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Which way to turn? Effect of direction of body asymmetry on turning and prey strike orientation in starry flounder *Platichthys stellatus* (Pallas) (Pleuronectidae)

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Starry flounder *Platichthys stellatus*, a rare polymorphic flatfish exhibiting a large-scale geographic cline in the frequency of right-eyed (dextral) and left-eyed (sinistral) morphs, was studied to investigate whether foraging behaviour (turning angle and prey strike orientation) differed between dextral and sinistral laboratory-raised juveniles. *Platichthys stellatus* foraging on brine shrimp *Artemia* sp. nauplii tended to strike dorsally at prey ('left' to an observer for dextral flounder and 'right' to an observer for sinistral flounder), although this effect was stronger for sinistral fish. This dorsal tendency also increased with body size. Non-strike behaviours (movements between strikes) were ventrally biased for both morphs. Maximum turn angles were larger for both morphs towards the dorsal side than the ventral side during prey strikes but were the same during non-strike behaviours. The positioning of the eyes of the juvenile starry flounder was skewed towards the dorsal midline rather than being symmetrically placed between dorsal and ventral margins on the eyed side of each fish. The migrating eyes of dextral fish, however, were significantly closer to the dorsal midline than in sinistral fish. This, in addition to the more dorsally oriented prey strikes in sinistral fish, suggests that the morphs are not simple behavioural mirror images of one another and therefore may differ ecologically.

Key words: asymmetry; flatfish; foraging behaviour; Pleuronectiformes; predation; vision.

INTRODUCTION

The starry flounder *Platichthys stellatus* (Pallas) (Pleuronectidae) is highly unusual among flatfishes because it is polymorphic for direction of body asymmetry: some individuals have both eyes on the left (sinistral morph) and others have both eyes on the right (dextral morph) (Hubbs & Kuronuma, 1942). While direction of body asymmetry differs among flatfish species, significant polymorphism within species is rare: limited to seven of *c.* 715 species (Munroe,

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2005). Starry flounder also exhibit a striking geographical cline in the proportions of sinistral and dextral morphs: sinistrality increases from 50% in central California to 100% in Japan (Hubbs & Kuronuma, 1942). The great age of this polymorphism [*c.* 2·2 million years since the divergence of the polymorphic, North Atlantic *Platichthys flesus* (L.) from the polymorphic North Pacific *P. stellatus*; Borsa *et al.*, 1997] hints at an adaptive explanation, but the factors that maintain this enduring polymorphism and that gave rise to the even more baffling circum-Pacific cline in *P. stellatus* remain mysterious. Differences between the two morphs in anatomical traits that affect function and performance in other fishes (*e.g.* head shape, gill-raker number and caudal peduncle size), however, suggest they may segregate ecologically (Bergstrom, 2007). To determine whether body asymmetry direction has any effect on behaviour, turning and prey striking activities were compared between dextral and sinistral laboratory-raised juveniles. In other words, do mirror-image flatfishes exhibit mirror-image behaviours?

Several morphological asymmetries in flatfishes may affect foraging behaviour in their largely two dimensional world. Starry flounder, like other pleuronectids, use a mixed foraging strategy: they target small, benthic invertebrates and occasionally small fishes swimming above the substratum (Orcutt, 1950). Mixed flatfish foragers tend to use a combination of visual and olfactory cues to identify prey (de Groot, 1971; Gibson, 2005), and swim on or just above the bottom for short, discontinuous bursts during active searching. Compared to symmetrical teleosts that have primarily monocular visual fields of *c.* 180° anteriorly (Cobcroft & Pankhurst, 2006), the few visually oriented flatfish species that have been studied have visual fields approaching 360°, with a binocular field of view of *c.* 40° anteriorly (Fujimoto *et al.*, 1992). Visual acuity may shift between monocular and binocular fields of view, with improved depth perception in the latter. Therefore, the degree to which the eyes have migrated away from the dorsal midline may influence foraging behaviour if it affects the position of the field of binocular vision.

In addition, other asymmetries in starry flounder morphology may affect their foraging behaviour; for example, the placement of their nostrils, and the positioning of their dorsal and anal fins. For a dextral fish lying with the right side up, its dorsally oriented nostrils will be positioned off to the 'left' side of the eyes, although whether this off-centre positioning of the nostrils affects olfaction such that odours are more easily detected dorsally is unknown. In addition, the positioning of the dorsal and anal fins imposes a lateral bias once the fish completes metamorphosis and lies on one side. The dorsal fin is considerably longer than the anal fin in most flatfishes and therefore, for a dextral fish, it will have a longer fin on its 'left' (dorsal) side than its 'right' (ventral) side. This inequality in fin length may affect the ability to turn in one direction or the other.

