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Orientation and food search behaviour of a deep sea lobster in turbulent versus laminar odour plumes

Robert Major[1,2*] and Andrew Jeffs[1]

Abstract

New Zealand scampi (*Metanephrops challengeri*) is a commercially important deep-water lobster species that is caught by bottom trawling on areas of muddy seafloor on the continental shelf below 300 m. Efforts are being made to develop lower impact potting methods to harvest scampi, however, they can only be caught when out of their burrows and searching for food. This emergent food searching behaviour appears to be associated with periods of higher tidal flow. Such water flow will increase turbulence along the sea floor, which has been observed to improve the efficiency of chemosensory food searching in some lobster species. Consequently, this study examined the food search behaviour of scampi in response to odours from two types of bait (mackerel and mussel) in both turbulent and laminar flows. Scampi were more efficient at foraging in the turbulent flow than in the laminar flow, using shorter search paths in response to both types of bait. Scampi in the turbulent flow reached the mussel bait 44% faster and with lower mean heading angles than in laminar flow. However, there was no difference between the flow regimes for the mackerel bait. The pattern of orientation behaviour was similar under both flow regimes, suggesting that the scampi were using the same orientation strategy, but it was more accurate in turbulent flows. The results show that the foraging efficiency of scampi improves in turbulent conditions and that this may explain their increased emergent behaviour during periods of higher tidal flows.

Keywords: Orientation, *Metanephrops challengeri*, Foraging behaviour, Chemically-mediated food search behaviour, Chemoreception, Behavioural assay

Background

New Zealand scampi (*Metanephrops challengeri*) is a commercially valuable lobster species that lives in depths of 200–600 m around much of the New Zealand coast [1, 2]. Scampi are the target of a deep sea trawl fishery which has an annual catch quota of 1191 t and generates an estimated NZ$11 million a year of sales [2, 3]. Deep sea bottom trawling for scampi damages the sea floor, has high levels of bycatch and uses large quantities of fuel [4–6]. Pots (also known as creels) are used in northern hemisphere fisheries to target the ecologically similar Norway lobster (*Nephrops norvegicus*) [1, 7]. The proposed development of a potting fishery for scampi, replicating the northern hemisphere creel fishery, would result in a more sustainable method for harvesting scampi by reducing the collateral environmental impacts and improving the fuel efficiency [8, 9]. In addition, live scampi landed by using potting methods can sold into higher-value markets for live seafood [6, 7, 10]. Effective baits need to be identified for a potting fishery to be economic [11]. Initial laboratory experiments to identify superior baits for scampi found behavioural responses were inconsistent among candidate baits [12].

Scampi, like other lobsters, search for food by tracking attractant chemicals that are released from the food source and transported to the animal as plumes of chemical odour by the localised hydrodynamics [12–14]. Diffusion disperses chemicals in fluids that are not moving, which creates a concentration gradient away from the

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source [15]. Advection is the dominant force governing the transportation of the odour chemicals in moving fluids. The variations in the velocity of the moving fluids create small-scale hydrodynamic features, such as eddies, which are collectively known as turbulence [15, 16]. The complexity of the odour plume is affected by the characteristics of the turbulence of the fluid movement [17]. Consequently, particles of different molecular weights can be distributed throughout the plume in similar concentrations and ratios to what was originally released from the bait [15]. This creates filaments of the attractant chemicals in high concentrations interspersed with areas without attractants, forming a three-dimensional distribution of odorant chemicals [13, 18, 19]. The spatial variations in odour concentrations are more pronounced in higher turbulence conditions and there are shorter periods between the passage of high concentration filaments of chemicals past a fixed point (known as intermittency), when compared to low turbulence [15, 20].

In order to navigate the odour landscapes that they live in, crustaceans use a range of orientation strategies which depend on the structure of odour plumes [21], the hydrodynamics of their environments [22], the morphology of their sensory systems [23], and their locomotory abilities [24]. The simplest of these orientation strategies is odour-gated rheotaxis, which is when an animal moves upstream after being stimulated by the attractant chemical [16]. This has been suggested to be the primary orientation strategy for blue crabs (*Callinectes sapidus*), and is used in combination with spatial comparisons of the chemical signals (chemo-tropotaxis) to maintain contact with the plume and progress toward the source [25]. In contrast, lobsters have been suggested to use a form of eddy-chemotaxis, simultaneously employing the chemosensors and mechanoreceptors on the antennules to make spatial and temporal comparisons of eddies of odorant chemicals [19, 26, 27]. As turbulence affects the spatial complexity of odour plumes and the intermittency that crustaceans encounter the filaments of odorant chemicals in the plume, it has a significant effect on the foraging behaviour of a number of crustacean species, which are tuned to the turbulence they encounter in their natural habitat [28–30].

New Zealand scampi are similar to other endobenthic crustaceans that either burrow or bury themselves in the sediment, and must emerge from their burrows in order to search for food [1, 31]. Emergence behaviour in Norway lobster and New Zealand scampi has been investigated through variations in catch rates [32–34], as the lobsters avoid capture by benthic trawls when they are either inside or at the entrance of their burrows versus emergent and foraging on the open seabed [35]. The emergence patterns of Norway lobsters are typically driven by the diel cycle. In shallow areas on the continental shelf (0–200 m) Norway lobster emerge nocturnally with crepuscular peaks, and in deeper areas, on the continental slope (400 m), emergence patterns are weakly diurnal [32, 36]. Other studies have observed Norway lobster catch rates to vary in relation to tidal state [34]. Similarly, the emergence patterns of New Zealand scampi, which only live on the continental slope (>200 m), have been observed to peak at dawn and potentially during periods of higher tidal flow in both tagging studies and investigations of catch rate variation [33, 37]. As scampi may be foraging for food during periods of change in tidal flows, which generates turbulence at the seafloor [38, 39], there is the potential that the chemosensory systems and orientation strategies of New Zealand scampi may be tuned to turbulent rather than laminar flow.

Therefore, the aim of this research is to improve our understanding of the behavioural response of New Zealand scampi to odours from two types of bait (mackerel and mussel) in both turbulent and laminar flow regimes in an experimental seawater flume in the laboratory.

Methods

Experimental animals

A total of 100 scampi were obtained from a depth of 300 m on the Chatham Rise, 250 km off the east coast of New Zealand (42–43°S, 176–177°E) in July 2015 using a short duration bottom trawl at slow speed. Scampi in good condition upon landing were transferred into aquaria with seawater adjusted to their ambient temperature at point of capture (10 °C). The scampi were transported to the laboratory at the Cawthron Aquaculture Park in Nelson, New Zealand, where they were held in a recirculating aquaculture system at 10.5 °C with a salinity of 36 ppt. The scampi were held in individual enclosures in plastic tanks under red light ($\lambda > 600$ nm) for at least a week to acclimatise to the system prior to commencing experiments. During acclimatisation the scampi were fed every three days with squid. Food was withheld from the scampi for 7 days before they were used in behavioural experiments to ensure they were responsive to food odour cues. The transport and holding of the scampi, as well as the experimental procedures, were approved by the Animal Ethics Committee of the Nelson Marlborough Institute of Technology (AEC2014-CAW-02).

