Fisheries Research, 8 (1989) 63-80
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

The Swimming and Orientation Behaviour of the Norway Lobster, *Nephrops norvegicus* (L.), in Relation to Trawling

P.L. NEWLAND*
Department of Zoology, The University, Glasgow G12 8QQ (Gt. Britain)
C.J. CHAPMAN**
Department of Agriculture and Fisheries for Scotland, Marine Laboratory, P.O. Box 101, Victoria Road, Aberdeen AB9 8DB (Gt. Britain)

(Accepted for publication 6 March 1989)

ABSTRACT

Newland, P.L. and Chapman, C.J., 1989. The swimming and orientation behaviour of the Norway lobster, *Nephrops norvegicus* (L.), in relation to trawling. *Fish. Res.*, 8: 63-80.

A towed sledge, fitted with television and photographic cameras, was used to observe the behaviour of *Nephrops norvegicus* in relation to tidal currents in the sea and to an experimental rig which simulated the ground gear component of a trawl. Analysis of video recordings suggested that, in their foraging behaviour, most *Nephrops* faced the gear and moved downstream. Reaction distances to the ground gear rig were short and 50% of *Nephrops* were touched by the gear before starting to swim. The majority of *Nephrops*, initially facing towards the approaching gear, reacted to it by swimming directly away at an angle of about 90°. This "herding" effect was not shown if *Nephrops* were initially facing away from the gear. In this case most animals responded by lifting their tails and swimming directly back over the ground gear. These observations are discussed in relation to the behaviour of *Nephrops* to commercial trawl gear.

INTRODUCTION

The Norway lobster, *Nephrops norvegicus*, often reacts to a sudden disturbance by initiating a series of "tail-flips", which propel the lobster backwards through the water (Newland, 1985; Newland et al., 1988a). This tail-flip swimming in brought about by a series of rapid flexions and extensions of the abdominal muscles. The main biological function of such swimming appears to be the avoidance of predators, but it is clear that this escape response also plays

---

*Present address: Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, Gt. Britain.

**Author to whom correspondence should be addressed.

a crucial role in the process of capture by trawls. Recent observations of trawls by Main and Sangster (1985) indicate that *Nephrops* must be induced to swim up and over the ground gear for capture to be achieved, otherwise they are likely to escape under the net. The swimming behaviour of *Nephrops* may also influence trawl selectivity, since escape through the meshes is more likely with the streamlined posture adopted during swimming (unpublished diving observations by J. Main and G.I. Sangster, 1985).

Recent developments in fishing gear design include nets that divide the fish catch by species (Main and Sangster, 1982a) and divide some species of fish from *Nephrops* (Main and Sangster, 1982b, 1985). In a recent paper, Newland et al. (1988a) have shown that the average swimming height of *Nephrops* rarely exceeds 0.5 m, thus providing a biological basis for the design of such "separator" trawls. With the present interest in these trawls for use in *Nephrops* fisheries (Anon., 1984; Ashcroft, 1984; Bennett, 1985), and the need to improve mesh selection for *Nephrops* in conventional gears (Briggs, 1983, 1986), additional information on the swimming behaviour of *Nephrops* in relation to trawls is needed.

The approach adopted in the present work was to examine the behaviour of *Nephrops* in response to one component of the trawl, the ground gear. In the commercial trawl, the ground gear is attached to the lower fishing line and its main function is to provide good bottom contact for the trawl net with a minimum of wear and damage. In our experiments, short lengths of three types of ground gear were stretched between the runners of a large sledge carrying television and photographic cameras. Obviously, this experimental method cannot replace observations on the full-scale trawl. Main and Sangster (1985), however, suggested that the events leading to the capture of *Nephrops* in trawls were largely confined to the central region of the ground gear*, so that our approach can provide useful information to complement observations on the whole trawl and perhaps aid their interpretation.

Our studies also considered the orientation of *Nephrops* to water currents in the sea in view of the possible influence of tidal cycles on *Nephrops* catches (Storrow, 1912; Farmer, 1975).

METHODS

Field experiments were carried out during two cruises of the University Marine Biological Station (Millport) R.V. "Aora" in November 1983 and August 1984. The work was carried out on commercial *Nephrops* grounds in the Firth of Clyde, Scotland, at Loch Striven (55°55′N, 05°04′W) and in the Cumbrae–Bute main channel (55°45′N, 04°58′W). The sea-bed on these grounds con-

---

*Hereafter, the term ground gear refers to the experimental rig (illustrated in Fig. 1) and the term trawl ground gear refers to the full-size trawl component (illustrated in Fig. 9).

sisted of mud with a high proportion of fine silt and clay particles. The water depth varied from 55 to 73 m, but on any one sledge run the depth variation was usually <5 m.

The basic framework of the sledge was constructed from 30-mm-diameter aluminium alloy tubing attached to mild steel runners 0.3 m wide (Fig. 1). The overall dimensions of the sledge were 1.6 m long, 2.6 m wide and 1.78 m high. Floats and weights were attached to the sledge to maintain stability during launch and recovery. The sledge, without camera equipment, weighed 125 kg in air.

Three types of ground gear were tested: 13-mm-diameter large-link chain, 50-mm-diameter rubber discs on 8-mm-diameter wire, and 32-mm-diameter sisal rope weighted with 50-mm-diameter lead rings (see Figs. 2 and 6). The 2.5-m lengths of the ground gear were fixed at various points on the sledge runners to vary the angle of attack relative to the towing direction.