Curiously, the extent of jaw asymmetry varies considerably among flatfishes, ranging from little or no asymmetry in the primitive Psettodidae, through partial jaw asymmetry with teeth only on the blind side in some Pleuronectidae, to extreme jaw asymmetry in the highly derived Cynoglossidae (Chapleau, 1993). In addition, whereas some flatfishes exhibit pronounced kinematic asymmetries when feeding, *e.g. Pleuronichthys verticalis* Jordan & Gilbert (Gibb, 1995), feeding kinematics are only weakly asymmetric in others, *e.g. Xystreurys liolepis* Jordan & Gilbert (Gibb, 1996). Although the weak asymmetries in form and kinematics that do exist are simply reversed in opposite-eyed individuals of *X. liolepis* [the one polymorphic flatfish whose feeding has been studied in detail (Gibb, 1996)], the effect of direction of body asymmetry on turning and prey striking behaviour is unknown.

In this study, 1) whether starry flounder exhibit a dorso-ventral bias (lateral bias to an observer) during foraging activities and 2) whether any detected directional biases differed between morphs and between striking and non-striking behaviours were tested. These findings could indicate if there is a functional advantage to turn one direction or another while foraging, which may be due, among other things, to a lateral bias in binocular visual field of view, olfactory sensitivity or locomotor capacity. If dextral and sinistral starry flounder both exhibit the same directional bias during foraging, they will be manoeuvring in opposite directions from the perspective of an onlooker, since dorsal is towards the left in dextral fish and towards the right in sinistral fish. This may have ecological implications if their prey are also lateralized in form or response to predation, as seen in scale-eating cichlids (Nakajima *et al.*, 2004).

MATERIALS AND METHODS

Starry flounder juveniles were raised in captivity from fertilized eggs at the Bamfield Marine Science Centre, British Columbia, Canada, beginning in March of 2005. Larvae were fed live rotifers *Brachionus plicatilis* daily and post-metamorphic juveniles were fed live brine shrimps *Artemia* sp. nauplii daily. By August 2005, 23 juveniles had grown to a mean ± S.D. standard length (L_S) of 17·6 ± 3·0 mm (range 12·2–24·4 mm), actively fed on *Artemia* sp. for several minutes at a time immediately after feeding, and were accustomed to feeding in the presence of an observer.

To quantify feeding and locomotory behaviours, each juvenile was placed in a separate glass container (100 mm long, 80 mm wide, 70 mm tall) that was filled to 50 mm deep with fresh sea water and set in a water-bath of 10° C. A 10 × 10 mm grid was placed beneath each container. The fish were allowed to acclimate for 24 h and were fasted during this time. After 24 h, a digital video camera was placed on a tripod directly above each container in turn, and each fish was fed freshly hatched *Artemia* sp. nauplii at a density of 20 nauplii ml^{-1}. Immediately after adding *Artemia* sp. to the container, the fish's foraging behaviour was recorded for 3 min.

The following were recorded from the 3 min video clips: each juvenile's L_S and asymmetry morph (sinistral or dextral), the number of strikes made at prey, the direction of each strike (straight ahead, anatomical dorsal or anatomical ventral), the angle of dorsal or ventral strikes (relative to the resting fish's midline immediately prior to the strike) and the number, direction and angle of all non-strike behaviours, which included moving around, pausing and turning in the container between strikes. This foraging strategy is commonly used in flatfishes, and searching for prey occurs during these frequent pauses and turns between strikes (Holmes & Gibson, 1983; O'Brien *et al.*, 1990). Angles were scored as positive if they were dorsal and negative if they were ventral. Angles of $\leq 2°$ were not scored as turns but as straight-ahead motions. Behaviours that occurred when juveniles were against the side of the container were excluded from analysis as the container wall restricted their movement.

The direction of each turn was tested for independence of the previous turn's direction by recording the number of times a dorsal turn was preceded by a dorsal turn (DD), a dorsal turn preceded by a ventral turn (VD), a ventral turn preceded by a dorsal turn (DV) and a ventral turn preceded by a ventral turn (VV), and comparing these frequencies to those expected based on the total frequency of dorsal and ventral turns for that fish. Only one fish showed a significant (before sequential Bonferroni correction) departure from the expected turn sequences (χ^2, d.f. $= 2$, $P < 0{\cdot}05$; non-significant after sequential Bonferroni correction), and this individual showed an excess of DV and VD turn sequences relative to DD and VV sequences. Since the main concern was that an excess of DD or VV sequences due to non-independence would bias indications of turning preference, this individual fish was included in the analysis.