Behavioural assay

The flume was 1.5 × 0.5 × 0.3 m (L × W × D), and supplied by 10 μm and carbon filtered seawater at 10.5 °C, pumped into the manifold at 10 l min^{-1}, flowing at 1 cm s^{-1} and passed through a corflute collimator before reaching the behavioural arena (Fig. 1). The experimental arena was a 1 m long section of the flume containing

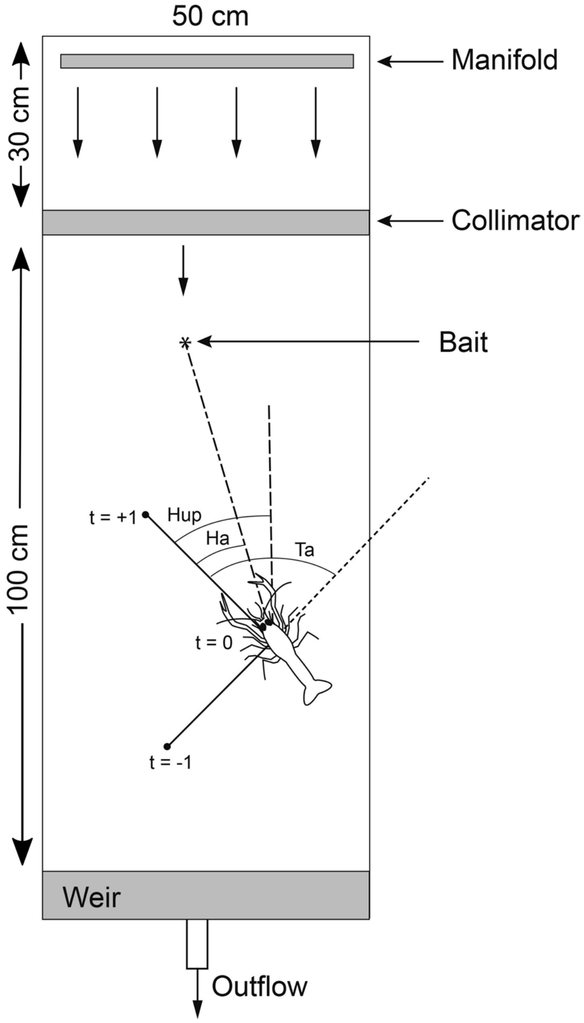

Fig. 1 Overhead diagram of the experimental behavioural flume showing the five orientation parameters that were measured in this study over three successive positions in video recordings ($t = -1, 0$, and $+1$). The *short dashed line* represents the scampi's projected path (if it had continued in a *straight line*), from which a turn angle value (TA) at point $t = 0$ is calculated. Heading angle (HA) is calculated from the difference of the bearing the scampi is travelling on and the bearing directly to the bait (short/long alternating *dashed line*). The *long-dashed line* represents a path that is *straight upstream*, from which a *heading angle* relative to upstream (HUp) is calculated

seawater 30 cm deep, which extended from the end of the collimator to a weir at the opposing end of the flume that the seawater flowed over and discharged through an outlet. Individual scampi were transferred in a darkened container from their holding tanks to the experimental flume nearby. The scampi was then placed at the end of the flume arena next to the outflow weir and allowed to move around the entire arena for a 30 min acclimatisation period. The scampi were then gently ushered back to the starting point immediately in front of the outflow weir using a mesh gate to ensure the scampi were in the correct position for the experiment to start. Five grams of defrosted bait material was placed in a polyvinyl chloride (PVC) mesh bag and suspended at the antennule height of the scampi, 2 cm above the floor of the tank. If the scampi displayed any stress-related behaviour, such as tail flicking, during the transport or acclimatisation period the scampi was replaced with another animal and the acclimatisation process was repeated.

Once the bait was in position a further 30 s was allowed for an odour plume to develop in the flume, then the mesh gate was carefully removed so as not to disrupt the plume or scampi and the experiment was allowed to run for 30 min. The experiments were conducted under infrared light and filmed from an overhead position using a Brinno TLC1200 time-lapse camera in ASAP mode. The flume was completely emptied and thoroughly cleaned between experiments.

Two baits were tested in the flume, the gonad of green-lipped mussel (*Perna canaliculus*) and tissue of New Zealand jack mackerel (*Trachurus declivis*). These baits were chosen because previous experiments had observed that scampi responded to the mackerel bait faster during the detection period than to the mussel gonad indicating differences in their chemical attractiveness to scampi [12]. Fifteen replicates were conducted for each combination of bait type (mussel versus mackerel) and flow regime (turbulent vs laminar) for a total of 60 experiments. Captive male and female scampi were randomly selected for use in the experiments from the 100 scampi available, however, given the limited supply of scampi maintaining an exact 50:50 sex ratio for the experiment was difficult and therefore a total of 28 females and 32 males were used. No gravid females were used and any scampi that had recently moulted were excluded from experiments. The orbital carapace length (OCL) of each scampi was measured (mm) after the experiment, and no scampi were subjected to repeated experiments.

Flow regimes

The two contrasting water flow regimes, "turbulent" and "laminar" were created in the flume by altering the seawater inflow arrangements. The usages of these terms are not as formal fluid dynamic descriptors, and are used to be able to distinguish clearly between the two flow treatments. Turbulent flow in the flume was generated by passing water entering the flume through only one collimator. Laminar flow was generated by passing the incoming water through two collimators arranged in series. The flow rates of seawater were consistent for both treatments, i.e., $10\ \mathrm{l\ min^{-1}}$. The varying flow fields were visualised in the flume by releasing food dye from a hypodermic needle at the bait position supplied by a peristaltic pump (Fig. 2). In the laminar flow the plume that was released was in a consistent stream and not broken into filaments. In the close up overhead image of the plume at the point of release (Fig. 2a) the small pulses of dye from the peristaltic pump can be seen, and these are also observed in the overhead image of the entire flume photo (Fig. 2c) as the stream of dye moves along the flume. In contrast the close up image of dye plume in the turbulent flow (Fig. 2b) shows how the eddies and structures in the flow break the dye stream into a number of small filaments that are interspersed with clear water, a pattern that continued to develop across the entire length of the flume (Fig. 2d).

Behavioural phase analyses

Aspects of chemically-mediated food search behaviour have been categorised into a number of behavioural phases that can be quantified [40]. These phases of food search behaviour have been adapted and used in New Zealand scampi [12], and consist of:

1. *Time to detection*—the time taken from when the mesh gate enclosing the scampi is removed until detection of the bait odour by the scampi. Indicated by a marked increase in the movement of appendages that contain the chemosensitive sensilla, including flicking or grooming of the antennae and antennules, beating of mouthparts and digging with, or wiping of dactyls.
2. *Detection period*—the time from the commencement of detection behaviour until the beginning of the search period. The scampi typically continue to display detection behaviour during this period.
3. *Search period*—from when the scampi starts locomotion or orientates into the water current, to the time it arrives at the bait.
4. *Time to reach bait*—time for all of the other behavioural phases combined, i.e., from the time the barrier is lifted to when the scampi reaches the bait.

These phases of behaviour were quantified by assessing the video recording of the bait-seeking behaviour of each scampi.