An underwater television camera (Hydroproducts SDA 125) was mounted vertically at the centre of the sledge with its domed window 1.02 m above the plane of the sledge runners. Illumination for the camera was provided by two 500-watt quartz iodide lamps fitted with red perspex filters to minimise any

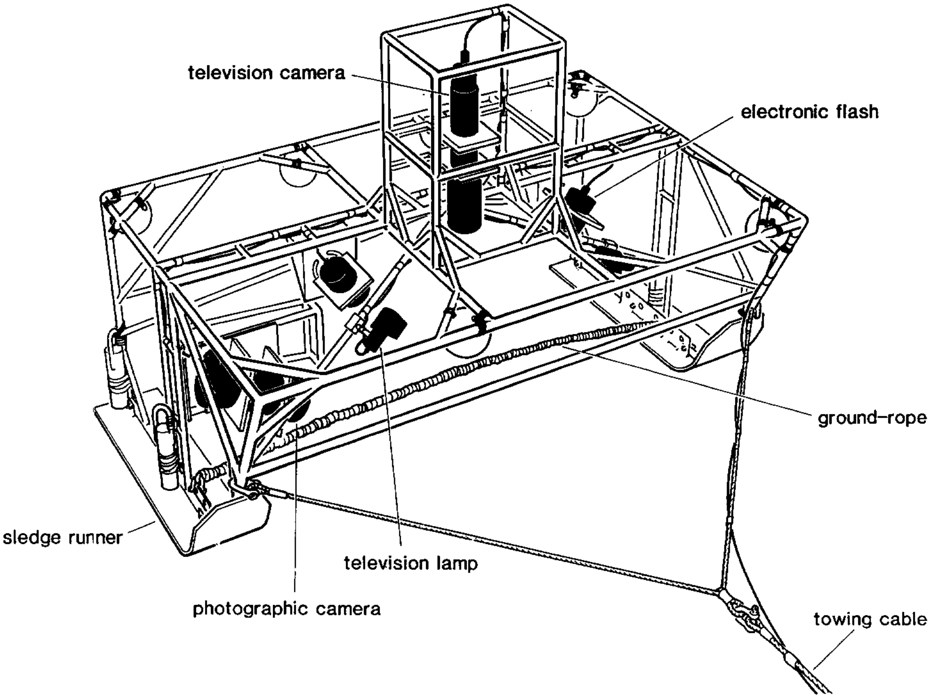

Fig. 1. Drawing of the towed sledge showing the arrangement of television and photographic cameras and lighting systems to observe the behaviour of *Nephrops* in relation to different types of ground gear (rubber disc type illustrated).

disturbance effect on *Nephrops* (Chapman, 1985). A Hassalblad photographic camera (type EM with 50-mm, f 1.4 lens) in an underwater housing was mounted on the starboard side of the sledge and pointed obliquely downwards to the centre of the sledge path (see Figs. 2 and 6). A pair of electronic flash units (Osprey type OE 4000A) were mounted on each side of the sledge, but in practice the best results were obtained using the port-side flash alone. The camera and flash were triggered remotely from the ship, through a cable connection, using the TV picture as a reference.

Video signals from the TV camera were relayed to the ship through a multicore cable and were then mixed with a time marker (For-A type VTG33F) before storage on a video cassette recorder (Sony U-matic) and monitor display. The video tapes were copied onto a second recorder (National Panasonic VHS) for analysis. Single-frame analysis was performed on the recordings using an image analyser (HVS). The analyser mixed a set of cross-hairs with the video signal and the coordinates of the intercept were displayed and transferred automatically to a microcomputer (Tuscan S-100). Analysis programs, written in Microsoft–Basic, provided data on the towing speed of the sledge, *Nephrops* size, their reaction distance, distance travelled, mean and maximum swimming velocities, and orientation before and during swimming.

Fig. 2. Electronic flash photography by Hassalblad camera viewing obliquely downwards across the path of the sledge towing sisal ground gear. Arrows mark the edges of the sledge track from a previous run. Note shallow depth of sinking of the sledge runner into the soft mud, estimated to be about 40 mm. Measurements of the width of such tracks from the TV monitor were used to check calibration of the TV field of view. Printed from original colour negative.

The field of view of the camera was calibrated from the lens acceptance angles given by the camera manufacturer. Additional calibration checks were provided by measurements of the spacing between lead weights on the sisal ground gear (see Fig. 6) and measurements of the width of tracks in the sediment left by the sledge runners on previous tows (Fig. 2; see also Chapman, 1985). These measurements suggested that the sledge runners were sinking about 40 mm into the sediment. Allowing for this sinking, the area of sea-bed viewed by the TV camera was calculated to be 1.0 m wide by 0.73 m high. The towing speed of the sledge was estimated at intervals by timing the passing of conspicuous objects from the top to the bottom of the TV monitor (representing a distance on the sea-bed of 0.73 m). The average towing speed was about 0.6 m s^{-1}. This relatively slow speed was necessary in order to keep the sledge on the sea-bed and to facilitate clear observations. Trawls used in *Nephrops* fishing are usually towed faster; 1–1.5 m s^{-1}.

The orientation of *Nephrops*, when first seen, was measured and analysed in relation to the tidal current, the Earth's magnetic field and the towing direction (Fig. 3) using circular statistical tests (Batschelet, 1981). The latter two parameters were obtained from compass readings on-board "Aora" which were recorded every 10–15 min. A current meter (Aanderaa) was moored 1 m above the sea-bed in a depth of 60 m, to the north of the working area in Loch Striven (55°55.3′N, 05°03.35′W). Data on time, temperature, current speed and direction were stored on magnetic tape within the meter housing. Bottom

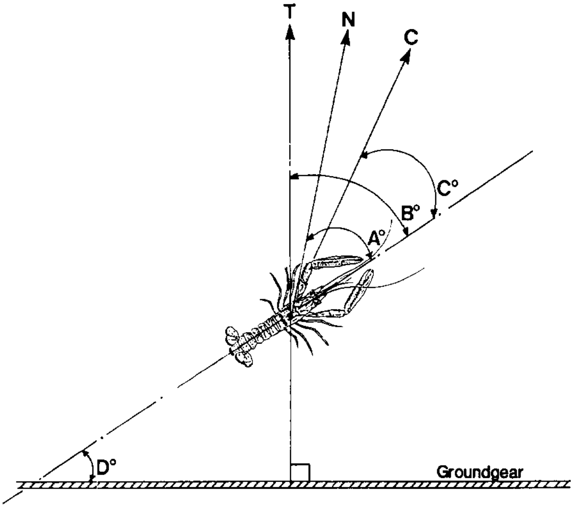

Fig. 3. Diagram showing angular measurements, derived from video analysis, giving orientations of *Nephrops*: A°, to compass direction north (N); B°, to towing direction (T); C°, to direction of tidal current (C). In one group of experiments the orientation of the ground gear was perpendicular to T so that the orientation of *Nephrops* to the gear (D°) is (90−B°). In other experiments the ground gear was orientated at 35° to T.

temperatures during the experiments were 9.3°C (August 1984) and 11.5°C (November 1983).