An ANCOVA was run with signed angle of turn as the dependent variable, morph (dextral, sinistral) and type of behaviour (prey strike or non-strike) as factors, and L_S as a covariate. The dependence of strike angle on body size did not differ between behaviours or morph (two- or three-way interaction terms involving the covariate, L_S all $P > 0{\cdot}05$); therefore, the ANCOVA was re-run with these interaction terms removed to test for main effects of morph, behaviour and L_S on mean signed turn angle.

An ANCOVA was also run with the maximum absolute angle turned for each individual fish as the dependent variable, morph (dextral and sinistral), type of behaviour (prey strike or non-strike) and direction of turn (dorsal or ventral) as factors and L_S as a covariate. Again slopes did not vary among factors (two-, three- and four-way interactions terms involving L_S; all $P > 0{\cdot}05$); therefore, the ANCOVA was re-run with interaction terms that included the covariate removed.

The degree of eye migration between sinistral and dextral starry flounder was compared by measuring the angle each eye had migrated from the dorsal midline. Frontal photographs were taken of a sample of 40 formalin-fixed adult starry flounder (180–380 mm L_S) from Denman Island, British Columbia. Using the anterior tips of the premaxilla and dorsal fin as reference points, the angles from the dorsal midline to the dorsal and ventral edges of each orbit were measured and averaged to give the migration angle of the midpoint of each eye. The angle of eye departure from the dorsal midline was compared between dextral and sinistral morphs with *t*-tests. All animals were handled in compliance with the Canadian Council on Animal Care (University of Alberta BioSciences Animal Policy & Welfare Committee approved protocol 414607).

RESULTS

Fish performed, on average, 25 prey strikes during the 3 min period (ranging from nine to 53 strikes per fish), and 35 non-strike behaviours (from 16 to 54 per fish) including moving backward, moving forward, backward turns, forward turns and stationary turns (rotation only).

Mean signed turn angle differed significantly between striking and non-striking behaviours ($P < 0{\cdot}001$) and between morphs ($P = 0{\cdot}01$) and became more dorsally biased with increasing L_S ($P = 0{\cdot}001$; Table I and Figs 1 and 2). During both strike and non-strike behaviours, sinistral fish were more dorsally oriented

TABLE I. Results of main effects of ANCOVA on mean signed turning angle, with interaction terms involving standard length (L_S) removed (all were non-significant). Behaviour is either a strike or a non-strike; morph is either sinistral or dextral

Factor	MS	d.f.	*F*	*P*
Behaviour	5058·03	1	28·12	<0·001
Morph	1186·06	1	6·60	0·01
Behaviour × morph	3·03	1	0·02	0·90
L_S	2153·08	1	11·97	0·001
Error	179·85			

