

Morphological evidence of correlational selection and ecological segregation between dextral and sinistral forms in a polymorphic flatfish, *Platichthys stellatus*

C. A. BERGSTROM

Systematics & Evolution Group, Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada and Bamfield Marine Science Center, Bamfield, BC, Canada

Keywords:

asymmetry;
competition;
correlational selection;
ecomorphology;
Pleuronectiformes;
trophic specialization.

Abstract

Phenotypic polymorphisms in natural systems are often maintained by ecological selection, but only if niche segregation between morphs exists. Polymorphism for eyed-side direction is rare among the ~700 species of flatfish (Pleuronectiformes), and the evolutionary mechanisms that maintain it are unknown. *Platichthys stellatus* (starry flounder) is a polymorphic pleuronectid flatfish exhibiting large, clinal variation in proportion of left-eyed (sinistral) morphs, from 50% in California to 100% in Japan. Here I examined multiple traits related to swimming and foraging performance between sinistral and dextral morphs of *P. stellatus* from 12 sites to investigate if the two morphs differ in ways that may affect function and ecology. Direction of body asymmetry was correlated with several other characters: on an average, dextral morphs had longer, wider caudal peduncles, shorter snouts and fewer gill rakers than sinistral morphs. Although the differences were small in magnitude, they were consistent in direction across samples, implying that dextral and sinistral starry flounder may be targeting different prey types. Morphological differences between morphs were greatest in samples where the chances of competitive interactions between them were the greatest. These results suggest that the two morphs are not ecologically identical, may represent a rare example of divergent selection maintaining polymorphism of asymmetric forms, and that correlational selection between body asymmetry and other characters may be driven by competitive interactions between sinistral and dextral flatfish. This study is one of very few that demonstrates the ecological significance of direction in a species with polymorphic asymmetric forms.

Introduction

Asymmetry, or lateral bias in trait expression, is a common phenomenon of life. Divergence in form between left and right versions of a character is often associated with functional specialization between them, and as such, selection for asymmetry may occur if this specialization incurs greater fitness to the individual. Ear

positional asymmetry in owls (Norberg, 1978), claw shape asymmetry in lobsters (Govind & Pearce, 1986; Pratt & McLain, 2002), wing pattern asymmetry in male speckled wood butterflies (Windig & Nylin, 1999), and hemispheric brain asymmetry in vertebrates (Bisazza *et al.*, 1998) all are examples of specialization of function between left and right sides that have ecological and adaptive importance.

At the population level, asymmetry can exhibit lateral monomorphism, where all individuals are biased in the same direction, or lateral polymorphism, where conspicuous morphological asymmetry is present in both left-biased and right-biased forms in various proportions.

Correspondence: C. A. Bergstrom, Bamfield Marine Science Center, Bamfield, British Columbia, Canada V0R 1B0.
Tel.: +1-250-728-3301; fax: +1-250-728-3452;
e-mail: cbergstr@bms.bc.ca

In both cases, there may be adaptive significance to the asymmetry regardless of the direction of bias. However, cases of lateral polymorphism raise the issue of the significance of direction: why are both left- and right-biased individuals occasionally present in the same species? Does the direction of bias affect ecological interactions? To date, there is little understanding of the evolutionary and developmental mechanisms resulting in lateral polymorphism or of the importance of the actual direction of asymmetry (but see Palmer, 2004).

In general, polymorphisms are maintained by frequency-dependent selection or by variable selection causing specialization of each morph to a specific micro-niche (Fisher, 1930; Maynard Smith, 1989). The importance of frequency-dependent selection (Gross, 1985; Sinervo & Lively, 1996; Rainey *et al.*, 2000) and variable selection (Cain & Sheppard, 1954; Hedrick, 1986; Smith, 1993; Sandoval, 1994; Reimchen, 1995; Smith & Skúlason, 1996) in maintaining variation within species is widespread across taxa. In the case of lateral polymorphisms, negative frequency-dependent selection is a plausible mechanism that maintains variation in human handedness (Raymond *et al.*, 1996; Billiard *et al.*, 2005), direction of bill crossing in crossbills (Benkman, 1996), and mouth twisting direction in scale-eating cichlids (Hori, 1993), but examples of ecological segregation between lateral morphs and variable selection (frequency independent) maintaining lateral polymorphisms are rare.

Platichthys stellatus (starry flounder), a pleuronectid flatfish found in the north Pacific, demonstrates a remarkable geographical pattern in body asymmetry, and is an excellent species with which to study the evolutionary mechanisms maintaining lateral polymorphism. *Platichthys stellatus*, like all flatfish, exhibits conspicuous lateral asymmetry in numerous traits; most obvious of which is the migration of one eye to the other side of the head during metamorphosis (Fig. 1a). Additional changes related to eye migration include asymmetrical pigmentation (Fig. 1b), and a behavioural shift from larvae that exhibit upright, open-water swimming to juveniles and adults that lie on the ocean floor, eyed side up (Norman, 1934). *Platichthys stellatus* is unusual in that it exhibits lateral polymorphism for the side of the body on which the eyes lie, dextral fish having both eyes on the right and sinistral fish having both eyes on the left (Fig. 1c). The evolution of lateral polymorphism in flatfish is rare (seven of approximately 715 species), and occurred independently throughout the order Pleuronectiformes (Munroe, 2005). Of these seven polymorphic species, only *P. stellatus* exhibits a large-scale geographical cline in the proportion of dextral and sinistral morphs across its range. A polymorphic congeneric, *P. flesus*, also exhibits geographical variation in this proportion throughout Europe (Fornbacke *et al.*, 2002) but this is much less than the variation seen in *P. stellatus*.

In the early 1900s, reports of the relative frequency of sinistral and dextral morphs of *P. stellatus* demonstrated a remarkable shift from equal numbers of both morphs in central California, to 75% sinistral morphs in Alaska and 100% sinistral morphs in Russia and northern Japan (Hubbs & Kuronuma, 1942). Although there is moderate heritability of body asymmetry direction in *P. stellatus* (Policansky, 1982; Boklage, 1984; C. A. Bergstrom & A. R. Palmer, unpublished), the mechanisms that maintain the geographical shift in relative frequency of lateral morphs in this species remain an enigma. Detection of other traits that are correlated with lateral morph may illuminate ecologically functional differences between morphs, and would suggest that the polymorphism is maintained by selection on correlated characters (Lande & Arnold, 1983; Shine *et al.*, 1998). Correlational selection of this kind is likely to operate in most polymorphic species (Sinervo & Svensson, 2002), and this would not be the first instance of lateral morphs differing in other traits besides asymmetry direction: sinistrally coiled snails from two genera (*Partula* and *Cerion*) differ in shell width compared with their dextral counterparts (see Gould *et al.*, 1985 and references therein).

