likely to be the most noisy and visually obvious strategy, covering the maximum area in the forager's odour. This may be a constraint on this foraging type. Catfish (*Silurus glanis*) can detect and follow the wake of guppies (*Poecilia reticulata*) over a minute after the guppy has left the position where the catfish contacts the trail (Pohlmann et al. 2001). If wake and sensory characteristics were similar in deep-sea fish cross-current foragers would leave an instantaneous wake length of 1800 m km^{-2} at fish densities of 300 km^{-2} and swimming speed of 0.05 m s^{-1}. The slow swimming and apparently streamlined body of *Coryphaenoides* may be important in reducing turbulence around the body in order to prevent a noisy and luminescent wake from forming. Differential vulnerability to predation as well as energetic constraints may influence the observed ontogenetic changes in foraging strategy (McLellan 1977; Mauchline and Gordon 1984; Cronin et al. 1996; Drazen et al. 2001). Even in large animals such as *C. armatus* the sub-lethal cropping of their tails by *Bathysaurus mollis* (Campbell et al. 1980) may be a significant additional cost of this overt foraging strategy.

None of the models presented completely describes the behaviour of *C. armatus* around bait as demonstrated by baited camera experiments (Bagley 1993; Priede and Merrett 1998). The cross-current foraging strategy model produces arrival time data which match well to trawl abundances, and accurately describes the buildup in fish numbers which occurs around large baits, such as marine mammal carcasses (Jones 1999). However, the peak number of fish predicted is much greater than observed in the field. The main alternative model, that fish sit and wait for the plume to reach them, then move upstream, predicts peak fish numbers more accurately but the form of the relationship between fish numbers and time is not consistent with the observed patterns.

Various possible explanations exist for these discrepancies, the identification of which is the major objective of these models. Low feeding motivation or animals remaining at previously encountered food sources could explain reduced numbers of arrivals. A second possibility is that at any time a mixture of active foraging and sit and wait strategies may be employed by individuals within the *C. armatus* population. The proportion foraging actively rather than remaining on the bottom, might be related to satiation. Ontogenetic variations in foraging strategy would also explain the differences in size frequency distribution in *C. armatus* observed from trawls and baited cameras (Priede et al. 1994a). However, at 4,000 m *C. armatus* individuals animals smaller than those seen at baits make up less than 15% of the population of this species as determined by trawling (D. Bailey et al., unpublished trawl data) so this alone is not sufficient to reduce fish arrival numbers in the way observed.

A mixed strategy could explain the lower than expected number of fish arriving at the bait and the stable fish numbers over a period of day observed at large food falls (Jones et al. 1998). This pattern can also be explained fully by a drifting foraging pattern but only if drifting animals detect the bait source by auditory means from a range of around 120 m. These models assume a staying time of 60 min. Greater staying times require much lower rates of arrival in order for numbers to build up to the numbers of fish observed.

Very long staying times of greater than 24 h have been recorded for zoarcids at large baits with numbers of these species continuing to rise over a period of days (Jones et al. 1998; Witte 1999). Benthic zoarcid eelpouts are thought to be negatively buoyant sit-and-wait predators so their numbers should only continue to rise while there is a continued increase in the area of seabed exposed to the odour plume at sufficient concentration to attract the fish. Either zoarcids are very sensitive to odour plumes and can follow them to the source for several hours or these animals employ a different method of foraging. Low but continuous rates of attraction are most consistent with a drifting strategy, as observed in midwater eelpouts (Robison 1999). The observation that the predominant mode of life of two-line eelpouts (*Bothrocara brunneum*) was to hover above the bottom (Ferry 1997) is consistent with this.

The bias in fish arrivals from a downstream direction is typically considered to be evidence of plume following (Wilson and Smith 1984). Terrestrial hunters may also approach targets from down-current in order to surprise them, even if the prey was detected by other means. The relatively small fields of view available typically does not determine direction of approach until the animal is very close to the bait so long- and close-range bait detection methods may differ and therefore give false impressions of foraging strategy (Wilson and Smith 1984).

Other complexities of fish behaviour such as the possibility of inter- and intra-specific interactions between animals have also not been included in the models. Density-dependency in fish staying time may explain the abrupt drop-offs in fish numbers in the models where, in reality, numbers of fish often fall rapidly at first and then more slowly (Priede et al. 1994b; Smith et al. 1997; Jones et al. 1998). Direct inter-specific interactions at bait have been observed in shallow marine fish and invertebrate scavengers (Godo et al. 1997; Tamburri and Barry 1999; Morton and Yuen 2000) and suggested for deep-sea fish species (Armstrong et al. 1992). Further deviation from the model predictions may exist where staying time (Priede et al. 1994b), odour detection thresholds and the proportion of fish foraging vary between populations of fish with differing levels of satiation (Løkkeborg et al. 1995).

Conclusions

The numbers of fish attracted to bait and their rates of arrival and departure may give valuable clues as to the foraging behaviour of the animals. This is particularly valuable in the deep-sea where behaviour prior to feeding is difficult to study. As the metabolic and sensory capabilities of animals are fundamentally linked to their foraging strategies laboratory data may give valuable insights into the animals' behaviours. Much new field data will be required, including swimming speeds before feeding and the metabolic costs of swimming in order to construct a full energy budget for foraging as has been achieved for shallow-water species (Ware 1975). The effects of hydrography and hydrology on deep-sea fish foraging behaviour are as yet poorly understood as are the olfactory and visual performance of foragers and the strength and type of cues relevant to these animals. Even complex patterns of fish attraction such as those in response to small, rapidly consumed, baits can be modelled and the theoretical effects of fish satiation level, swimming speed, and staying time determined.

A single small bait item is the most complex situation to understand as the characteristics of the attractant are constantly changing. The process of bait consumption results in a poorly understood feedback between the animals present and the attractiveness of the bait. The models presented can only make predictions of the most likely, average, arrival rates of animals; only pooled data from a high number of lander deployments is likely to closely match predictions of even the most complete model. Experimentation isolating odour, sound, and light as attractants is a potentially useful approach as the strength of each can then be controlled and standardised between experiments.

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