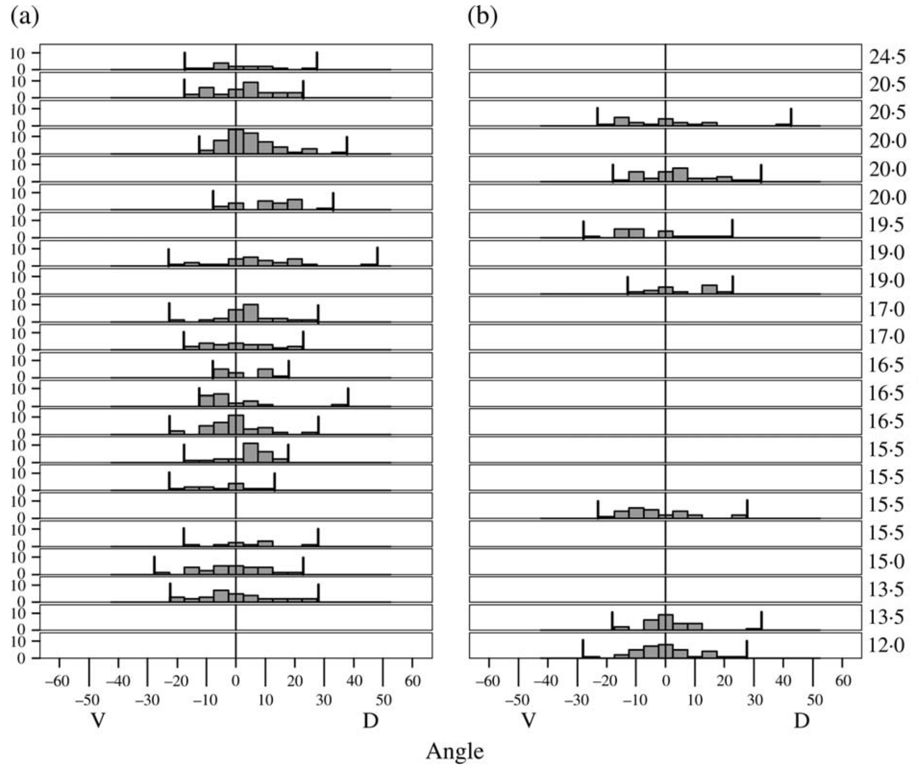

FIG. 1. Frequency histograms of prey strikes, showing direction and magnitude of turns for individual (a) sinistral and (b) dextral starry flounder. Values on *x*-axis are angles; ventral directed turns (V) are negative, dorsal directed turns (D) are positive, straight strikes are zero. Fish are ordered by standard length with increasing size from bottom to top. Short vertical lines mark the maximum ventral and dorsal turn angles for each fish.

than dextral fish (Fig. 3). In prey strikes, sinistral fish were more dorsally oriented whereas dextral fish did not show a turn direction preference. In addition, the ratio of total number of dorsal to ventral strikes was higher for sinistral fish (mean ± S.E. 1·84 ± 0·35, $n = 15$) than dextral fish (1·02 ± 0·22, $n = 7$), consistent with the difference in mean signed turn angle. In non-striking behaviours, both dextral and sinistral individuals tended to turn ventrally (Fig. 3), and this ventral bias did not differ among non-strike activities (forward, backward and stationary turns; one-way ANOVA, d.f. = 2 and 737, $P > 0{\cdot}05$).

Maximum turn angles were significantly greater for non-strike behaviours than for strikes ($P < 0{\cdot}001$) and dextral fish tended to make slightly larger turns than sinistrals although this effect was not significant ($P > 0{\cdot}05$; Table II and Fig. 4). Due to the suggestive behaviour-by-turn-direction interaction term in Table II, two separate ANCOVAs were run for strike and non-strike behaviours, and with only morph and turn direction as factors and L_S as a covariate. The dependence of maximum turn angle on body size did not differ between morphs or turn direction for either behaviour (all two- and three-way interaction terms involving L_S were $P > 0{\cdot}05$); therefore, the ANCOVA was re-run with the interaction terms involving the covariate removed to test for main effects.