The results were derived from the analysis of 30 h video recording supplemented by 315 flash photographs (Figs. 2 and 6).

RESULTS

Size composition of the Nephrops *population*

The total body lengths of 22 *Nephrops* measured from the TV picture had a mean and SD of 97.0 ± 18.7 mm; equivalent to a carapace length of 29.0 ± 6.2 mm (Pope and Thomas, 1967). This compares with mean carapace lengths of 28.8 ± 4.0 mm and 26.7 ± 5 mm for samples of 170 male and 76 female *Nephrops*, respectively, caught by a 70-mm mesh commercial trawl fished on the same grounds.

Initial orientation of Nephrops *on the sea-bed*

These observations were made in Loch Striven where the current meter was moored. The meter showed that the main tidal current components were in the north–south direction, with velocities varying over the tidal cycle from 0 to 0.1 m s^{-1}. In Fig. 4 the initial orientation of *Nephrops*, as first seen by the TV camera, is shown relative to compass direction (N) for three combinations of water current and towing direction. The predominant orientation of *Nephrops* appears to be facing downstream (i.e. tail-on to the current). With a southerly tide the mean orientation of *Nephrops* was 193°; close to the mean

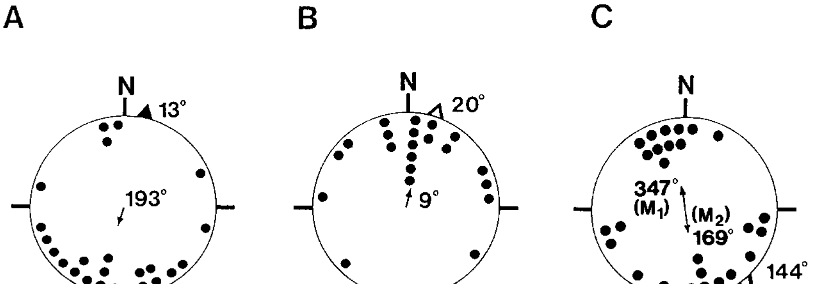

Fig. 4. Polar diagrams showing initial orientation of fully emerged *Nephrops* on the sea-bed for three combinations of water current and towing direction. (A) Northerly tow heading, southerly current; (B) southerly tow, northerly current; (C) southerly tow and current. Each point indicates the direction faced by individual *Nephrops*. Open arrow head, mean current direction; closed arrow head, mean towing direction; centre arrows, mean orientations of *Nephrops*. All orientations are given relative to compass north (N). See Table 1 for further details.

direction of current flow of 199° (Fig. 4A). On a northerly tide the mean *Nephrops* and current orientations were 9° and 20°, respectively (Fig. 4B). In both cases the current direction was contained with the 95% confidence interval for the *Nephrops* orientation vector (Table 1). A different set of results was obtained when the sledge was towed close to the direction of the tide (Fig. 4C). In this case, the orientation of *Nephrops* appeared to have a bimodal distribution, with one group of 15 animals facing downstream as before, and a second group of 11 animals facing upstream. The calculation of the mean vector and associated statistical tests were performed on each of these groups separately (vectors $\mathbf{M}_1$, $\mathbf{M}_2$ in Fig. 4C and Table 1). The analysis procedure recommended by Batschelet (1981) for certain types of bimodal distribution was not followed because although the two modes in Fig. 4C are opposite, they are clearly unequal ($\mathbf{M}_2$ has a wider confidence interval than $\mathbf{M}_1$). The mean orientation of one group of *Nephrops* ($\mathbf{M}_2$) was 169°; reasonably close to the mean direction of current of 144°.

A cue which may have accounted for the orientation of the second group of 11 *Nephrops* in Fig. 4C could be a stimulus from the sledge and/or ground gear, since a few of these lobsters seemed to be turning to face the sledge when first sighted on the TV monitor. The orientation data in Fig. 4 are examined in Fig. 5 in relation to three factors; the Earth's magnetic field (as indicated by the research vessel's compass heading), the direction of tidal current and the sledge towing direction (see also Fig. 3). Both current and towing directions gave rise to clear unimodal distributions (Fig. 5B and C), confirming the tendency for most *Nephrops* to face downcurrent and towards the approaching sledge. There was no evidence that *Nephrops* orientation is influenced by the Earth's mag-

TABLE 1

Initial orientation of *Nephrops*. Analysis of data from Fig. 4. The direction of the mean *Nephrops* orientation vector, water current and towing directions are given relative to magnetic north (N). Separate vectors ($\mathbf{M}_1$, $\mathbf{M}_2$) are given for each part of the bimodal distribution in Fig. 4C

	A	B	C	
Water current				
Mean direction (°)	199	20	144	
Towing				
Mean direction (°)	13	187	192	
			($\mathbf{M}_1$)	($\mathbf{M}_2$)
Nephrops				
No. of observations	24	22	11	15
Mean orientation (°)	193	9	347	169
95% confidence interval (°)	±35	±30	±12	±31
Mean vector length	0.46	0.57	0.95	0.64
Probability in Rayleigh test	<0.005	<0.001	<0.001	0.001