The objective of the present study is to investigate if there is evidence of ecological segregation between sinistral and dextral *P. stellatus*. This would support the hypothesis that the direction of asymmetry is associated with fitness, and that the cline in lateral morph frequencies is adaptive. I investigated variation in multiple morphological traits of *P. stellatus* to assess whether the sinistral and dextral morphs are anatomical mirror images of each other, and if not, whether any differences exist that may affect function and ecology. If morphological differences between sinistral and dextral morphs are because of competition and character displacement, I expected to find larger differences where competition was stronger (in localities with almost equal proportions of both morphs). In addition, I compared the frequency of sinistral *P. stellatus* from a number of recent samples from around the North Pacific to those reported in the earlier part of the 20th century. Temporal consistency in the relative proportion of sinistral *P. stellatus* would not be expected if the cline were entirely because of random processes, unless population sizes were extremely large.

Materials and methods

Samples of *P. stellatus* were collected from 12 sites throughout the north Pacific by beach seine or otter trawl. All samples were collected from May to October between 1999 and 2004 except for one (Columbia River mouth), which was collected in 1988. Some samples were fixed in 10% formalin and stored in 75% ethanol before being photographed and examined for this study (Columbia River mouth, Sakhalin Island); some were fixed and stored in 95% ethanol (Kuril Island, Puget Sound, Victoria); the rest were photographed and

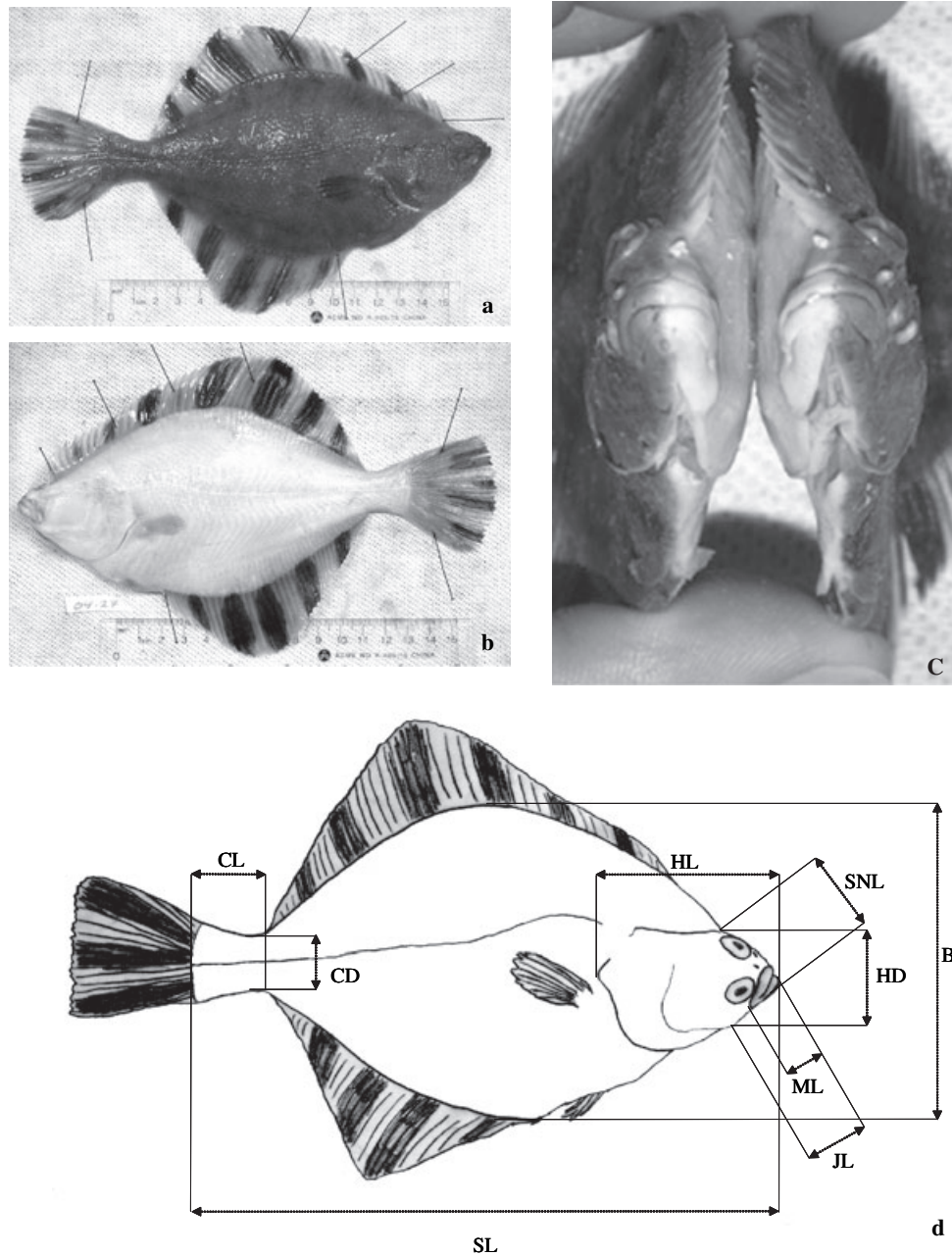


Fig. 1 *Platichthys stellatus* morphology showing (a) eyed side of a dextral individual, (b) blind side of the same individual, (c) anterior view of dextral (on left) and sinistral (on right) *P. stellatus* juveniles, and (d) sketch of dextral *P. stellatus* showing traits measured for this study: BD = body depth; CD = caudal peduncle depth; CL = caudal peduncle length; HD = head depth; HL = head length; JL = jaw length; ML = mouth length; SNL = snout length; SL = standard length.

examined fresh. Sample sizes ranged from 12 to 59 with an average of $30 (\pm 4.4 \text{ SE})$, for a total of 355 fish. The following samples were from the University of Washington Fish Collection Museum: Columbia River mouth (catalogue no. 1988-IX:30), Kuril Islands (no. 43598), Puget Sound (no. 48377), Sakhalin Island (no. 46120). Alaskan samples were collected by the Alaskan Depart-

ment of Fish and Game and the National Oceanic and Atmospheric Administration. The Denman Island and Hecate Strait samples were collected by the Canadian Department of Fisheries and Oceans. The Victoria and Bamfield samples were collected by the author.