Tracking analyses

Orientation pathways were digitized using the TrackMate plug-in for ImageJ available in the FIJI package

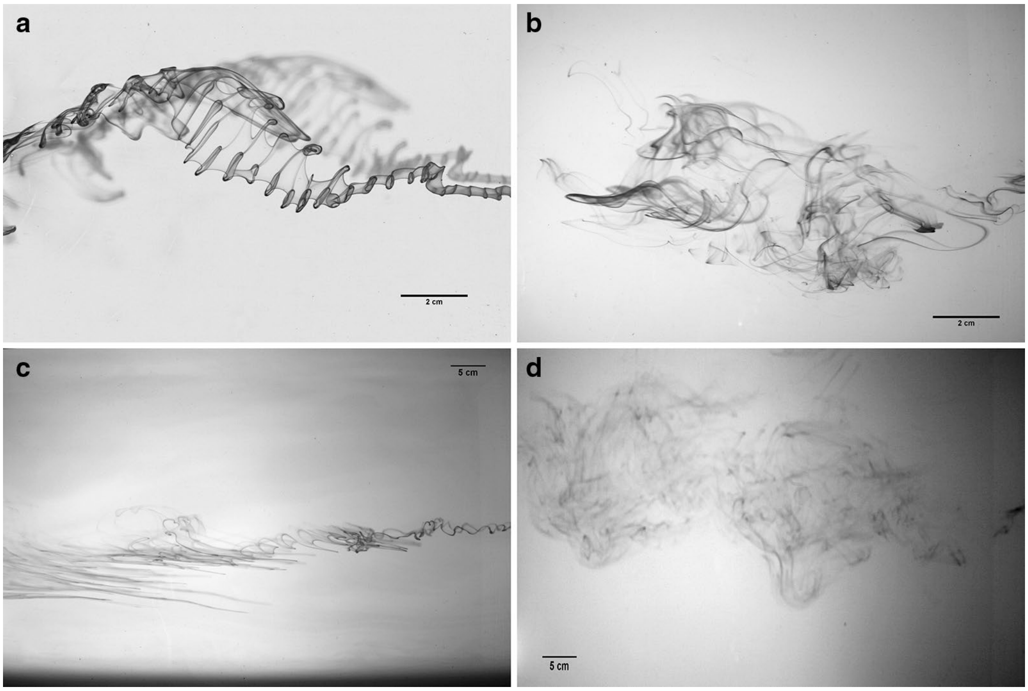

Fig. 2 Images of the dye tracer plumes generated by food dye released from a hypodermic needle via a peristaltic pump into the water flow in the experimental flume under the two different flow regimes. **a** Close up overhead image at the point of release of the dye plume generated in the laminar flow; **b** close up overhead image at the point of release of the dye plume generated in the turbulent flow; **c** overhead image of entire flume showing the structure of the dye plume generated in the laminar flow; **d** overhead image of the entire flume showing the dye plume generated in the turbulent flow

[41] for those scampi that successfully reached the bait, i.e., 14 scampi for the turbulent mackerel treatment, 12 scampi for both the laminar mackerel and turbulent mussel gonad treatments and 9 scampi for the laminar mussel gonad treatment. Digitizing was undertaken at one frame per second and x and y spatial co-ordinates were obtained for each movement of the scampi. As the scampi can orientate in a range of directions without changing its spatial location a single reference point where the cephalothorax meets the abdomen was used as the spatial reference for digitizing and calculating five orientation parameters (Fig. 1). These parameters were adapted from previous research [27, 28, 42] and consisted of:

- *Walking speed*—Distance travelled by the scampi to go from the point in the previous frame to the current point (one second difference between frames).
- *Turn angle*—The difference between the bearing that the scampi walked to get to the current point and the bearing that the scampi turns to move to the next point in the subsequent frame. Hence, low turn angles indicate that the scampi were walking in a straight line.
- *Heading angle*—The angle between a direct bearing to the bait from the scampi's current position and the heading that it is moving in. Hence, higher heading angles indicate that the scampi is orientating further away from the bait.
- *Heading angle upstream*—The angle between a direct bearing upstream from the scampi's current position and the heading that it is moving in. Hence, a heading upstream of zero would indicate rheotaxis and the scampi orientating directly into the current.
- *Tortuosity ratio*—A measure of the directness of the orientation pathway taken by the scampi from the origin to bait destination [43], that is calculated by dividing the direct distance from the origin to the bait by the total distance travelled by the scampi. Hence, the closer tortuosity ratio is to 1 the more direct the pathway is.

Statistical analyses

For each combination of baits and flow conditions log–likelihood ratios (G-test) were used to compare the proportion of the scampi successfully reaching the bait. General linear models (GLM) were used to determine the effect of the type of bait, flow regime, size and sex of the scampi on the mean time taken for each phase of chemically mediated food search behaviour. When the flow regime was observed to have a significant effect on the phases of behaviour post hoc t-tests with a Holm correction were used to compare effect of the flow regimes within each of the bait treatments. Data for the measures of the time taken to complete each behavioural phase were tested for normality and homoscedasticity using Shapiro and Levene's tests respectively. When the raw data did not meet these assumptions, it was transformed using either natural logarithm or square-root functions.

For all five of the orientation parameters (walking speed, turn angle, heading angle, heading upstream, tortuosity ratio), a mean value was calculated for each scampi over the duration of the search period when they were actively looking for the bait, and then used in the subsequent statistical analyses [28]. General linear models were then used to compare each of the orientation parameters in relation to the experimental treatments, i.e., type of baits, flow regime, as well as testing for any effect due to size and sex of the scampi. When the GLMs found a significant difference between the flow treatments for an orientation parameter, the means for the laminar and turbulent flow regimes within each of the bait treatments were compared using post hoc t-tests with a Holm correction for protecting against inflated Type I error rate due to multiple comparisons. General linear models were run using the base R program [44], and multiple comparisons using the Multcomp package [45].

The GLMs for both the phases of chemosensory behaviour and orientation parameters were structured as so: $Y = \alpha + \beta_1 \mathit{Flow} + \beta_2 \mathit{Sex} + \beta_3 \mathit{Size} + \beta_4 \mathit{Bait}$, with flow, sex and bait as fixed variables, while size was included as a continuous variable.

To investigate the relationship between the means and the variances of the different orientation parameters with the distance the scampi were from the bait, the means and variances of each parameter were binned into 5 cm distance intervals from the bait, and then analysed using either linear or 2nd order polynomial regression analyses. The curves and intercepts of the regressions for the two flow regimes were compared for each of the two types of bait using an analysis of covariance (ANCOVA). All means are reported with standard errors (SE).

Results

Success in reaching the baits

Fourteen of the 15 (93%) scampi reached the mackerel bait and 12 of the 15 (80%) scampi reached the mussel bait within the 30 min maximum experimental period in the turbulent flow. Twelve of the 15 scampi (80%) reached the mackerel bait and 9 of the 15 scampi reached the mussel bait (60%) in the laminar flow. The different flow regimes did not alter the success rates for scampi reaching the baits, either overall ($G_1 = 5.03$, $P > 0.05$), or for either the mackerel ($G_1 = 1.20$, $P > 0.05$) or mussel ($G_1 = 1.45$, $P > 0.05$) baits alone.

Behavioural phases

Overall, scampi in the turbulent flow had lower mean search periods ($t_{1,44} = 2.02$, $P = 0.049$) and mean total time to bait ($t_{1,44} = 2.132$, $P = 0.039$) regardless of the type of bait. Scampi search periods and total time to the mussel bait were both shorter in the turbulent flow compared to the laminar flow (Search period: $t_{1,17} = 2.35$, $P = 0.046$, 160.8 ± 32.5 vs 318.6 ± 60.3 s respectively; total time to bait: $t_{1,17} = 2.39$, $P = 0.042$, 567.8 ± 93.0 vs 1001.0 ± 130.3 s respectively) (Fig. 3). In contrast, no differences were observed in any of the scampi behavioural phases in response to the mackerel bait. Sex and size of the scampi did not significantly affect either search period or total time to bait for either of the baits.

Orientation behaviour

Flow regime was observed to significantly affect the heading angle of the scampi ($t_{1,38} = 2.78$, $P = 0.008$). In the mussel gonad treatment the scampi had a mean heading angle that was 15.2° lower in the turbulent versus the laminar flow ($t_{1,17} = 2.07$, $P = 0.048$). The mackerel treatment also trended in this direction with the scampi having a mean heading angle 14.5° lower when searching in the turbulent flow versus the laminar flow, but this was not significant ($t_{1,19} = 1.83$, $P > 0.05$). No significant differences were observed in the means of the other two spatial orientation parameters (turn angle and heading upstream) due to the two flow or bait treatments (Fig. 4). Sex and size of the scampi did not significantly affect any of the orientation parameters.