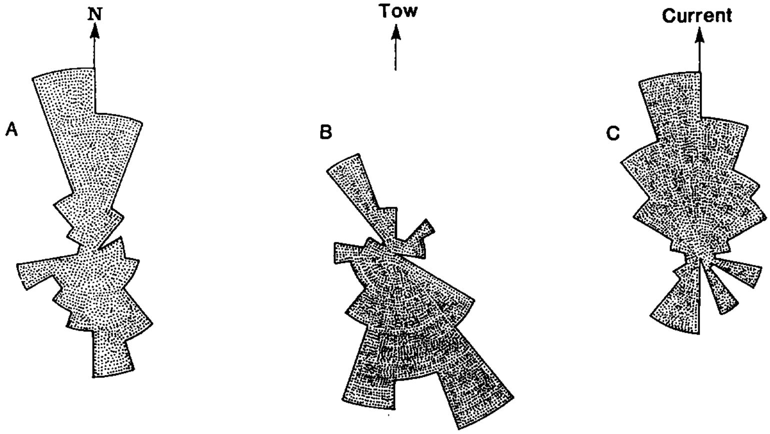

Fig. 5. Diagrams to show the angular frequency distributions (grouped in 20° sectors) of *Nephrops* initial orientation in relation to (A) compass, (B) towing and (C) current directions, shown by arrows (scale: length of arrow = three animals; number of observations = 73). Each diagram was compiled by superimposing the three polar plots of Fig. 4 after aligning the relevant environmental vector.

netic field. The bimodal distribution of *Nephrops* orientation in relation to this parameter (Fig. 5A) follows from the response to water currents and the fact that the tide flows mainly north and south in Loch Striven. The orientation of *Nephrops* was unlikely to have been influenced by sea-bed gradients and topography. Apart from the presence of the burrows of *Nephrops* and other organisms, the sea-bed was featureless and fairly uniform in depth within the distance covered by each sledge run.

Responses to the ground gear

Reaction distance

Under towing conditions each type of ground gear formed a shallow catenary (Figs. 2 and 6) moving over the mud surface. The chain ground gear tended to "dig" into the mud and generated a large cloud of disturbed sediment (Fig. 6A). The other two gears were lighter and tended to bounce lightly over the sea-bed producing little disturbed sediment (Fig. 6B–F). The TV camera was positioned such that the centre of the ground gear was just visible at the bottom of the screen, and the maximum visible range ahead of the ground gear was 0.65 m. Any responses of *Nephrops* beyond this range would not have been detected in our experiments. It was noted earlier that, at the maximum visible range, some fully emerged *Nephrops* appeared to be turning to face the ground gear. This turning would have been initiated before the *Nephrops* were seen, suggesting that *Nephrops* may have detected the sledge's approach from at least 0.65 m away. In addition, some *Nephrops* in their burrow entrances (Fig.

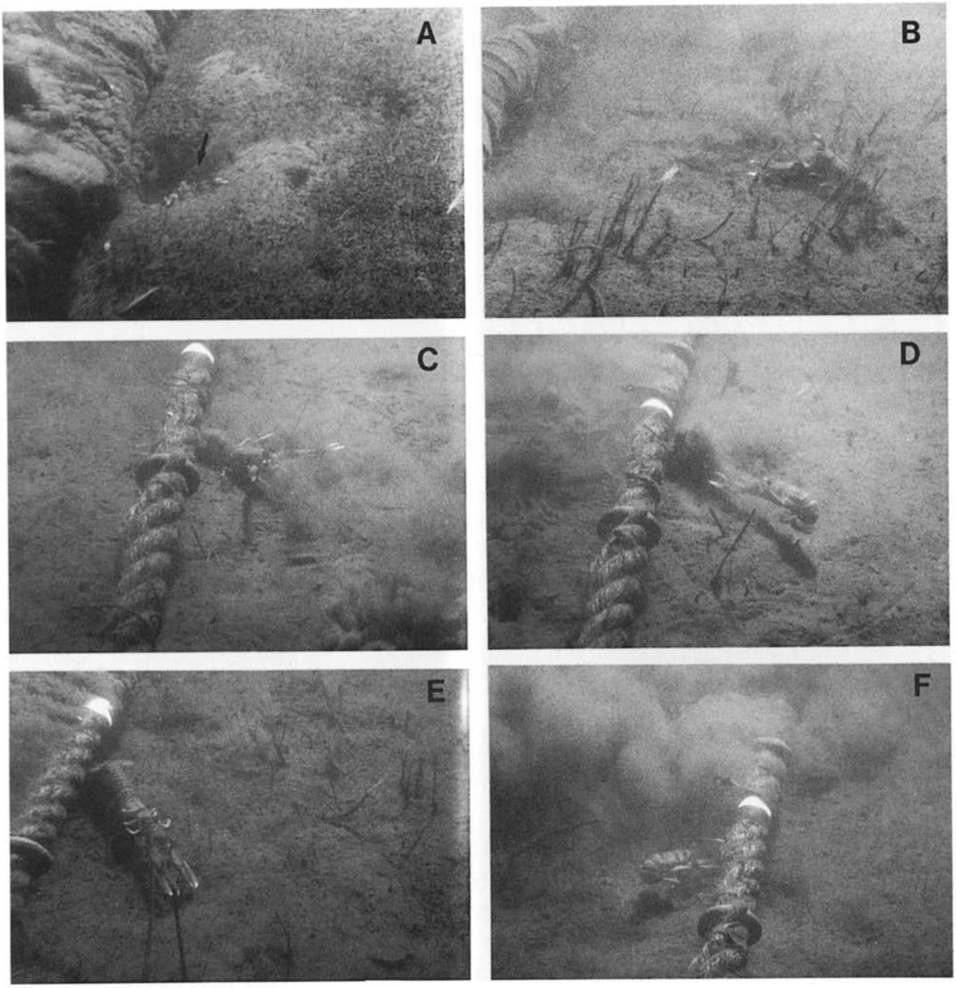

Fig. 6. Electronic flash photographs by Hassalblad camera illustrating *Nephrops* responses to ground gear: (A) in burrow entrance (arrowed); (B) facing approaching sledge, chelae held in defence posture with claws open; (C) *Nephrops* walking backwards towards ground gear; (D) tail-flip swimming in front of ground gear; (E) tail-flip swimming towards gear about to be initiated while lobster is "grooming" its carapace with pereiopods; (F) tail-flip swimming back over the ground gear. Chain ground gear in (A), note the extent of disturbed sediment; rubber disc gear in (B); sisal rope with lead weights in (C)-(F), centre marked by white tape. Printed from original colour negatives.

6A) were observed to respond at the maximum range by a slight movement out of the burrow, followed by a rapid withdrawal into the burrow as the ground gear passed over. This withdrawal was usually accomplished by tail-flip swimming that left a cloud of disturbed sediment in the burrow entrance. No *Nephrops* were induced to leave their burrows completely.