Fish were scored for asymmetry morph (fish with both eyes on the left side are sinistral and with both eyes on

the right side are dextral), gill raker number, several metric traits likely to affect feeding and swimming performance, and age class. Fish were placed into age classes based on standard length (juveniles ≤ 200 mm SL, adults > 200 mm SL; Orcutt, 1950), but only three samples (Bamfield, Denman Island, and Hecate Strait) contained both age classes.

The proportion of sinistral and dextral morphs was compared among samples and between age classes within samples when possible using G tests and log-linear analysis. The correlation between the proportion of sinistral fish and proximity to northern Japan among samples was tested using linear regression. Comparisons of proportions of morphs in recently caught samples (samples used in the current study, which were collected in 1988 and later) were compared with those of older samples reported in the literature from the same areas (Hubbs & Kuronuma, 1942; Orcutt, 1950; Forrester, 1969) using G tests.

The left and right sides of each fish were photographed with a digital camera, and linear measurements (all in mm) were taken using tpsDig (© F. James Rohlf; version 1.4) and Excel (© Microsoft Corporation). Metric traits taken from the photographs included: standard length, body depth, mouth length, head length, jaw length, snout length, head depth, and depth and length of the caudal peduncle (Fig. 1d). Bilateral traits (head length, mouth length, jaw length and gill raker number) were measured on both left and right sides of the body and converted to a mean per fish ($[L + R]/2$). A subset ($n = 59$) of fish were re-measured from the original photographs to estimate repeatability (intra-class correlation coefficient; see Lessells & Boag, 1987) all of which were ≥ 0.90 . All metric traits were natural log transformed ($\ln[x + 1]$) and gill raker number was square-root transformed. As fish varied in overall size both within and among samples, all transformed metric traits were size standardized before further analysis. First, residuals were calculated from regression for each trait against standard length within each sample to adjust for size within samples. Second, the adjusted mean for each trait (from an ANCOVA with sample site as a factor, standard length as the covariate and the interaction term 'site \times covariate' removed) was added back to fish in each sample to adjust for size among samples while still retaining among-sample variation in growth rates of traits (Vamosi & Schluter, 2004; Østbye *et al.*, 2005). Therefore, values for metric traits were adjusted to the mean standard length (276 mm) for all individuals in the study. This allowed me to create a new variable for each trait that was independent of size that I could use in multivariate analyses.

Univariate comparisons of all traits were made among sample sites and between laterality morphs with two-way ANOVAs (type III because of unequal sample sizes). A discriminant factor analysis was run on all size-standardized metric traits and gill raker number, using asymmetry

morph (sinistral or dextral) as the grouping variable to determine what percentage of morphs can be classified correctly based on anatomical features aside from their body asymmetry.

Results

Current geographical patterns of frequencies of sinistral *Platichthys stellatus*

The frequency of sinistral flounder ranged from 0.45 to 1.00 and differed significantly among sample sites (log-linear: morph by sample site interaction $G_{11} = 49.85$; $P < 0.001$; Fig. 2). There were neither significant differences in the proportion of sinistral morphs between younger and older age classes (morph by age interaction $G_1 = 0.06$; $P = 0.81$), nor was there a significant interaction between age and sample site (morph by age by sample site interaction $G_{11} = 2.41$; $P = 0.99$).

Recent counts of sinistral vs. dextral *P. stellatus* morphs from samples encompassing a broad geographical range (from the mouth of the Columbia River to Japan) did not differ significantly from those published between 1942 and 1969 (Table 1; Hubbs & Kuronuma, 1942; Orcutt, 1950; Forrester, 1969). Recent frequencies

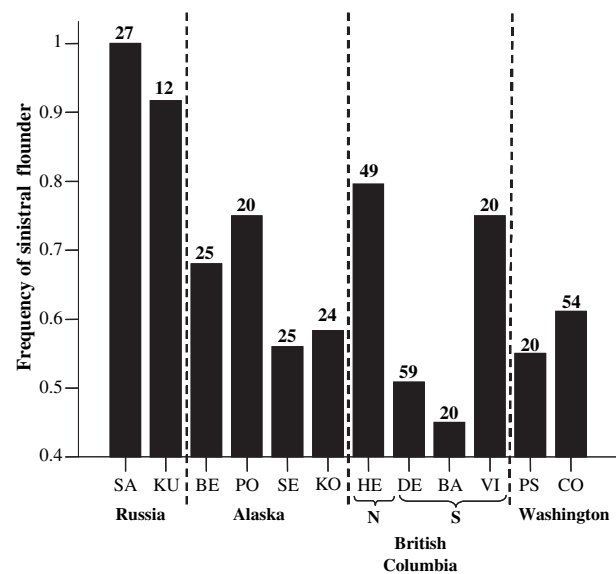


Fig. 2 Frequency of sinistral *Platichthys stellatus* from 12 sample sites. Samples are ordered from left to right by increasing distance from Japan. Sample sizes given above bars. Vertical dashed bars separate regions. Russian samples: SA = Sakhalin Island, KU = Kuril Islands; Alaskan samples: BE = Belkofski Bay, PO = Port Moller, SE = South-eastern Bering Sea, KO = Kodiak Island; Northern British Columbia sample: HE = Hecate Strait; Southern British Columbia samples: DE = Denman Island, BA = Bamfield, VI = Victoria; Washington state samples: PS = Puget Sound, CO = Columbia River mouth.

Table 1 Previously published proportions of sinistral (*S*) and dextral (*D*) *Platichthys stellatus* morphs compared with recent proportions using *G* tests and Fisher's exact tests when appropriate.