Tortuosity ratio

Scampi began the search period on average 70.4 ± 2.5 cm from the bait, and travelled 225.7 ± 34.0 cm in search of the bait. Neither the flow regime or the bait treatment was observed to affect the distance from the bait from where the scampi started their search path. Turbulent flow significantly reduced the tortuosity of the scampi's search paths to baits ($t_{1,38} = 3.04$, $P = 0.004$). The tortuosity ratios of the search path show that the scampi were 24.8% more direct to the mackerel bait ($t_{1,19} = 2.18$, $P = 0.038$) and 52.2% more direct to the mussel bait ($t_{1,17} = 2.10$, $P = 0.045$) in the turbulent flow in comparison with their respective laminar flow results (Fig. 5).

Orientation parameters relative to the distance from the bait

Heading angle

Scampi had higher mean heading angles relative to distance when searching for the mackerel bait in the laminar flow regime versus the turbulent flow regime ($F_{1,44} = 6.63$, $P = 0.016$) (Fig. 6). For both types of bait and flow regimes the mean heading angle of the scampi tended to start higher at the outset of food search and reached the lowest around 40–45 cm from the bait and

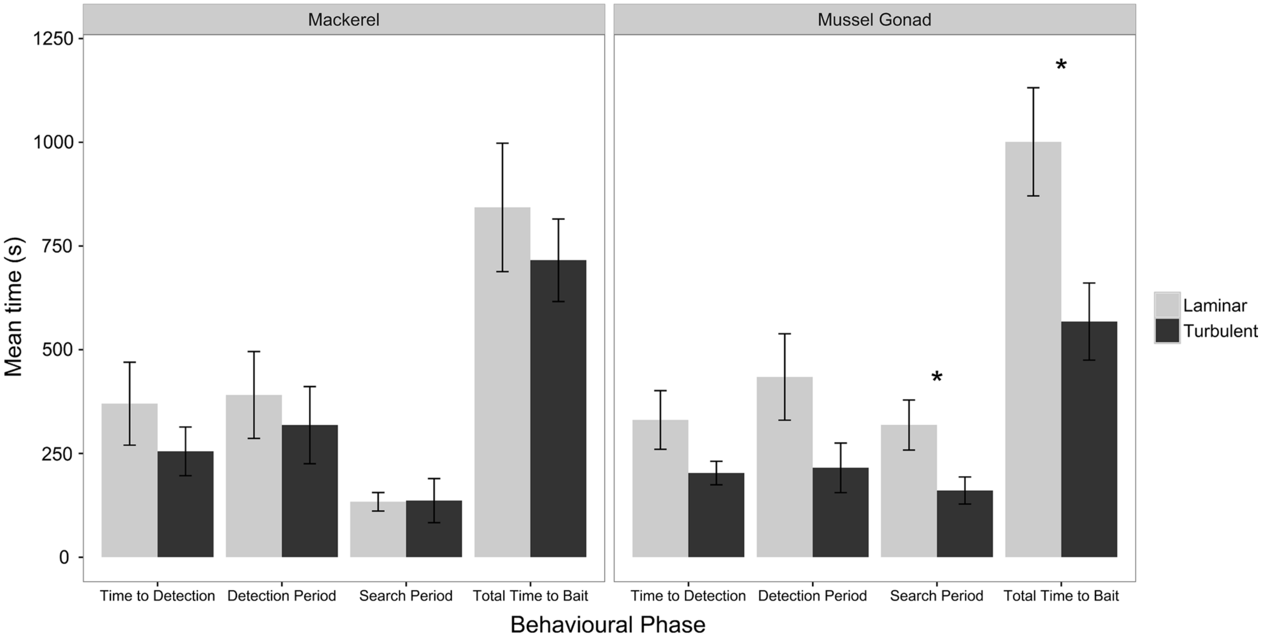

Fig. 3 The mean (±SE) time taken for each of the food search behavioural phases of scampi in response to the mackerel and mussel baits under the laminar and turbulent flow regimes. *Asterisk* denotes a significant difference ($P < 0.05$) between the mean time taken to complete the behavioural phase between the laminar and turbulent flow regimes

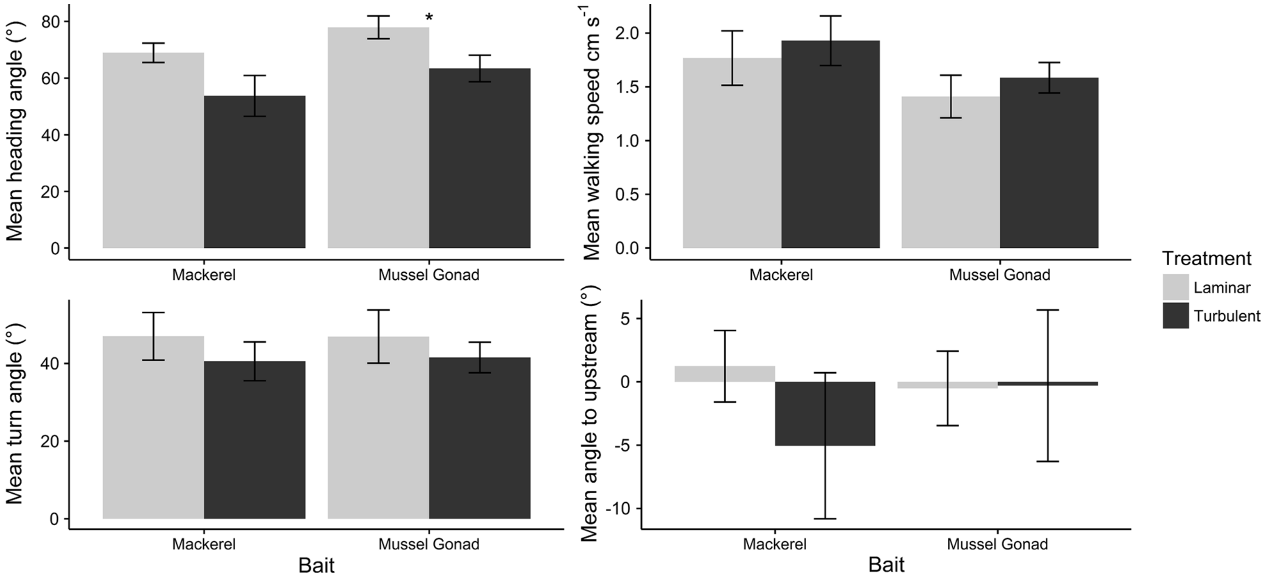

Fig. 4 The mean (±SE) for each of four orientation parameters for the entire tracked path in response to the mackerel and mussel baits under the turbulent and laminar flow regimes. *Asterisk* denotes a significant difference ($P < 0.05$) between the laminar and turbulent flow regimes within a bait treatment