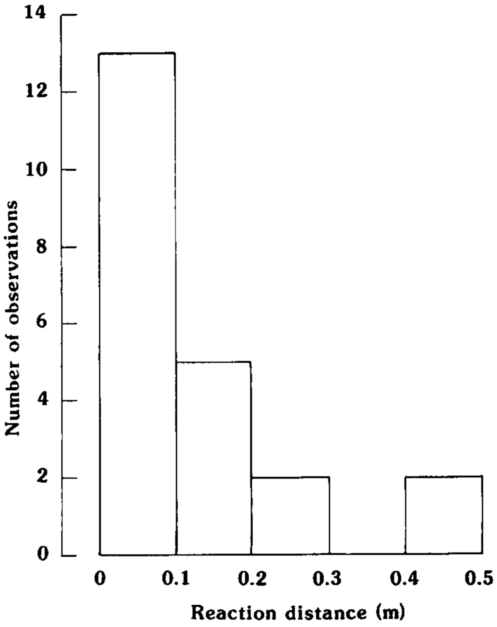

Fig. 7. Histogram showing the frequency distribution of distance from the ground gear at which *Nephrops* commenced tail-flip swimming (reaction distance) (number of observations = 22).

The majority of *Nephrops* observed on the mud surface, away from any burrows, responded to the ground gears by tail-flip swimming (Fig. 6C–F). The distance from the gear at which swimming first commenced varied from zero (i.e. swimming only occurred after contact with the ground gear) to 0.5 m (Fig. 7). Roughly half of the *Nephrops* began swimming only after contact with the ground gear. Taking these into account, the overall mean reaction distance for all types of ground gear was 0.10 ± 0.14 m. The form of the histogram in Fig. 7 and the fact that the maximum reaction distance recorded was 0.5 m suggests that *Nephrops* were unlikely to have commenced swimming beyond the visible range of the TV camera. A few *Nephrops* were seen escaping through gaps caused by the tendency of the fibre rope and rubber disc ground gears to "bounce" over the uneven sediment surface.

Orientation to ground gear

The direction of swimming adopted by *Nephrops* depended upon their initial orientation; whether they were facing towards or away from the approaching ground gear. As noted earlier, most *Nephrops* were initially orientated facing downstream (Fig. 5C) and towards the approaching ground gear (Figs. 5B and 6B). This follows from the fact that on most runs the sledge was towed against the tide. Also, when the sledge was towed with the tide about half the *Nephrops* were observed to be facing the approaching ground gear (Fig. 4C). In each case, *Nephrops* facing the ground gear responded by tail-flip swimming away from the gear in the towing direction (Fig. 6D).

A different pattern of swimming was observed in those *Nephrops* that were initially facing away from the approaching sledge towed with the tide. Some of these *Nephrops* walked backwards towards the approaching gear (Fig. 6C), and after contact with it were stimulated to swim up and over the ground gear (Fig. 6E and F). Most of these lobsters were quickly overtaken by the sledge and were lost from the camera field, so that little detail of their swimming paths was observed. One individual, initially tail-on to the ground gear, turned round and swam away from the gear (Fig. 8B).

Figure 8 indicates that the direction of *Nephrops* swimming, in most cases, was roughly perpendicular to the ground gear, irrespective of whether the gear

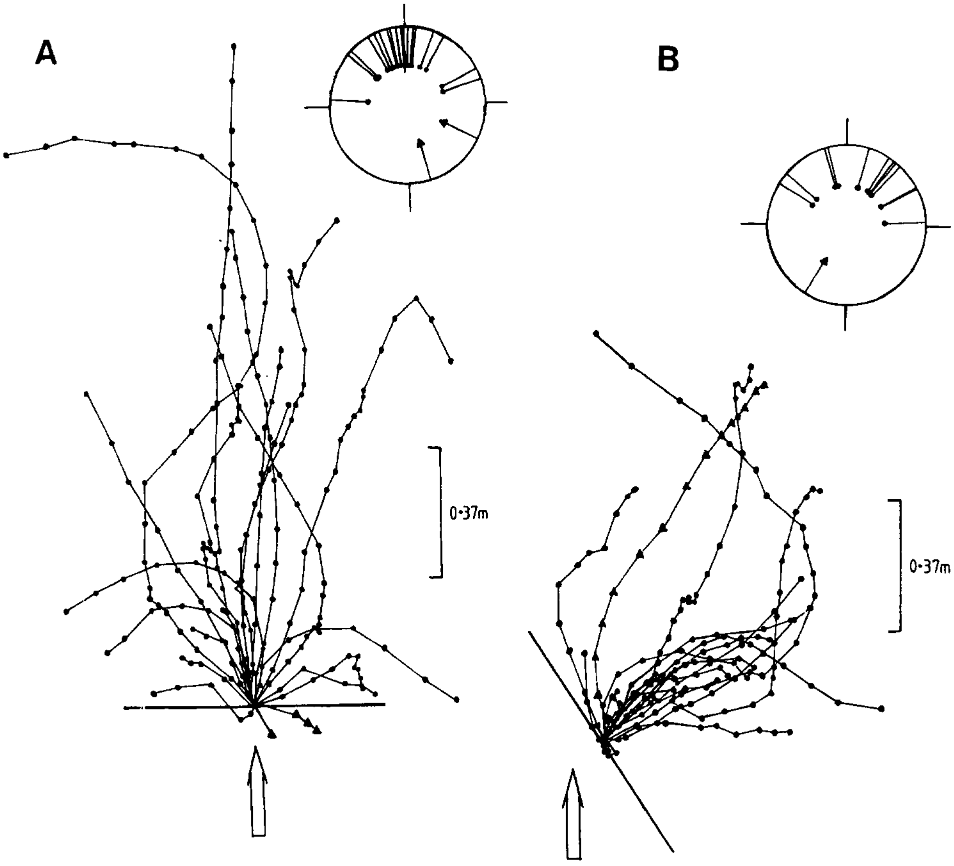

Fig. 8. Direction of swimming paths in response to ground gear orientated at 90° (A) and 35° (B) to the towing direction (shown by arrows). Insets show the initial orientations with respect to the gear before starting to swim; (●) *Nephrops* facing towards gear; (▲) *Nephrops* facing away from gear. Time between data points, 0.08 s.

was orientated 90° or 35° to the direction of tow. Some *Nephrops* swam in a curved path to either side of the sledge (Fig. 8A).