Locality	<i>n</i>	<i>S</i>	<i>D</i>	% <i>S</i>	Author	<i>G/P</i>
Columbia R. (WA)	225	136	89	60.4	Hubbs & Kuronuma (1942)	0.01/0.93
	54	33	21	61.1	Current study	
Puget Sound (WA)	8972	4629	4343	51.6	Hubbs & Kuronuma (1942)	0.09/0.83
	20	11	9	55.0	Current study	
British Columbia (Canada)	7671	5093	2578	66.4	Forrester, 1969	0.81/0.38
	148	93	55	62.8	Current study*	
Alaska	5129	3488	1641	68.0	Hubbs & Kuronuma (1942)	0.72/0.40
	94	60	34	63.8	Current study†	
Japan	476	476	0	100.0	Hubbs & Kuronuma (1942)	Fisher's <i>P</i> = 0.08
	39	38	1	97.4	Current study‡	

G/P = *G*-test statistic/*P*-value. All data for the table, aside from the recent samples collected for this study, were taken directly from Hubbs & Kuronuma (1942) and Forrester (1969).

*Samples BA, DE, HE, and VI combined.

†Samples BE, KO, PO, and SE combined.

‡Samples KU and SA (Russian samples just north of Japan).

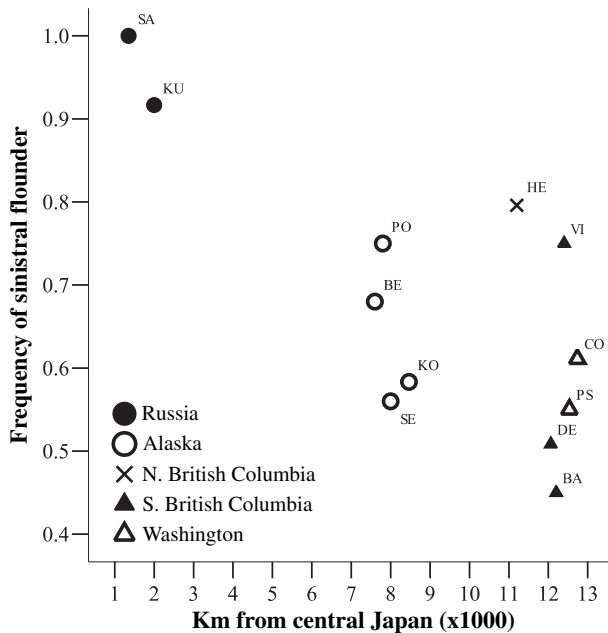


Fig. 3 Frequency of sinistral *Platichthys stellatus* in recent samples as a function of the distance in kilometres from central Japan. See Fig. 2 for sample sizes and site names.

of sinistral morphs had a significant negative correlation with distance along shore from central Japan (linear regression $r^2 = 0.56$; $t = -3.57$; $P < 0.005$; Fig. 3), consistent with previous findings by Hubbs & Kuronuma (1942). However, this correlation was primarily driven by the two Russian samples: when they were excluded, the remaining north American samples still showed a weak negative slope but it was no longer significant ($r^2 = 0.06$; $t = -0.70$; $P = 0.50$). In particular, the samples from Alaska and British Columbia exhibited

variation in frequency of sinistral morphs from locality to locality.

Morphological divergence between sinistral and dextral fish

Sinistral and dextral *P. stellatus* morphs were not mirror images of each other, but instead differed subtly yet significantly in several morphological traits. Significant differences were found between morphs in both the depth and length of the caudal peduncle (Table 2). Dextral morphs exhibited greater caudal dimensions in eight of 10 (caudal depth) and nine of 10 (caudal length) polymorphic samples (Fig. 4a,b). Caudal length exhibited a marginally significant interaction between sample site and morph because of large differences between morphs in some samples (e.g. Puget Sound, Kodiak Is.) but small differences in others (e.g. Victoria). Snout length also differed between morphs, but the difference depended on sample locality (Table 2): sinistral morphs had shorter snouts than dextral morphs in Alaska but relatively longer snouts in British Columbia and Washington (Fig. 4c). Differences in head depth between sinistral and dextral morphs also depended on sample site (Table 2). Sinistral fish had considerably deeper heads than dextral fish in the Hecate Strait and in Puget Sound, but in other samples differences were either slight or in the opposite direction (Fig. 4d). Finally, sinistral fish had more gill rakers than dextral fish across the sampled geographic range, and although the effect was marginally non-significant (Table 2), this trend was evident in nine of the 10 polymorphic samples (Fig. 4e; binomial $P = 0.02$). Differences between sinistral and dextral morphs were on an average less than 5% of trait size for each of these traits (Appendix S1 in Supplementary Material).

Table 2 Two-way ANOVA results showing differences in means of individual morphological traits among sample sites and between morphs.

Trait	Factor	MS	F	d.f.	P
Gill raker no.	Site	0.152	8.46	11	< 0.001
	Morph	0.056	3.10	1	0.08
	Site × morph	0.003	0.19	9	0.99
	Error	0.018	–	–	–
Body depth	Site	0.053	24.80	11	< 0.001
	Morph	0.004	1.76	1	0.19
	Site × morph	0.002	0.85	9	0.57
	Error	0.002	–	–	–
Mouth length	Site	0.108	24.31	11	< 0.001
	Morph	0.008	1.70	1	0.19
	Site × morph	0.004	0.89	9	0.54
	Error	0.004	–	–	–
Head length	Site	0.068	37.97	11	< 0.001
	Morph	< 0.001	0.01	1	0.94
	Site × morph	0.002	1.03	9	0.42
	Error	0.002	–	–	–
Jaw length	Site	0.068	24.82	11	< 0.001
	Morph	0.001	0.35	1	0.56
	Site × morph	0.002	0.70	9	0.71
	Error	0.003	–	–	–
Snout length	Site	0.096	11.81	11	< 0.001
	Morph	0.008	9.97	1	0.33
	Site × morph	0.020	2.43	9	0.01
	Error	0.008	–	–	–
Head depth	Site	0.046	14.49	11	< 0.001
	Morph	0.001	0.41	1	0.53
	Site × morph	0.008	2.55	9	0.01
	Error	0.003	–	–	–
Caudal depth	Site	0.068	26.07	11	< 0.001
	Morph	0.020	7.66	1	< 0.01
	Site × morph	0.002	0.71	9	0.70
	Error	0.003	–	–	–
Caudal length	Site	0.015	3.19	11	< 0.001
	Morph	0.115	24.80	1	< 0.001
	Site × morph	0.010	2.14	9	0.03
	Error	0.005	–	–	–

Factors with values of $P \leq 0.10$ are in bold face.