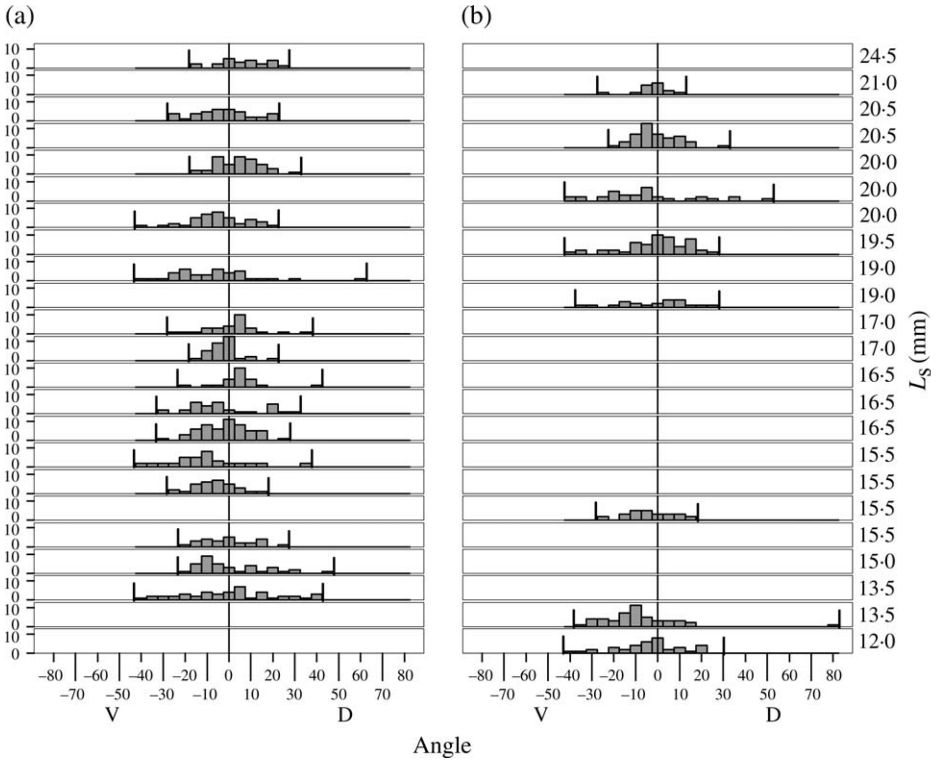

FIG. 2. Frequency histograms of non-prey strikes, showing direction and magnitude of turns for individual (a) sinistral and (b) dextral starry flounder. Values on the *x*-axis are angles; ventral directed turns (V) are negative, dorsal directed turns (D) are positive, straight movements are zero. Fish are ordered by standard length with increasing size from bottom to top. Short vertical lines mark the maximum ventral and dorsal turn angles for each fish.

Dorsal turns were larger than ventral turns for both morphs during prey strikes ($P < 0{\cdot}001$) but not during non-strikes ($P > 0{\cdot}05$; Table III and Fig. 4).

Both eyes were oriented *c.* 4° further from the dorsal midline in sinistral than dextral fish (Fig. 5). Although the angle of midline departure for the non-migrating eye did not differ significantly between morphs [*t*-test, d.f. = 53, $P > 0{\cdot}05$; Fig. 5(a)], the migrating eye was significantly further away from the dorsal midline in left-eyed than right-eyed fish [*t*-test, d.f. = 53, $P < 0{\cdot}05$; Fig. 5(b)]. Regardless of morph, the positioning of both eyes was dorsally biased, rather than symmetrically placed between dorsal and ventral margins on the eyed side of each fish. The non-migrating eye was, on average, 8·4° ventral to a line perpendicular to the substratum at the anatomical midline, while the migrating eye was 52° dorsal to this line. If the eyes were symmetrically placed dorso-ventrally, these angles would be the same.

DISCUSSION

Flatfishes see their world in a decidedly unusual way because both eyes lie on the same anatomical side of the body: the upper surface to an observer.

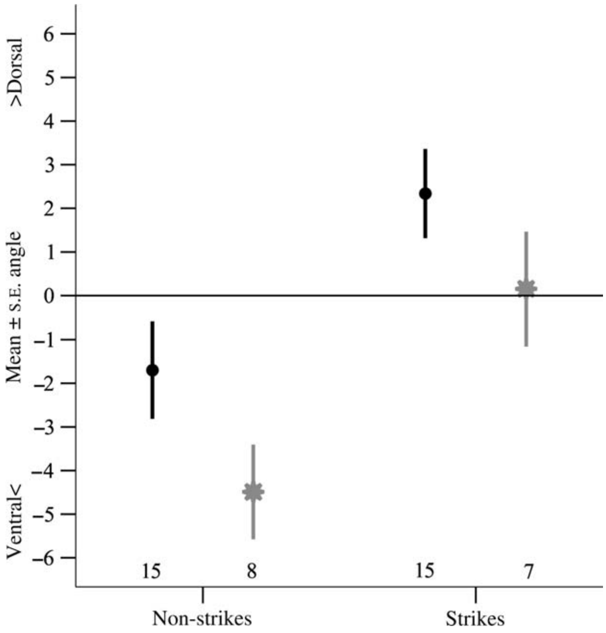

FIG. 3. Mean ± S.E. signed turn angles for sinistral (●) and dextral (✱) fish during non-strike and strike behaviours. Numbers under each bar represent number of individuals used to compute that mean. In all cases, strike turns were more dorsal than non-strike turns, and sinistral fish turned more dorsally than dextral fish. Non-strike behaviours for all fish were comprised of backwards movements (mean ± S.E. turn angle $= -1.71 \pm 0.77$; $n = 23$), forwards movements (mean ± S.E. turn angle $= -2.07 \pm 0.82$; $n = 23$) and stationary turns (mean ± S.E. turn angle $= -4.19 \pm 1.24$; $n = 23$), did not differ significantly from each other, and were therefore pooled.