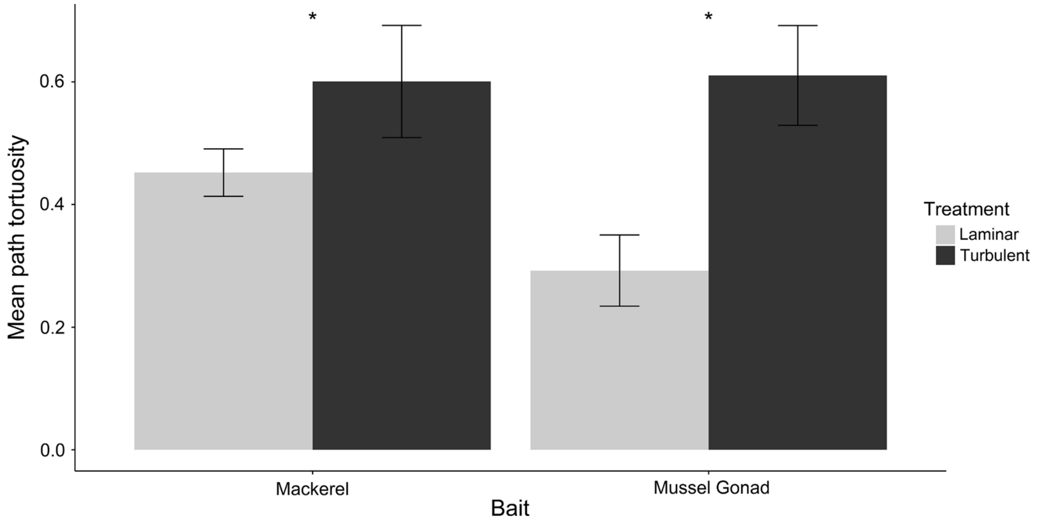

Fig. 5 The mean (±SE) tortuosity ratio of the paths for the scampi in response to the mackerel and mussel gonad baits under the turbulent and laminar flow regimes. The closer the ratio is to 1 the more direct the pathway. *Asterisk* denotes a significant difference ($P < 0.05$) between the two flow regimes within a bait type

then tended to increase again in the immediate vicinity of the bait. This trend was not as pronounced for the mussel bait in laminar flow. The variability in the heading angles among individual scampi appeared to alter with distance from the bait for each of the bait and flow combinations (Fig. 7). For example, heading angles of scampi were least variable at the outset and conclusion of the food search in response to the mackerel in laminar flow and mussel in turbulent flow. In contrast, the heading angle of scampi was more variable at the conclusion of food search for mackerel in turbulent flow, whereas for scampi searching for mussel in a laminar flow regime there was no pattern to the variability in their heading angles over the duration of their food search.

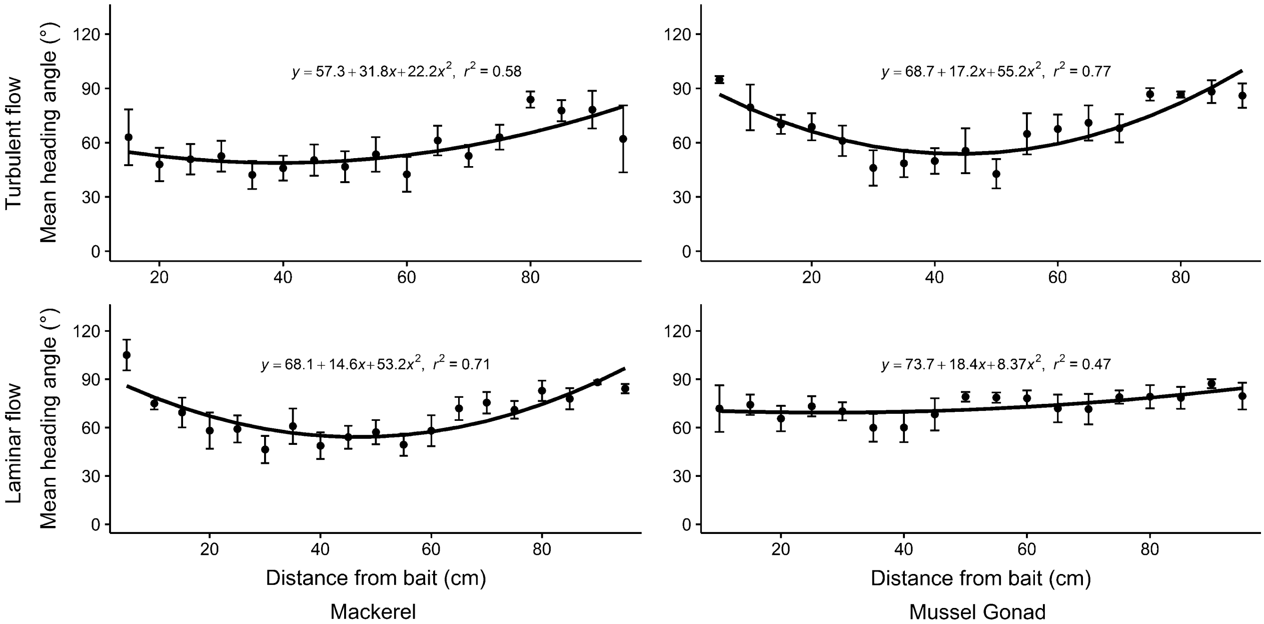

Fig. 6 Mean (±SE) heading angles of the scampi at varying distances from two types of bait (mackerel and mussel) in two flow regimes (turbulent and laminar). All regressions were significant ($P < 0.05$)

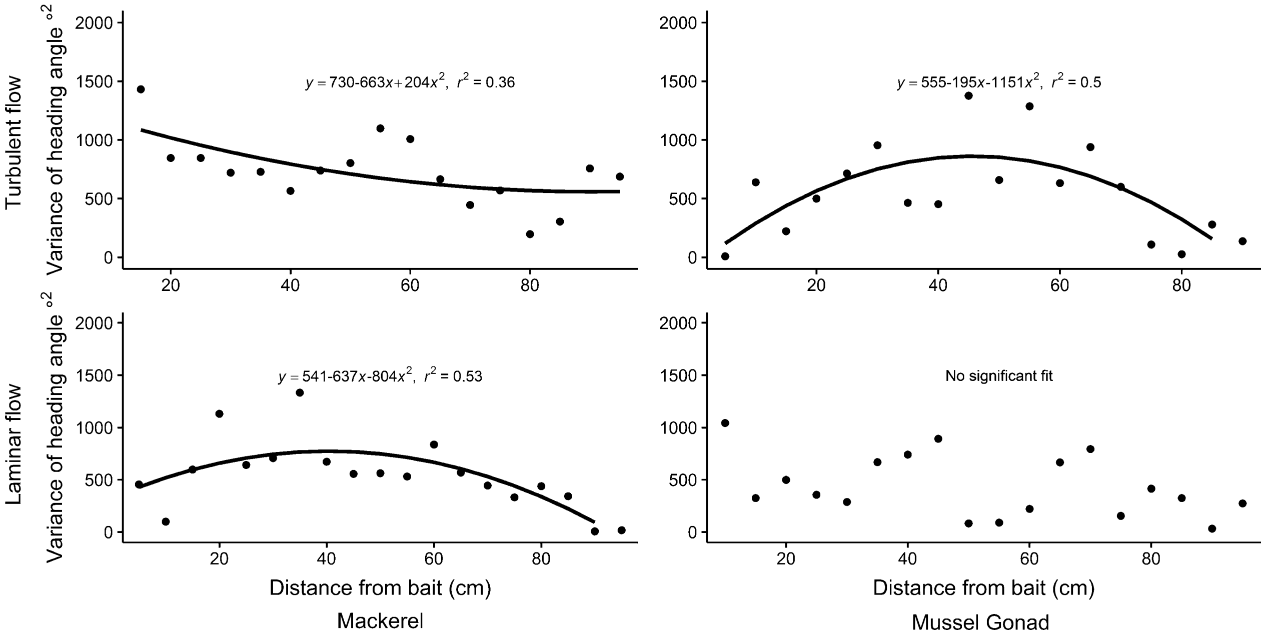

Fig. 7 Variance of the mean heading angle of the scampi at varying distances from two types of baits (mackerel and mussel gonad) under two flow regimes (turbulent and laminar). All regressions were significant ($P < 0.05$)