Nephrops *swimming speed*

Most *Nephrops* were induced to swim in front of the ground gear, but the distance travelled before passing out of the camera field of view was generally small (about 1 m). These swimming sequences were usually composed of a few brief bouts, between which the *Nephrops* resettled on the sea-bed before being stimulated to recommence swimming (as shown by closely grouped points on some swimming paths in Fig. 8). For the relatively short duration that they could be followed, it was clear that most *Nephrops* were capable of swimming faster than the average sledge towing speed of 0.6 m s^{-1}. The horizontal component of *Nephrops* swimming speed was estimated from measurements of the distance and duration of each bout. From these data, the average speed of *Nephrops* swimming in front of the ground gear was found to be 0.84 ± 0.27 m s^{-1}. The maximum speed recorded was 1.8 m s^{-1}. There was no evidence that speed over a swimming bout was influenced by the sledge towing speed.

DISCUSSION

Orientation to water currents

In our experiments the swimming behaviour of *Nephrops* to one trawl component, the ground gear, was divisible into two categories dependent on the direction of the stimulus, and hence, on the initial orientation of the lobsters on the sea-bed. This orientation appeared to be governed primarily by the direction of tidal flow.

The influence of water currents on *Nephrops* behaviour has recently been demonstrated in flume tank experiments by Newland et al. (1988b). These flume studies showed that *Nephrops* adopted a downstream orientation (i.e. tail-on to the current), and usually walked downstream, in water flow speeds exceeding 0.02 m s^{-1}. Direct measurement of forces acting on the bodies of *Nephrops* revealed that the downstream orientation of the body experienced the least hydrodynamic drag. The drag forces experienced by *Nephrops* on the mud surface are likely to be higher during spring tides and this may inhibit burrow emergence and contribute to reduced catches at spring tides (Storrow, 1912; Farmer, 1975; Chapman, 1980).

Swimming behaviour in relation to the sledge and ground gear

The majority of *Nephrops* were initially facing the approaching sledge (Figs. 5B and 6B) and they responded by swimming directly away from the ground gear in a direction roughly perpendicular to it (Figs. 6D and 8). The paths taken had little elevation (Fig. 6D; see also Newland et al., 1988a). The relatively small number of *Nephrops* initially facing away from the approaching sledge (Figs. 5B and 6C) swam up from the sea-bed and then back over the ground gear so that no herding took place (Fig. 6F). In the full-scale trawl these lobsters would have quickly entered the net. The two patterns of swimming observed in our experiments have been studied in aquarium experiments by Newland et al. (1988a), and the underlying neuromuscular physiology has been deduced by comparison with work on the freshwater crayfish, *Procambarus clarkii* (Wine and Krasne, 1982). Swimming is initiated by an escape reflex mediated by two pairs of giant fibres in the ventral nerve cord (different pairs of fibres are activated in the two categories of swimming).

The direction of swimming, normal to the ground gear, was observed for two different orientations of the gear with respect to the towing direction (Fig. 8). This was to be expected in the case of gear set at 90° to the towing direction (Fig. 8A) because the initial orientation of most *Nephrops* was already normal to the approaching ground gear. A different situation arises for ground gear orientated at 35° to the towing direction (Fig. 8B). The average orientation of *Nephrops* on the sea-bed is now no longer normal to the approaching gear, resulting in asymmetrical stimulation of mechanical sense organs on the body. In this situation, Newland (1985) and Newland and Neil (1987) have shown that the tail-flip swimming response is redirected away from the stimulated side by a combination of abdomen rotation and steering movements of the uropods, so that the final swimming orientation of *Nephrops* is still roughly perpendicular to the ground gear (Fig. 8B).

Nephrops *behaviour in relation to fishing gear*

The basic components of a typical demersal trawl are illustrated in Fig. 9. For the purpose of discussion it is useful to divide the area swept by the gear into two regions, namely, that between the wings of the trawl, swept by the trawl ground gear (i.e. to the right of the broken line through point A in Fig. 9), and the regions on each side between the otter board and the wing end of the net, swept by the sweeps and bridles. These two regions may be referred to as the catching zone and the peripheral herding zones.

Our observations suggest that the majority of fully emerged *Nephrops* within the net catching zone would be induced to swim, provided the trawl ground gear maintains good contact with the sea-bed. Those *Nephrops* orientated tail-on to the gear would be expected to tail-flip backwards (Fig. 6E and F) over the trawl ground gear into the net opening, whereas *Nephrops* facing towards the gear are likely to swim away from the trawl ground gear in a direction normal to it (Figs. 6D and 8). This herding of *Nephrops* in front of the trawl ground gear would only last for a relatively short distance because of the short reaction distances (Fig. 7) and the limited swimming speed of *Nephrops* com-

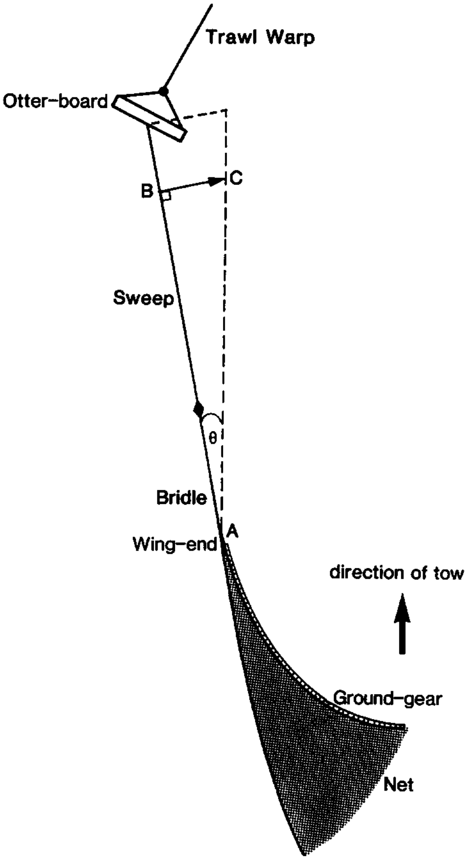

Fig. 9. Simplified diagram of part of *Nephrops* trawl gear (port side only) showing major components discussed in the text. Broken line through A constructed to show angle of attack (θ) of bridle/sweep in relation to their herding effect. The arrow BC represents the swimming path of a *Nephrops*, normal to the sweep at B.