Because both eyes are protrusible and independently moveable, one benefit of this arrangement is a nearly 360° combined field of view (Gibson, 2005). In the few flatfish species that have been studied, however, binocular vision is limited to 40–50° anteriorly and *c.* 10° posteriorly (Gibson, 2005), although this varies among species (Fujimoto *et al.*, 1992). In addition, unlike most other fishes,

TABLE II. Results of main effects of ANCOVA on maximum turning angle, with interaction terms involving standard length (L_S) removed (all were non-significant). Behaviour is either a strike or a non-strike; morph is either sinistral or dextral; turn direction is either dorsal or ventral

	MS	d.f.	*F*	*P*
Behaviour	2231·74	1	18·42	<0·001
Morph	381·66	1	3·15	0·08
Turn direction	414·12	1	3·42	0·07
Behaviour × morph	84·04	1	0·69	0·41
Behaviour × turn direction	396·14	1	3·27	0·07
Morph × turn direction	67·72	1	0·56	0·46
Behaviour × morph × turn direction	101·59	1	0·84	0·36
L_S	2·86	1	2·86	0·10
Error	121·15			

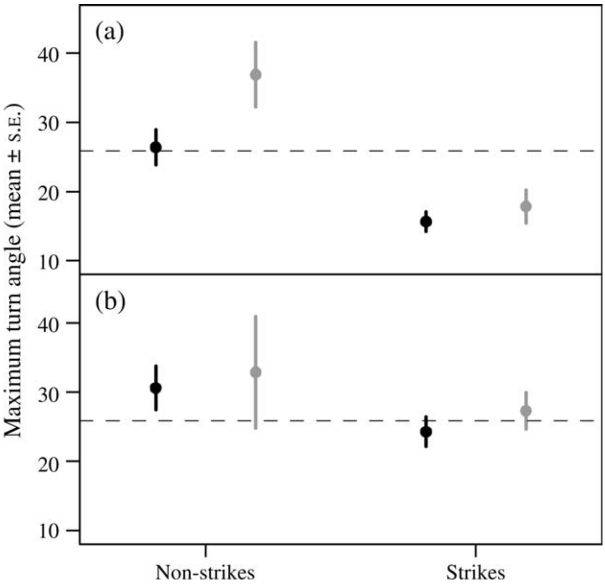

FIG. 4. Mean ± S.E. maximum turn angles in degrees as a function of direction of turn (a) ventral and (b) dorsal, asymmetry morph [sinistral (●) and dextral (●) fish] and behaviour (non-strikes and strikes). Horizontal dashed line represents the mean maximum angle for all fish (25·9°). Maximum turn angles were less pronounced for strikes than non-strikes, but tended to be larger (both dorsally and ventrally) for dextral than sinistral fish and larger for dorsal strikes than ventral strikes. See Fig. 3 for sample sizes.

where both eyes see symmetrically positioned fields of view to either side of the midplane, the eyes in flatfishes see fields of view that are skewed towards the dorsal midline (Fujimoto *et al.*, 1992). The non-migrating eye lies near or slightly ventral to the lateral midline [Fig. 5(a)], while the migrating eye lies about half way between the lateral midline and the dorsal margin of the head

TABLE III. Results of main effects of ANCOVA on maximum absolute turning angle for strikes and non-strikes separately, with interaction terms involving standard length (L_S) removed (all were non-significant). Morph is either sinistral or dextral; turn direction is either dorsal or ventral

Behaviour	Factor	MS	d.f.	*F*	*P*
Strike	Morph	61·93	1	1·27	0·27
	Turn direction	775·64	1	15·93	<0·001
	Morph × turn direction	1·64	1	0·03	0·86
	L_S	5·59	1	0·12	0·74
	Error	48·69			
Non-strike	Morph	437·22	1	2·33	0·14
	Turn direction	0·10	1	0·01	0·98
	Morph × turn direction	175·41	1	0·93	0·34
	L_S	555·59	1	2·96	0·09
	Error	187·79			