The two Russian samples were composed entirely of sinistral fish (Sakhalin and Kuril Islands), resulting in an unbalanced design for the above two-way ANOVAs. However, removing these samples from the analyses resulted in only trivial changes in the statistic values, and did not alter the results (significance vs. non-significance) of the original ANOVAs.

Age was included as a third factor in the ANOVAs for those localities where both age classes were present (Bamfield, Denman Island and Hecate Strait), and had a significant main effect on head length and depth as well as caudal peduncle depth (all $P < 0.04$). Adults had shorter, deeper heads and deeper caudal peduncles than did juveniles. However, interactions with age and asymmetry morph were not significant (two-way interactions all $P > 0.24$; three-way interactions all $P > 0.07$).

Discriminant function analysis with backwards elimination of variables tested whether sinistral and dextral fish could be classified correctly by the morphological traits used in this study. The single resulting factor was driven by three variables: increasing discriminant score corresponded with increasing caudal peduncle length, shorter snout length and fewer gill rakers. The discriminant function revealed highly significant separation of sinistral and dextral morphs (Wilk's $\lambda_9 = 0.833$; $P < 0.001$) and correctly classified 72% of the individual fish from the entire data set as either sinistral or dextral. Dextral morphs had greater discriminant function means than sinistral morphs in every polymorphic sample, six of which were significant (Fig. 4f). However, the magnitude of the difference in factor scores between morphs differed among samples from quite large (e.g. KO, CO) to almost none (e.g. SE).

To determine why some samples had larger morphological differences between morphs than others, I calculated the absolute difference in mean discriminant score between morphs for all polymorphic samples. This difference decreased slightly as the sample frequency of sinistral morphs increased (Fig. 5), although the correlation was non-significant ($r = -0.49$; $P = 0.15$). However, those samples that exhibited a significant difference at $\alpha = 0.05$ in discriminant scores between morphs had proportions of sinistral fish that were significantly lower (mean 54% sinistral) than those that did not exhibit a significant difference (mean 71% sinistral; $t_1 = 3.35$; $P < 0.05$; Fig. 5). In other words, samples that had approximately equal numbers of sinistral and dextral morphs were morphologically more dissimilar than those that were dominated by sinistral morphs. This was not because of differences in sample size: proportion of sinistral fish was uncorrelated with total sample size ($r < -0.01$; $P = 0.99$) and sample size of dextral fish ($r = -0.50$; $P = 0.15$). Similarly, the differences between morphs were not significantly related to sample size (total sample size: $t = 0.74$; $P = 0.48$; sample size of dextrals: $t = 2.00$; $P = 0.10$).

Discussion

Surprisingly, sinistral and dextral morphs of *P. stellatus* are not mirror images of each other. Direction of body asymmetry is associated with several traits that, in other fishes, affect foraging and swimming performance. Gill rakers in particular are functionally associated with resource acquisition (Magnuson & Heitz, 1971; McPhail, 1984; Ruzzante *et al.*, 2003; Amundsen *et al.*, 2004). Fish that feed on smaller prey have numerous, long rakers, whereas those that target larger prey have few, short rakers (Link & Hoff, 1998). The difference in raker number between asymmetry morphs in *P. stellatus* was subtle, yet in nine of 10 polymorphic samples dextral morphs had fewer rakers than sinistrals (on average 12 rakers for dextrals vs. 12.5 for sinistrals), suggesting that