Turn angles

Overall, the scampi had lower turn angles relative to distance in the turbulent versus laminar flow ($F_{1,44} = 5.34$, $P = 0.028$). For both bait types and flow regimes mean turn angles were higher at the start of food search, and reached their lowest within 40–45 cm of the bait and then tended to increase again in the vicinity of the bait (Fig. 8). This increase in mean turn angles closer to

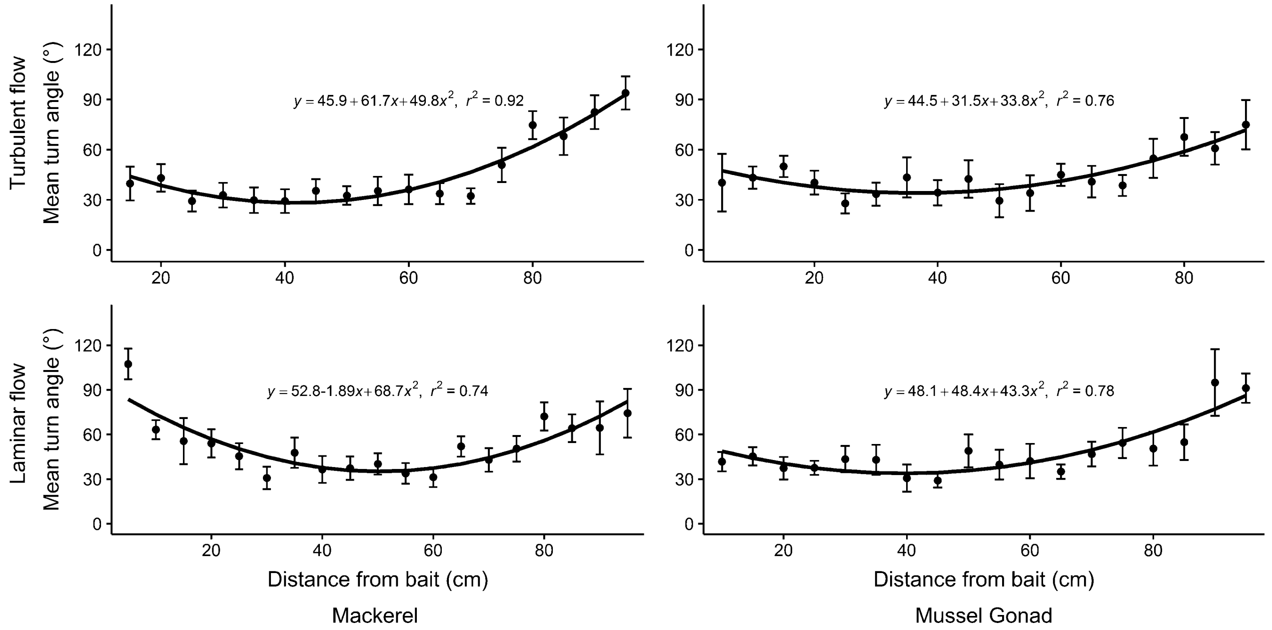

Fig. 8 Mean (±SE) turn angles of the scampi at varying distances from two types of bait (mackerel and mussel gonad) in two flow regimes (turbulent and laminar). All regressions were significant ($P < 0.05$)

the bait was more pronounced when the scampi were responding to the mackerel bait under laminar flow than under turbulent flow ($F_{1,19} = 9.94$, $P = 0.004$). The variance of the turn angle had a positive linear relationship to the distance from the bait for the mussel gonad in laminar flow indicating that the turn angle of the scampi was more variable at greater distances from the bait (Fig. 9).

Walking speed

The mean walking speed of scampi consistently increased as the scampi got closer to the bait for both baits in both flow regimes (Fig. 10). However, the increasing walking speed was more pronounced in scampi responding to mackerel bait in a turbulent flow versus those in a laminar flow ($F_{1,44} = 13.15$, $P = 0.001$).

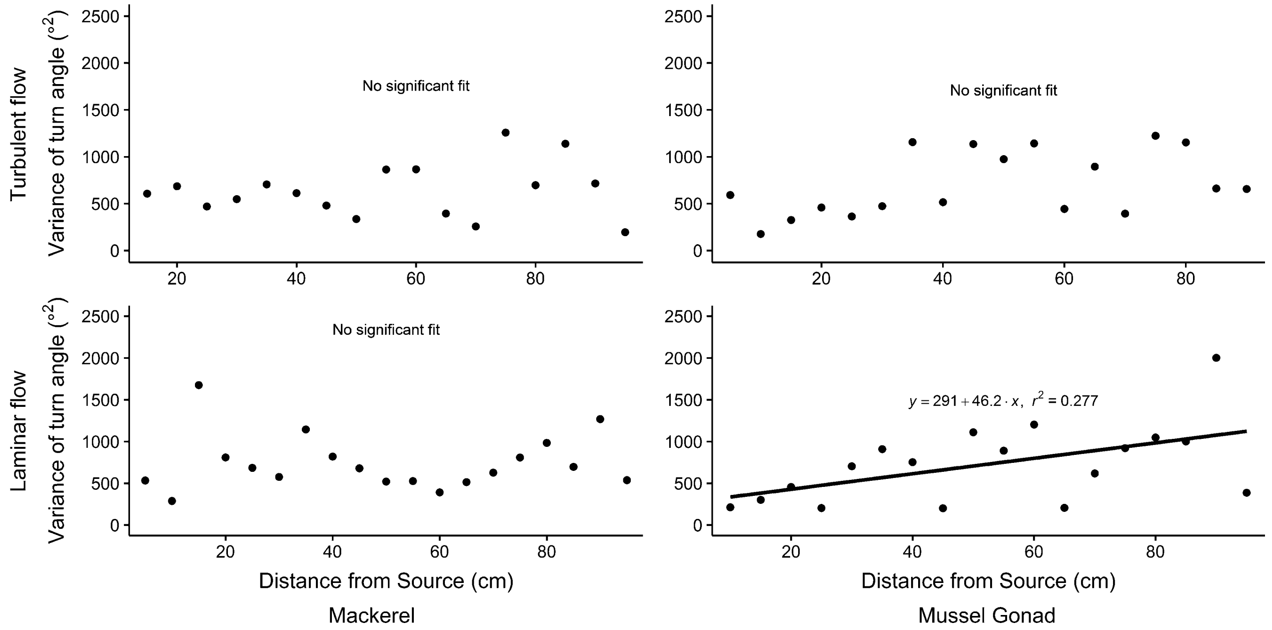

Fig. 9 Variance of the mean turn angles of the scampi at varying distances from two types of bait (mackerel and mussel gonad) under two flow regimes (turbulent and laminar flow). Regressions significant at $P < 0.05$