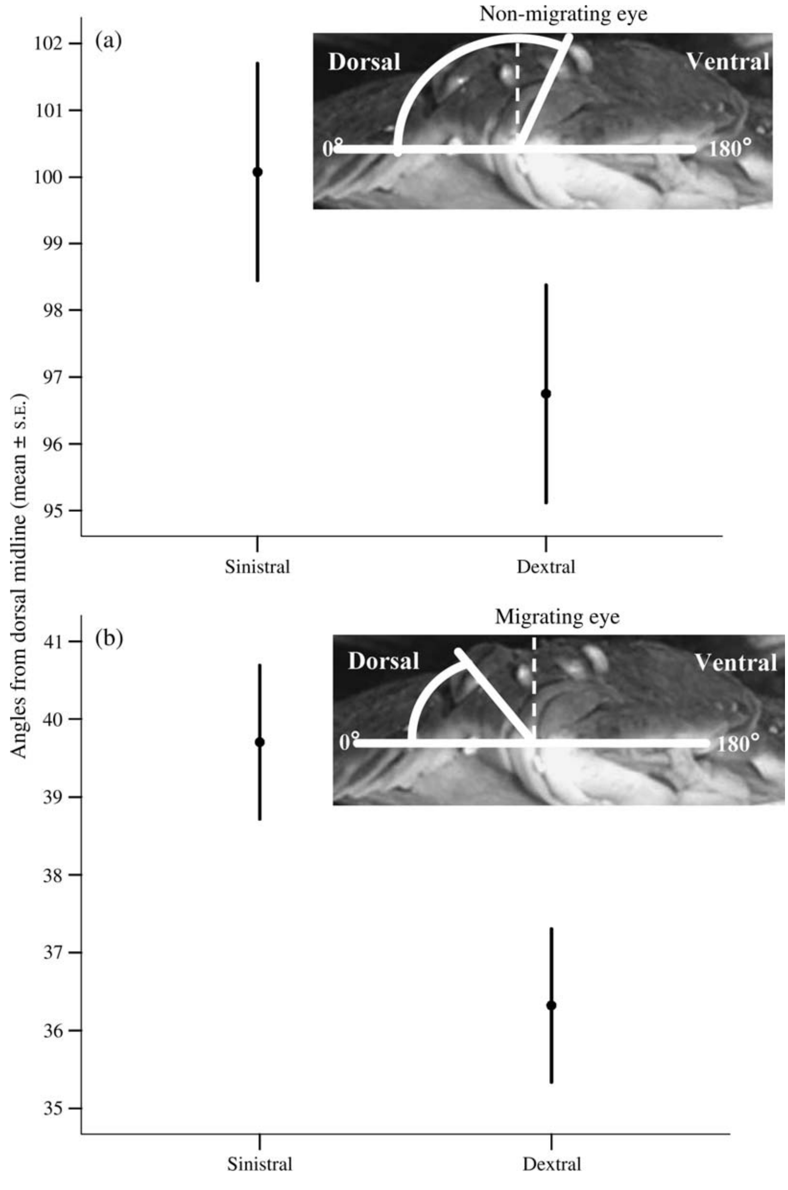

FIG. 5. Degrees of departure from the dorsal midline for (a) non-migrating and (b) migrating eyes of sinistral and dextral morphs of adult starry flounder (sinistral $n = 27$; dextral $n = 28$). The sinistral flounder in the photograph shows how angle of departure from the dorsal midline was calculated for each eye. Dashed vertical line shows 90° angle for reference, which is parallel to the lateral midline of the fish.

[Fig. 5(b)]. Taken together, flatfishes should generally have a wider binocular view towards their dorsal margin than their ventral margin when looking anteriorly (Fujimoto *et al.*, 1992).

Does a wider view dorsally influence the preferred orientation of turning or prey strike behaviour? The present results showed a small but significant dorsal bias to average strike angle, at least compared to non-striking turn angles, which tended to be more ventral (Fig. 3). In addition, maximum turn angles were *c.* 10° larger during dorsal prey strikes than ventral prey strikes (Fig. 4), while there was no difference for non-prey strikes. These results are consistent with the dorsal rotation of the neurocranium relative to the body prior to and during the strike of dextral *P. verticalis* (Gibb, 1995) and both sinistral and dextral *X. liolepis* (Gibb, 1996), both of which rotate the neurocranium more dorsally than most other percomorph fishes (Gibb, 1997). The excess of ventral non-strike turns in this study is also consistent with the 15% ventral turn excess of 'near-attack' turns (the 10 turns taking place just prior to striking) reported in plaice *Pleuronectes platessa* L. (Hill *et al.*, 2000) because nearly all recorded turns were within 10 turns prior to a prey strike. Pre-strike turn angles in flatfishes may therefore be generally ventrally biased whereas strike angles appear to be dorsally biased.

Maximum strike angles, which better define the field of view that elicits a prey strike than do average strikes angles, were dorsally biased with a mean dorsal maximum of *c.* 27° compared to a mean ventral maximum of *c.* 17° (Fig. 4). Significantly, the total 44° anterior prey striking range (dorsal maximum + ventral maximum) within which all prey strikes were elicited lies within the 40–50° range reported for the binocular field of view of other flatfishes (Gibson, 2005). The dorsal bias in the positioning of the eyes on one side of the body in *P. stellatus* suggests that the binocular field of view may be dorsally (lateral to the observer) biased, rather than symmetrically placed as in other teleosts. This, combined with the dorsal bias of maximum strike angles in *P. stellatus*, suggests that they strike at prey within their binocular field of view. The binocular field of view may be wider than the maximum prey striking range, but other mechanical constraints that cannot be ruled out at present might limit the latter. Strike success could not be reliably measured from the video, so it could not be determined whether dorsal strikes were more successful or not.