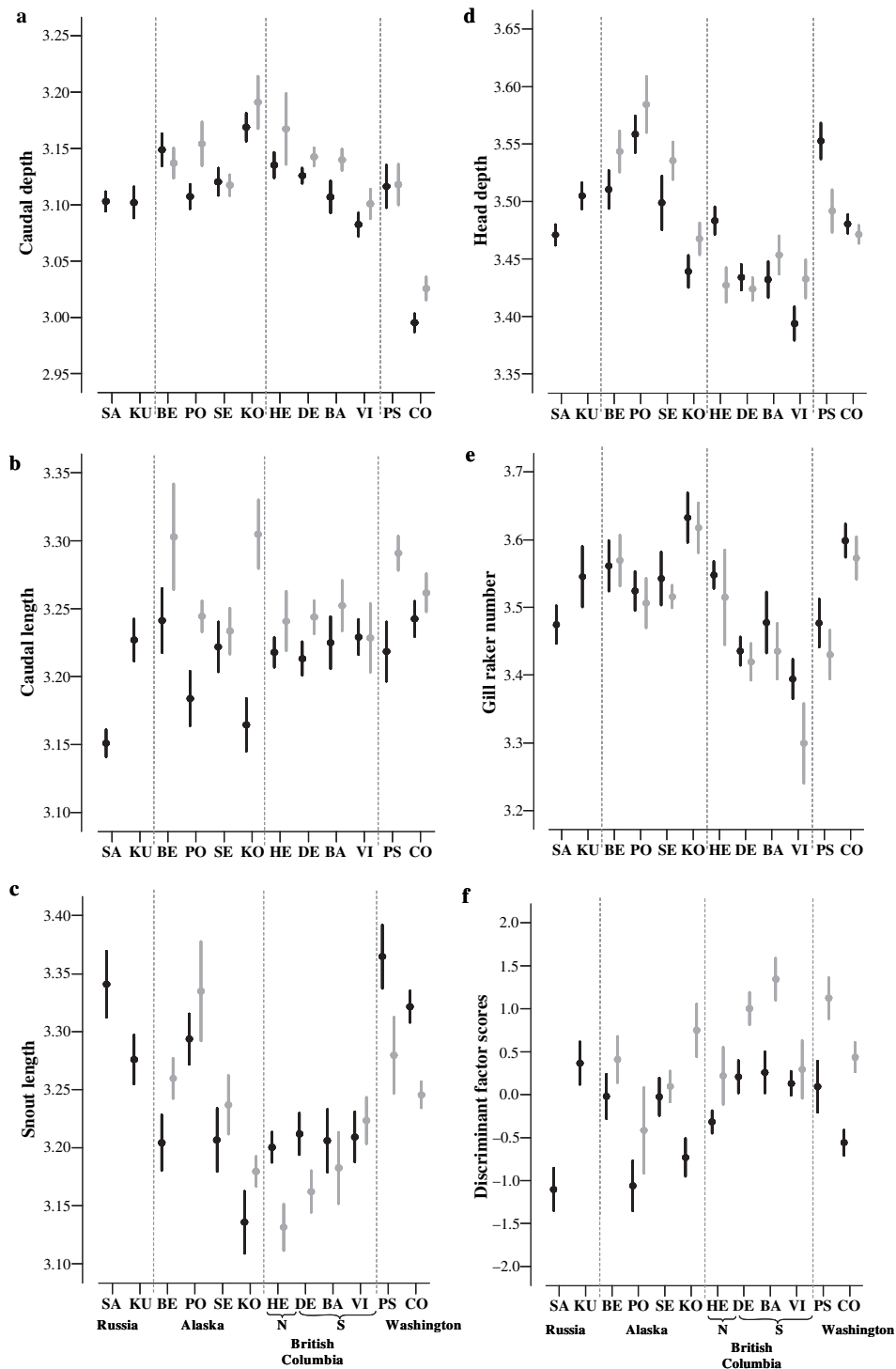


Fig. 4 Comparisons of trait means between lateral morphs and among sample sites. Black bars are sinistral flounder and grey bars are dextral flounder. Caudal peduncle depth (a), caudal peduncle length (b), snout length (c) and head depth (d) are all $\ln(x + 1)$ transformed; gill raker number (e) is square-root transformed. Discriminant factor scores (f) increase with longer caudal peduncles, shorter snouts and fewer gill rakers. Error bars are ± 1 standard error. Vertical dashed bars separate regions, and samples are ordered from left to right by increasing distance from Japan. See Fig. 2 for sample sizes and site names.

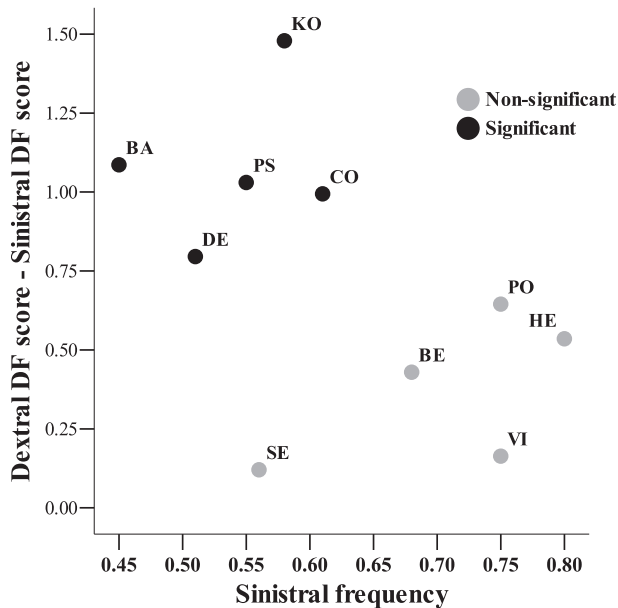


Fig. 5 Difference in mean discriminant function (DF) scores between dextral and sinistral *Platichthys stellatus* for each of the 10 polymorphic samples as a function of the frequency of sinistral fish in that sample. Samples with a significant difference in DF scores between morphs (black circles) had significantly lower sinistral frequencies than those with non-significant differences (grey circles; $t_1 = 3.35$; $P < 0.05$). See Fig. 2 for sample sizes and site names.

they may target larger prey. The strong association between raker number and trophic level across fish species implies that these consistent differences in raker number between asymmetrical forms in *P. stellatus* may be because of ecological segregation in prey acquisition. Differences in raker number are unlikely to be entirely because of sampling effects, as differences in the same direction arise across sample sites.

Differences in caudal peduncle size suggest that swimming performance may also differ between lateral morphs. The peduncle accounts for up to 88% of the propulsive thrust in fishes (Frith & Blake, 1991), and greater size is associated with greater thrust and fast-start velocity (Webb, 1984; Taylor & McPhail, 1985, 1986; Harper & Blake, 1990). Therefore, dextral flounders with larger peduncles may enjoy improved fast-start performance over their sinistral conspecifics. If dextral flounders are targeting larger prey, as suggested by their raker numbers, increased fast-start performance may be advantageous during pursuit if larger prey are also faster.

Snout length also differed between sinistral and dextral morphs, and although the overall main effect (ANOVA) was non-significant, snout length was included in the discriminant factor as one of the largest contributors to variation between morphs. In general, there is a trade-off between speed and strength of jaw movements as a

function of snout and jaw elongation: elongation allows for greater bite speed, whereas shortening allows for greater bite strength (Wainwright & Richard, 1995). *Platichthys stellatus* with more blunt snouts may be better suited for targeting harder prey that require greater bite strength to subjugate, whereas elongated snouts may be suited for softer prey. The differences in snout elongation between morphs may indicate ecological specialization between these two food types. The shorter snouts in dextral flounder, at least in the British Columbia and Washington state samples, is consistent with differences between lateral morphs in raker number and peduncle size, in that dextral fish may be targeting larger, faster or harder prey than sinistral fish.

The adaptive significance of the correlation between morph direction and other traits remains unknown, but several factors might be relevant. First, ecological selection may be acting on the direction of asymmetry and secondarily on correlated traits. For example, if dextrality enhances predation success on some prey, then correlational selection may act on raker number and peduncle size to improve foraging efficiency. In a symmetrical world this would be unlikely, but if some aspect of the flounders' environment was asymmetrical, this could place selection on the direction of body asymmetry. One possibility is asymmetrical prey. In pebble crabs, for example, the dextrally coiled shells of their snail prey puts crabs with larger dextral claws at an advantage over sinistral crabs (Shigemiyu, 2003), and this selection pressure likely affects traits other than claw asymmetry. If morphology of *P. stellatus* prey is asymmetrical, this may put one lateral morph at an advantage. Similarly, if the lateral morphs differ in the direction of their foraging behaviours, and if behavioural asymmetries also exist in their prey, one lateral morph might be favoured over another. Behavioural asymmetries occur in many vertebrates (for review see Bisazza *et al.*, 1998) and invertebrates (Ades & Ramires, 2002; Byrne *et al.*, 2002), and we are currently studying behavioural asymmetries in *P. stellatus* during prey capture.

Second, selection may be acting directly on other traits that are correlated with the direction of asymmetry in *P. stellatus*. For example, if selection in a heterogeneous environment is causing gill raker number to diverge, and raker number is genetically correlated with lateral morph, selection for raker number would put disruptive correlational selection on laterality. Flatfish from monomorphic species occasionally give rise to rare reversed-asymmetry individuals that differ morphologically in other traits (Gudger, 1935; Dawson, 1962; Houde, 1971; Bisbal & Bengston, 1993). If the original reversed *P. stellatus* were morphologically unique in a beneficial way, these 'hopeful monsters' (Goldschmidt, 1940) may have persisted and exploited new niche space.