pared to the trawl. Commercial trawls are usually towed at speeds between 1.0 and 1.6 m s^{-1} (2–3 knots) (Main and Sangster, 1982b, 1985), which are higher than the speeds that *Nephrops* accomplished in front of the sledge (0.84 m s^{-1}). This means that most *Nephrops* herded by the trawl ground gear will be quickly overtaken, probably within the first few tail-flips, irrespective of the initial orientation or the category of swimming trajectory involved. Consequently, a high proportion of the *Nephrops* lying in the catching zone are likely to be caught. From observations on full-scale trawls Main and Sangster (1985) came to the same conclusion. It seems that most *Nephrops* trawls are very efficient in the capture of *Nephrops*, although whether they are subsequently retained will depend on mesh selection in the codend and other parts of the net.

The effectiveness of bridles and sweeps in herding additional fish into the catching zone of trawls has received both theoretical and practical consideration by Bridger (1969), Foster (1969) and Hemmings (1969). In general, the herding of fish by sweeps and bridles is effective for certain combinations of towing speed, sweep/bridle length, angle of attack and otter-board spread which will allow fish the time to swim to the catching zone. This principle has never been considered in the case of *Nephrops*, since knowledge of their swimming performance was previously lacking. From direct observations of commercial *Nephrops* trawls, Main and Sangster (1985) concluded that little effective herding by sweeps and bridles took place, and they suggested that most *Nephrops* were likely to be overtaken and escape before reaching the net. On the other hand, some comparative trawling experiments showed that with a combined sweep and bridle length of 43 m, the *Nephrops* catch was 38% greater (by number) than for the same net fished with 12-m sweep/bridles (J.A. Sinclair, C.J. Chapman, unpublished data, 1979). The improvement in catch was noticeably better for the larger *Nephrops*, suggesting that swimming performance could be important.

The geometry of the herding components of a trawl may be considered in relation to the swimming performance of *Nephrops* with the aid of Fig. 9. For a given net, the angle of attack (θ) of the sweeps and bridles is dependent upon the length of the bridle/sweep combination and the spreading force exerted by the otter board. For effective herding to occur, a *Nephrops* stimulated to start swimming, normal to the sweep, at B must reach the point on the sea-bed denoted by C before the wing end of the net (A) arrives there. If the swimming speed of *Nephrops* is V_n and V_t is the trawl towing speed over the ground, then the times T_t and T_n for arrival of the trawl and the *Nephrops*, respectively, at C are

$$T_t = \mathrm{AB}/V_t \cos\theta$$

$$T_n = \mathrm{AB}\tan\theta/V_n$$

For herding to occur, T_n must be less than T_t and the maximum value of θ which satisfies this condition is given by

$$\theta = \sin^{-1} V_n/V_t \qquad (1)$$

We noted earlier that trawl towing speeds (1–1.6 m s^{-1}) were higher than the swimming speed of *Nephrops* measured in front of the sledge (0.84 m s^{-1}). These speeds were measured over a relatively short distance (about 1 m) before the *Nephrops* swam beyond the TV camera field, and there is some evidence that the swimming speed of *Nephrops* declines over successive bouts. Thus, the average swimming speed over a longer series of bouts was less than 0.84 m s^{-1} and, according to Newland et al. (1988a), was about 0.5 m s^{-1}. This is a more realistic figure for our calculations, since we are concerned with the

TABLE 2

Maximum distance along the combined sweep and bridle ($L = AB_{max}$), for different angles of attack (θ), at which herding into the catching zone could theoretically occur based on the swimming performance of *Nephrops*

Angle of attack (θ) (°)	Distance (L) (m)
5.0	137
7.5	91
10.0	68
12.5	54
15.0	45
17.5	38
20.0	33
22.5	29

TABLE 3

Measurements of sweep and bridle angle of attack (θ) and length (L) in *Nephrops* trawls during commercial fishing. For effective herding, $L \tan \theta$ should be close to 12. Metal "V" otter boards (2 m^2) were used in each case

Trawl type	θ (°)	L (m)	$L \tan \theta$	Reference
Boris 520[1]	7.4	61.2	7.9	Main and Sangster (1982b)
Boris 520[1]	9.5	61.2	10.2	Main and Sangster (1982b)
Cosalt 860	11.5	64.0	13.0	Main and Sangster (1985)
Hamilton 23 fathom	9.6	78.0	13.2	Galbraith (1985)
Hamilton 23 fathom[1]	9.2	78.0	12.6	
Cosalt 520	10.3	92.6	16.8	
Cosalt 520[1]	10.6	92.6	17.3	

[1] Net modified by incorporating a separator panel and twin codends.

limitations in swimming speed and endurance. For a trawling speed of 1.3 m s^{-1} (2.5 knots) and a *Nephrops* swimming speed of 0.5 m s^{-1}, the maximum angle of attack of bridles and sweeps which could permit herding leading to capture is about 23° (by substitution into eqn. 1).

The swimming endurance of *Nephrops* must also be considered. In aquarium experiments the average swimming distance achieved by *Nephrops* before failing to respond to a tactile stimulus was about 12 m (Newland et al., 1988a). Therefore, the distance BC must not exceed 12 m. This condition is satisfied if AB is chosen so that

$$L \tan\theta = 12 \qquad (2)$$

where L is the maximum permitted length of sweep along the axis AB. Values of L and θ satisfying eqns. (1) and (2) are given in Table 2.