The feeding kinematics (bone and muscle movements) of sinistral and dextral individuals of the polymorphic *X. liolepis* are largely mirror images of one another (Gibb, 1996), but does this apply to turn and strike orientations? Sinistral and dextral flatfishes are not complete anatomical mirror images of one another. First, although the eyes may lie on other side of the body, the viscera are always asymmetrical in the same direction (*e.g.* left-sided heart and liver and right-sided intestinal coils; Hubbs & Hubbs, 1945). Second, the left optic nerve is invariably dorsal to the right optic nerve within the Pleuronectidae, regardless of whether the eyes are on the left or right side of the body (Hubbs & Hubbs, 1945). Third, subtle divergence exists between sinistral and dextral starry flounder in head shape, gill-raker number and caudal peduncle size (Bergstrom, 2007). These differences taken together might yield turning and striking behaviours that are not mirror images of one another.

Indeed, the present results revealed some unexpected differences between sinistral and dextral starry flounders. First, sinistral fish were more dorsally biased in turn angles than dextral fish (Fig. 3 and Table I). While significant, these differences were not great (*c.* 3°), but the consistently more dorsal orientation of sinistral fish for both turning and striking behaviours suggests this difference is real. Sinistral fish also exhibited a higher ratio of dorsal to ventral turns (1·84) compared to dextral fish (1·02), which reinforces the conclusion that turns of sinistral fish are more dorsally biased than those of dextral individuals. Second, sinistral fish had slightly smaller maximum turn angles than dextrals. Although the effect was not significant ($P > 0{\cdot}05$), the same trend was consistent for both dorsal and ventral turns during both strikes and non-strikes (Fig. 4). Third, both eyes were positioned *c.* 4° more dorsally on dextral compared to sinistral fish (Fig. 5). Curiously, this is the reverse of what would be expected given the more dorsal turning bias of sinistral fish (Fig. 3): if the greater dorsal turning and striking bias of sinistral fish was due to a difference in eye positioning, eyes of sinistral fish should have been positioned more dorsally than dextral fish, but, instead, the opposite was observed. Eye position measurements were made on adult, wild-caught individuals, and so may have differed from the eye positions of juvenile, laboratory-raised individuals. Although eye positioning might have differed in juvenile, laboratory-raised individuals, allometry or rearing environment would probably not cause the opposite morphological tendency to occur. Some aspect of the morphology of dextral fish may enhance their ability to turn ventrally, resulting in ambidextrous strike behaviours despite the greater dorsal positioning of their eyes. Dextral fish tended to make larger turns both dorsally and ventrally than sinistral fish. These individuals may have a greater range of motion relative to sinistral fish that releases them from the limits of their dorsal binocular vision, which could put them at an advantage while foraging in a spatially random and symmetrical world.

Given that *P. stellatus* is in the relatively large, dextral family Pleuronectidae, the sinistral morph in this species might be considered a congenital 'oddball' that arose due to a developmental error. If true, perhaps the dorsal strike tendency and positioning of the eyes of the sinistral morph are erroneous consequences of an inferior developmental programme. This is probably unlikely because the sinistral morph is ubiquitous across the range of the species and is the more common of the two morphs. Although it may have arisen originally as a developmental anomaly, a pure developmental anomaly would not be expected to become so abundant relative to the ancestral dextral morph or to exhibit such a prolonged temporal persistence (Hubbs & Kuronuma, 1942). Therefore, the behavioural and morphological attributes unique to the sinistral morph are either neutral or reflect ecological specialization. Behavioural and morphological comparisons between dextral and sinistral individuals of other species are needed, particularly in normally monomorphic species reared in culture that tend to exhibit a much higher incidence of eye side reversal than observed among field-collected individuals (Schreiber, 2006).

Three clear conclusions emerge from the present study. First, juvenile starry flounder tend to turn and strike at prey in a dorsal direction relative to non-strike turns. Second, they appear to strike at prey within the binocular region of their anterior field of view. Third, dextral and sinistral starry flounder are not simple mirror images of one another, behaviourally or morphologically. These differences in foraging behaviour and position of the eyes are subtle yet consistent, as are morphological differences in head and tail form between dextral and sinistral starry flounder (Bergstrom, 2007). Collectively these differences all suggest that sinistral and dextral starry flounder differ ecologically, and that ecological mechanisms may maintain polymorphisms for direction of body asymmetry in this and other polymorphic flatfish species.

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