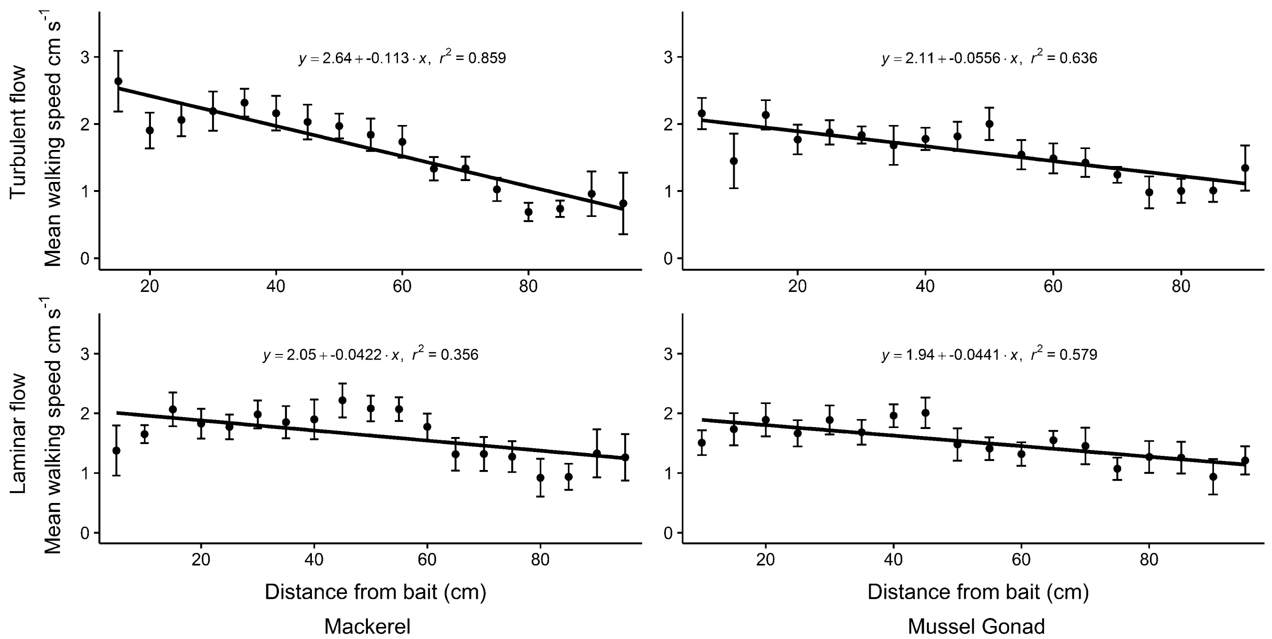

Fig. 10 Mean (±SE) walking speed of the scampi at varying distances from the two types of bait (mackerel and mussel) in two flow regimes (turbulent and laminar). All regressions were significant at $P < 0.05$

Heading upstream

The mean heading upstream was not affected by the distance the scampi were from the baits or the different flow regimes (Fig. 11). However, the variance of the heading angle upstream tended to increase as the scampi approached the bait (Fig. 12) and this was more pronounced for both baits in the turbulent versus the laminar flow ($F_{1,44} = 7.17, P = 0.010$).

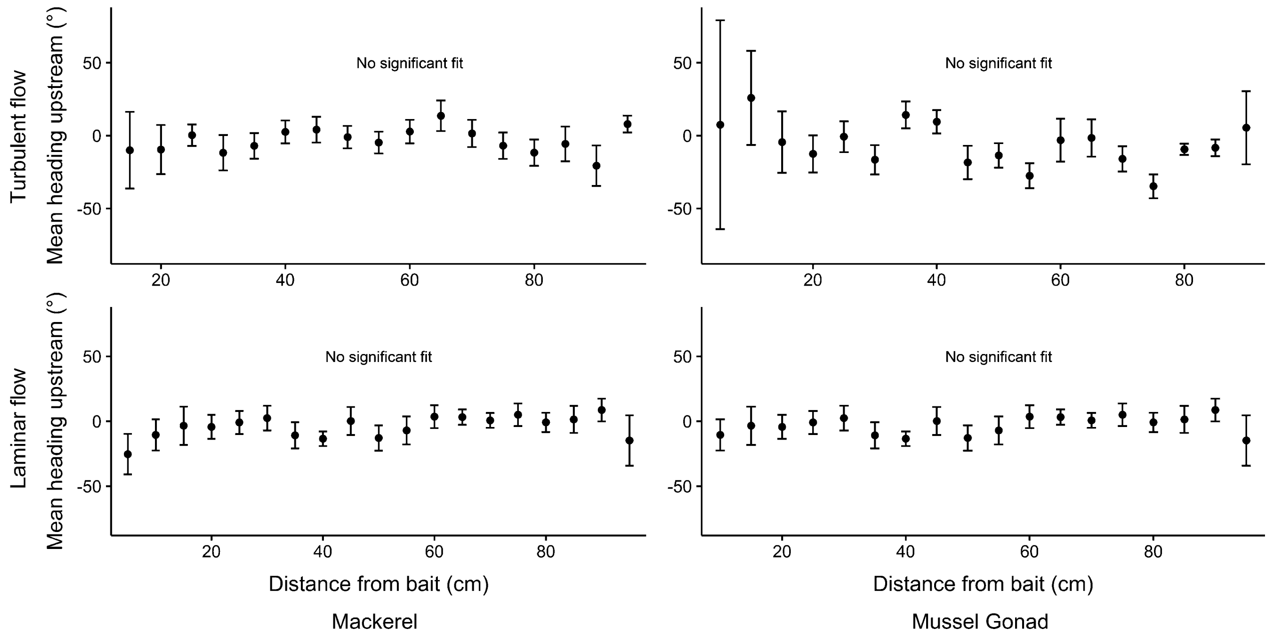

Fig. 11 Mean (±SE) heading upstream of the scampi at varying distances from two types of bait (mackerel and mussel) under two flow regimes (turbulent and laminar). None of the relationships were significant at $P < 0.05$

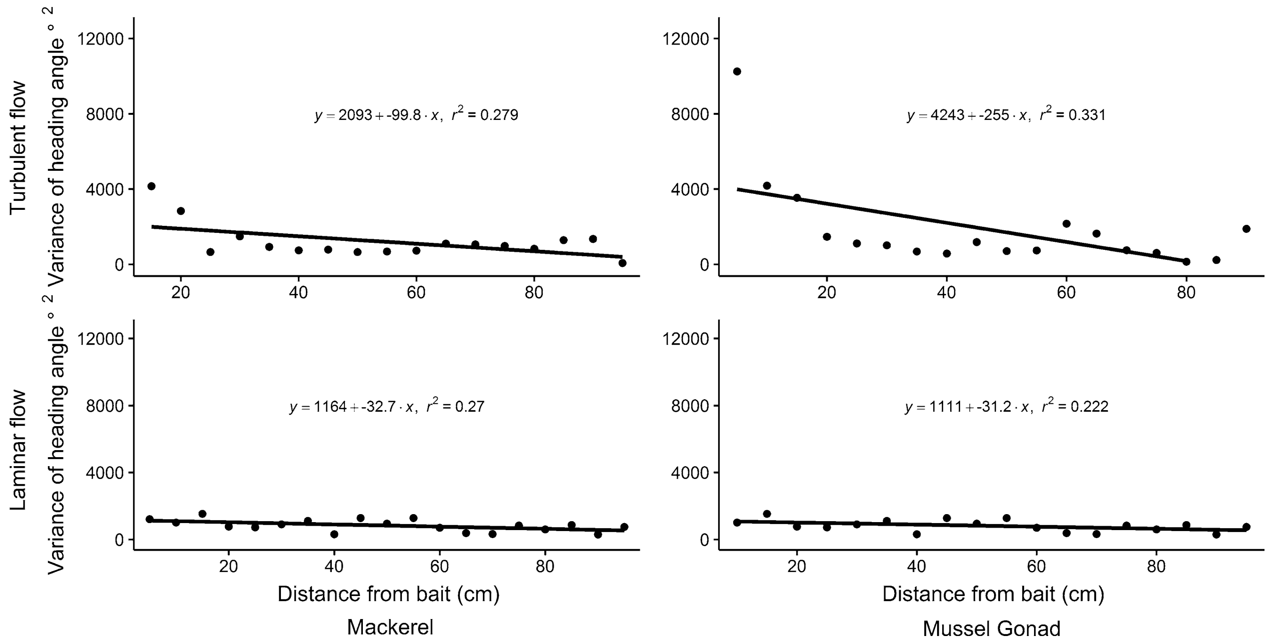

Fig. 12 Variance of the mean heading upstream of the scampi at varying distances from two types of bait (mackerel and mussel gonad) under two flow regimes (turbulent and laminar). All regressions were significant at $P < 0.05$

Discussion

Success in reaching the baits

The differences in experimental flow regimes (turbulent vs laminar) did not affect the success of the scampi in reaching either of the baits. This is consistent with other studies that have observed variations in search behaviour in lobsters in different flow regimes, but have not observed differences in success rates of lobsters reaching food odour sources [30]. This result indicates that the structure of the odour plume in both flow regimes and for both types of bait was suitable for the scampi to reliably track to the odour source.