There would be little advantage in using a sweep and bridle longer than L if *Nephrops* is the main species of interest. Interestingly, measurements of gear parameters during commercial fishing generally fall within the range of bridle/ sweep length and angle of attack that would theoretically produce effective herding of *Nephrops* (Table 3). For herding to take place in practical fishing the sweeps and bridles would have to move in close proximity to the sea-bed, otherwise they are likely to pass over the *Nephrops* without inducing a swimming response. In *Nephrops* fishing, the sweeps are generally made from heavy combination rope with lead cores, and the lower bridle is often of the rubber disc type (Figs. 1 and 6B), effectively extending the ground gear beyond the wing end of the net (Main and Sangster, 1982b, 1985).

ACKNOWLEDGEMENTS

One of us (P.L.N.) was supported by Research Studentship No. 82506659 from the SERC, which is gratefully acknowledged. For advice and technical assistance we thank C. Shand, who took part in the sea trials, B. Ritchie and R. Payne. We are very grateful to A.D. Hawkins, R. Jones, J. Main and D.M. Neil for their valuable comments on the manuscript. Special thanks to M. Parker and his crew on board the R.V. "Aora" (U.M.B.S., Millport).

REFERENCES

Anonymous, 1984. Report of the *Nephrops* Working Group. ICES CM 1984/K:4 (unpublished), 82 pp.

Ashcroft, B.A., 1984. Trials of fish/prawn separator trawls on fishing grounds in the Irish Sea, ICES Area VIIa. Sea Fish Industry Authority, Tech. Rep. 253 (unpublished), 23 pp.

Batschelet, E., 1981. Circular Statistics in Biology. Academic Press, London, 371 pp.

Bennett, D.B., 1985. The problems of small mesh *Nephrops* trawls in the Irish Sea - are separator trawls the answer? ICES CM 1985/K:38 (unpublished), 9 pp.

Bridger, J.P., 1969. The behaviour of demersal fish in the path of a trawl. In: A. Ben-Tuvia and W. Dickson (Editors), Proc. FAO Conf. Fish Behaviour in Relation to Fishing Techniques and Tactics, 19-27 October 1967, Bergen, Norway. FAO Fish. Rep. No. 62, pp. 695-715.

Briggs, R.P., 1983. Net selectivity studies in the Northern Ireland *Nephrops* fishery. Fish. Res., 2: 29-46.

Briggs, R.P., 1986. A general review of mesh selection for *Nephrops norvegicus* (L.). Fish. Res., 4: 59-73.

Chapman, C.J., 1980. Ecology of juvenile and adult *Nephrops*. In: J.S. Cobb and B.F. Phillips (Editors), The Biology and Management of Lobsters, 2. Academic Press, New York, pp. 143-178.

Chapman, C.J., 1985. Observing Norway lobster, *Nephrops norvegicus* (L.) by towed sledge fitted with photographic and television cameras. In: J.D. George, G.I. Lythgoe and J.N. Lythgoe

(Editors), Underwater Photography and Television for Scientists. Clarendon Press, Oxford, pp. 100-108.

Farmer, A.S.D., 1975. Synopsis of biological data on the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758). FAO Fish. Synop. No. 112, pp. 1-97.

Foster, J.J., 1969. The influence of fish behaviour in trawl design with special reference to mathematical interpretations of observations on the swimming speeds of fish and results of C.F. experiments. In: A. Ben-Tuvia and W. Dickson (Editors), Proc. FAO Conf. Fish Behaviour in Relation to Fishing Techniques and Tactics, 19-27 October 1967, Bergen, Norway. FAO Fish. Rep. No. 62, pp. 731-773.

Galbraith, R.D., 1985. *Nephrops* separator trawl drag measurements, "St Adrian II" — October, 1984. Scottish Fisheries Research Working Paper, 3/85 (unpublished), 20 pp.

Hemmings, C.C., 1969. Observations on the behaviour of fish during capture by the Danish seine net, and their relation to herding by trawl bridles. In: A. Ben-Tuvia and W. Dickson (Editors), Proc. FAO Conf. Fish Behaviour in Relation to Fishing Techniques and Tactics, 19-27 October 1967, Bergen, Norway. FAO Fish. Rep. No. 62, pp. 645-655.

Main, J. and Sangster, G.I., 1982a. A study of a multi-level bottom trawl for species separation using direct observation techniques. Scottish Fisheries Research Report (26), 17 pp.

Main, J. and Sangster, G.I., 1982b. A study of separating fish from *Nephrops norvegicus* L. in a bottom trawl. Scottish Fisheries Research Report (24), 8 pp.

Main, J. and Sangster, G.I., 1985. The behaviour of the Norway lobster, *Nephrops norvegicus* (L.), during trawling. Scottish Fisheries Research Report (34), 23 pp.

Newland, P.L., 1985. The Control of Escape Behaviour in the Norway Lobster, *Nephrops norvegicus* (L.). Ph.D. Thesis, University of Glasgow, 158 pp.

Newland, P.L. and Neil, D.M., 1987. Functional plasticity in a stereotyped motor act: redirection of the tail-flick in the Norway lobster, *Nephrops norvegicus*, by asymmetrical stimuli. Neurosci. Lett. Suppl., 29: S124.

Newland, P.L., Chapman, C.J. and Neil, D.M., 1988a. The swimming performance and endurance of the Norway lobster, *Nephrops norvegicus* (L.). Mar. Biol., 98: 345-350.

Newland, P.L., Neil, D.M. and Chapman, C.J., 1988b. The reactions of the Norway lobster, *Nephrops norvegicus* (L.), to water currents. Mar. Behav. Physiol., 6: 301-313.

Pope, J.A. and Thomas, H.J., 1967. Some biometric observations on *Nephrops norvegicus* (L.). J. Conseil. Int. Explor. de la Mer, 31: 265-271.

Storrow, B., 1912. The prawn (Norway lobster, *Nephrops norvegicus*) and the prawn fishery in North Shields. Dove Mar. Lab. Rep., New Series 1, 10-31.

Wine, J.J. and Krasne, F.B., 1982. The cellular organisation of crayfish escape behaviour. In: D.E. Bliss (Editor), The Biology of Crustacea, vol. 4. Academic Press, New York, pp. 241-292.