Correlational selection of the type represented by the above two scenarios is a common occurrence in polymorphic species (Svensson *et al.*, 2001; Sinervo &

Svensson, 2002). In a given system, the magnitude of the differences between morphs will be a dynamic product of the interaction between the strength of correlational selection that causes the two morphs to diverge, and the erosion caused by recombination that blurs differences between them (Svensson *et al.*, 2001). As spawning adults of dextral and sinistral starry flounder are found in the same trawl nets (Orcutt, 1950; C. A. Bergstrom, unpublished), and cross easily in the laboratory (Policansky, 1982; C. A. Bergstrom, unpublished), it is likely that the morphs cross-breed in the wild. Presumably, this recombination would destroy phenotypic correlations between lateral morph and other traits unless correlational selection was strong and consistent over time. Therefore, the subtlety and variation among sites in the differences in morphology between the two morphs (Fig. 5) are not surprising, especially if the loci that affect these traits are not tightly linked.

Finally, divergence in the traits found to be associated with lateral morph may be because of phenotypic plasticity. Plastic divergence within fish species is common (Hegrenes, 2001; Andersson *et al.*, 2005). Although there is moderate heritability of asymmetry direction in *P. stellatus* (Policansky, 1982; Boklage, 1984; C. A. Bergstrom, unpublished), the heritable variation of the correlated traits are unknown, so plasticity cannot be ruled out at present. Behavioural differences between morphs may subject them to different environmental cues that trigger plastic responses. However, even if the traits in question (gill raker number, caudal peduncle size and snout length) are entirely plastic, the consistent differences in morphology still suggest ecological segregation between lateral morphs because of behavioural divergence.

The suite of morphological differences between sinistral and dextral morphs, whether genetically or plastically determined, raises the interesting possibility that the morphs are divergent along some dimension(s) of niche space, and one possible driver of this is competition and character displacement. Character displacement occurs when two closely related species are more dissimilar in sympatry than in allopatry (Brown & Wilson, 1956), but could presumably also occur between morphs within a species if resource competition occurs between them. The same mechanism that causes displacement between closely related species may be causing dextral and sinistral starry flounder to be more dissimilar in those locations where competition between them is the strongest. For example, if the two morphs are competing for a resource, such as food, competition is expected to be the strongest in locations where the morphs are most likely to interact (i.e. where they are equally common). Some models of sympatric speciation driven by competitive interactions between morphs make this same assumption (Dieckmann & Doebeli, 1999). Data presented here are consistent with this: morphological differences are greatest between morphs from sites that

contain approximately equal numbers of both (Fig. 5). Morphological differences between morphs in raker number, peduncle size and snout shape could reduce competition between them, and these traits diverge in response to competitive interactions in a multitude of other fish species (Robinson & Wilson, 1994).

Geographical clines in phenotype, such as that seen in *P. stellatus*, are usually associated with clines in the selective landscape (Palmer, 1979; Lynch, 1992; Rolan-Alvarez *et al.*, 1997), yet random drift is also possible. However, temporal consistency in phenotype frequencies would be broken down by stochastic processes unless population sizes are very large. Comparisons of recently caught samples exhibit a negative correlation between the proportion of sinistral fish and distance from Japan (Fig. 3), consistent with earlier reports (Hubbs & Kuronuma, 1942). In addition, recent samples do not differ significantly from previous samples in the proportion of sinistral fish from site to site (Table 1). Both of these pieces of data suggest that, although there is some heterogeneity in the cline in recent North American samples, this cline has been stable over time and continues to show a shift from polymorphism in North American to monomorphism in Asia.

In conclusion, this paper demonstrates that ecological segregation and adaptive divergence driven by competition are possible mechanisms maintaining the geographical distribution of asymmetric forms in *P. stellatus*. Another study has suggested that inter-specific competition between dextral and sinistral flatfish is maintaining small-scale variation in sinistral proportions in European flounder (*P. flesus*) (Fornbacke *et al.*, 2002). This, combined with the current study, implicates competition as one likely driver of stable polymorphisms in body asymmetry in natural populations of flatfish. Although the functional advantage of asymmetry to flatfishes and other organisms is well understood in some cases, this study is a rare demonstration of the significance of ecological correlates with asymmetry direction, and thus enhances our understanding of lateral bias in a symmetrical world.

Acknowledgements

I am thankful to A. R. Palmer for guidance and suggestions that improved the morphometric analysis and manuscript, T. E. Reimchen for discussion, and E. Svensson and two anonymous reviewers for comments and suggestions that improved earlier drafts of this paper. All samples from Alaska were generously collected and donated by the Alaska Department of Fish and Game and the United States National Oceanic and Atmospheric Administration, two samples from British Columbia were collected and donated by the Canadian Department of Fisheries and Oceans, and museum specimens from Washington were provided by the University of Washington Fish Collection Museum. Financial support for

this research was provided by an Alberta Ingenuity Fund Post-doctoral Fellowship and a Bamfield Marine Science Centre Research Associate Award to C. A. Bergstrom and a National Science and Engineering Research Council Discovery Grant to A. R. Palmer.