Search efficiency

New Zealand scampi are more efficient at tracking food odours in more turbulent flow conditions. The higher efficiency was achieved by the scampi being more direct to the bait with a mean heading angle that was 14.9° smaller in the turbulent flows than in the laminar flows. This resulted in the scampi travelling between 24.8 and 52.2% less distance when foraging in the turbulent flow, and the scampi reaching the mussel gonad bait 44% faster in the turbulent flow. The dye visualisations in the tank highlight how the turbulent flow broke the plume into a greater number of filaments and dispersed these filaments across the width of the flume, compared to the single continuous narrow plume with only a small number of large filaments forming under laminar flow conditions. Filaments and microscale eddies in odour plumes create variation in odour concentration which have been highlighted as responsible for improving the efficiency of food search behaviour in a number of other lobster species [19, 46]. High variation in odour signal structure at the height of the antennules is associated with higher foraging speeds and greater success in blue crabs, but in rougher turbulent flows, this signal structure degrades due to increased mixing and results in less directed and slower movements of crabs toward odour sources [21, 22, 47]. In the current study less direct search paths were indicated by greater heading angles, higher turn angles and low tortuosity ratios. Less direct search paths were most commonly observed in laminar flow conditions. These results suggest that scampi are tuned to detect and respond to odour plumes with more complex structure that is typical of more turbulent water flow conditions.

The flow regime was observed to have more of an effect on the scampi searching for the mussel baits than the mackerel bait, with marked differences observed in search periods, heading angle, and turn angles between the two baits. These differences between the two baits are most likely due to differences in the mix and concentrations of the attractant chemicals released from the two baits [13]. Higher concentrations of chemical odours that elicit a strong food search behaviour will generate larger odour concentration gradients within odour plumes, especially across odour filaments and eddies which have been associated with facilitating the orientation response in lobsters [19, 28, 46]. Mussel gonad is known to be highly attractive to many crustaceans due to the high rate of release of amino acids, especially glycine [48, 49], which is known to stimulate food search behaviour in many crustaceans [48, 49]. Furthermore, the 5 g of mussel gonad was cut from several whole mussels for the experiments whereas only a single piece of mackerel tissue of the equivalent mass (5 g) was used. Consequently, the higher surface area to volume ratio of the experimental mussel bait would have further promoted the release of attractive chemicals into the resulting plume [50].

Walking speed is a temporal orientation parameter that has been observed to be an indicator of lobsters coming into contact with an odour filament and moving towards the source [46]. The current study did not observe a difference in mean walking speed due to the two flow regimes. However, when the walking speed was compared in relation to distance from the bait, the scampi had a larger increase in the walking speed as they approached the mackerel bait in the turbulent versus the laminar flow. This result is in contrast from previous studies that have observed lobsters to slow down as they approach the source of the odour [27]. Walking speeds of crustaceans are affected by the spatial arrangement of the odour signals [42] as the faster the crustacean progresses along the odour plume, the more regularly odorant filaments are encountered [51]. This result suggests that scampi were encountering more odour filaments as they approached the bait and sped up as a result during their approach.

Orientation strategies

Changes in the orientation parameters of scampi relative to their distance from the odour source is an indication of the orientation strategies that are being utilised, and changes in these parameters have been previously been used to identify when freshwater crayfish were altering their orientation strategies [30, 42, 52]. The results of this study suggest that the scampi were progressing up the plume as they encountered filaments of high concentration chemicals, a form of odour-gated rheotaxis, which uses chemical and rheotaxic information similar to other crustacean species [21, 52]. As both the turn and heading angles of the scampi initially decreased and then increased again as the scampi approached the baits, the results suggest that the scampi are using other sensors to spatially sense the plume and guide the rheotaxis [24, 53]. This is because the variabilities in turn and heading angles may be caused by encountering longer periods of odour intermittency further from the source, which makes spatial localisation more difficult [54]. As this pattern is consistent in both flow regimes and for both baits, it suggests that the scampi are likely to be utilising the same orientation strategy in both flow regimes. Consequently, in the turbulent flow the scampi were typically more accurate in determining their pathway once they were closer to the bait. This improved accuracy in turbulent flow may be due to the turbulence reducing the boundary layer and improving the performance of less sensitive secondary chemosensors located around the mouthparts and on the legs [27]. These secondary chemosensors are also known to play an important role in the final stages of localising baits in the American lobster (*Homarus americanus*) [27] and in the blue crab [22, 29].

Implications

In the deep sea benthic environment where scampi dwell the hydrodynamics can change markedly when the sheer stress from tidal currents generates turbulence and alters current speeds [38, 39, 55]. The results of this study suggest that scampi are tuned to search for food more efficiently during periods of higher turbulence and hence this may help to explain the association of the timing of emergence and feeding activity in scampi with periods of higher current flow [34, 37].

Deep sea lobsters use burrows as their primary defence to avoid predators, and emergence patterns of Norway lobster on the continental shelf are during periods low light to avoid visual predators [56]. However, at the depths scampi live, there is limited light and tidal cycles may be the only zeitgeber present [55]. Ling (*Genypterus blacodes*), are the primary predator of scampi, and scampi are often in the gut content of ling caught between 382 and 428 m [57]. Therefore, if scampi are tuned to emerge from their burrows due to tidal changes, then the adaption of foraging more efficiently in these turbulent conditions would reduce the time they are out of their burrows and available to predators. Consequently, a fishery using bait to attract scampi into pots should be targeting scampi during periods of higher tidal flows.

Conclusion

Chemosensory food searching in New Zealand scampi is more efficient in turbulent flow as a result of adopting more direct search paths. This improved food-finding accuracy suggests that scampi are using spatial sensing in addition to odour gated-rheotaxis, which utilises the secondary chemoreceptors on their walking legs and mouthparts, the performance of which is improved in turbulent flow conditions. In the wild, scampi display a pattern of emergent foraging behaviour associated with periods of stronger tidal flow. By having their chemosensory system and behaviour tuned to turbulent flow, scampi would be more efficient foragers when they are out of their burrow, enabling them to avoid predators. Therefore, these results have the potential to assist with improving the effectiveness of a developing pot fishery for scampi by targeting them during periods of higher tidal flow.

Abbreviations

ANCOVA: analysis of covariance; GLM: general linear model; HA: heading angle; HUp: heading upstream; OCL: orbital carapace length; PVC: polyvinyl chloride; SE: standard error; TA: turn angle.

Authors' contributions

RM and AJ Developed the experimental protocols and designed the experiments together. RM collected and analysed the data and drafted the manuscript. AJ Revised the manuscript for intellectual content. Both authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

Ethics approval and consent to participate

The transport and holding of the scampi, as well as the experimental procedures, were approved by the Animal Ethics Committee of the Nelson Marlborough Institute of Technology (AEC2014-CAW-02).

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