References

- Østbye, K., Næsje, T.F., Bernatchez, L., Sandlund, O.T. & Hindar, K. 2005. Morphological divergence and origin of sympatric populations of European whitefish (*Coregonus lavaretus* L.) in Lake Femund, Norway. *J. Evol. Biol.* **18**: 683–702.
- Ades, C. & Ramires, E.N. 2002. Asymmetry of leg use during prey handling in the spider *Scytodes globula* (Scytodidae). *J. Insect Behav.* **15**: 563–570.
- Amundsen, P., Bøhn, T. & Vågak, G.H. 2004. Gill raker morphology and feeding ecology of two sympatric morphs of European whitefish (*Coregonus lavaretus*). *Ann. Zool. Fenn.* **41**: 291–300.
- Andersson, J., Byström, P., Persson, L. & De Roos, A.M. 2005. Plastic resource polymorphism: effects of resource availability on Arctic char (*Salvelinus alpinus*) morphology. *Biol. J. Linn. Soc. Lond.* **85**: 341–351.
- Benkman, C.W. 1996. Are the ratios of bill crossing morphs in crossbills the result of frequency-dependent selection? *Evol. Ecol.* **10**: 119–126.
- Billiard, S., Faurie, C. & Raymond, M. 2005. Maintenance of handedness polymorphism in humans: a frequency-dependent selection model. *J. Theor. Biol.* **235**: 85–93.
- Bisazza, A., Rogers, L.J. & Vallortigara, G. 1998. The origins of cerebral asymmetry: a review of evidence of behavioural and brain lateralization in fishes, reptiles and amphibians. *Neurosci. Biobehav. Rev.* **22**: 411–426.
- Bisbal, G.A. & Bengston, D.A. 1993. Reversed asymmetry in laboratory-reared summer flounder. *Prog. Fish-Culturist* **55**: 106–108.
- Boklage, C.E. 1984. On the inheritance of directional asymmetry (sidedness) in the starry flounder, *Platichthys stellatus*: additional analyses of Policansky's data. *Behav. Brain Sci.* **7**: 725–762.
- Brown, W.L. & Wilson, E.O. 1956. Character displacement. *Syst. Zool.* **5**: 49–64.
- Byrne, R.A., Kuba, M. & Griebel, U. 2002. Lateral asymmetry of eye use in *Octopus vulgaris*. *Anim. Behav.* **64**: 461–468.
- Cain, A.J. & Sheppard, P.M. 1954. Natural selection in *Cepea*. *Genetics* **39**: 89–116.
- Dawson, C.E. 1962. Notes on anomalous American Heterosomata with descriptions of five new records. *Copeia* **1962**: 138.
- Dieckmann, U. & Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature* **400**: 354–357.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Oxford University Press, London.
- Fornbacke, M., Gombrii, M. & Lundberg, A. 2002. Sidedness frequencies in the flounder *Platichthys flesus* (Pleuronectiformes) along a biogeographical cline. *Sarsia* **87**: 392–395.
- Forrester, C.R. 1969. Sinistrality in *Platichthys stellatus* off British Columbia. *J. Fish. Res. Board Can.* **26**: 191–196.
- Frith, H.R. & Blake, R.W. 1991. Mechanics of the startle response in the northern pike. *Can. J. Zool.* **69**: 2831–2839.
- Goldschmidt, R. 1940. *The Material Basis of Evolution*. Yale University Press: New Haven, CT.
- Gould, S.J., Young, N.D. & Kasson, B. 1985. The consequences of being different: sinistral coiling in *Cerion*. *Evolution* **39**: 1364–1379.
- Govind, C.K. & Pearce, J. 1986. Differential reflex activity determines claw and closer muscle asymmetry in developing lobsters. *Science* **233**: 354–356.
- Gross, M.R. 1985. Disruptive selection for alternative life histories in salmon. *Nature* **313**: 47–48.
- Gudger, E.W. 1935. Abnormalities in flatfishes (Heterosomata). *J. Morphol.* **58**: 1–39.
- Harper, D.G. & Blake, R.W. 1990. Fast-start performance of rainbow trout *Salmo gairdneri* and northern pike *Esox lucius* during escapes. *J. Exp. Biol.* **150**: 321–342.
- Hedrick, P.W. 1986. Genetic polymorphism in heterogeneous environments: a decade later. *Annu. Rev. Ecol. Syst.* **17**: 535–566.
- Hegrenes, S. 2001. Diet-induced phenotypic plasticity of feeding morphology in the orangespotted sunfish, *Lepomis humilis*. *Ecol. Freshw. Fish* **10**: 35–42.
- Hori, M. 1993. Frequency-dependent natural selection in the handedness of scale-eating cichlid fish. *Science* **260**: 216–219.
- Houde, E.D. 1971. Developmental abnormalities of the flatfish *Achirus lineatus* reared in the laboratory. *U.S. Nat. Mar. Fish. Ser. Fish. Bull.* **69**: 537–544.
- Hubbs, C.L. & Kuronuma, K. 1942. Hybridization in nature between two genera of flounders in Japan. *Pap. Mich. Acad. Sci.* **27**: 267–306.
- Lande, R. & Arnold, S.J. 1983. Detecting selection on correlated characters. *Evolution* **37**: 1210–1226.
- Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *The Auk* **104**: 116–121.
- Link, J. & Hoff, M.H. 1998. Relationships of lake herring (*Coregonus artedii*) gill raker characteristics to retention probabilities of zooplankton prey. *J. Freshw. Ecol.* **13**: 55–65.
- Lynch, C.B. 1992. Clinal variation in cold adaptation in *Musdomesticus* – verification of predictions from laboratory populations. *Am. Nat.* **139**: 1219–1236.
- Magnuson, J.J. & Heitz, J.G. 1971. Gill raker apparatus and food selectivity among mackerels, tunas and dolphins. *Fish. Bull.* **69**: 361–370.
- Maynard Smith, J. 1989. *Evolutionary Genetics*. Oxford University Press, New York.
- McPhail, J.D. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): origin of the species pairs. *Can. J. Zool.* **71**: 515–523.
- Munroe, T.A. 2005. Systematic diversity of the Pleuronectiformes. In: *Flatfishes: Biology and Exploitation* (R. N. Gibson, ed.), pp. 10–41. Blackwell Science Ltd, Oxford.
- Norberg, R.A. 1978. Skull asymmetry, ear structure and function, and auditory localization in Tengmalm's Owl, *Aegolius funereus* (Linne). *Phil. Trans. R. Soc. Lond. B* **282**: 325–410.
- Norman, J.R. 1934. *A Systematic Monograph of the Flatfishes (Heterosomata). Vol 1: Psettodidae, Bothidae, Pleuronectidae*. British Museum of Natural History, London.
- Orcutt, H.G. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallus). *Calif. Fish Game Fish Bull.* **78**: 1–64.
- Palmer, A.R. 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* **33**: 697–713.

- Palmer, A.R. 2004. Symmetry breaking and the evolution of development. *Science* **306**: 828–833.
- Policansky, D. 1982. Flatfishes and the inheritance of asymmetries. *Behav. Brain Sci.* **5**: 262–266.
- Pratt, A.E. & McLain, D.K. 2002. Antisymmetry in male fiddler crabs and the decision to feed or breed. *Funct. Ecol.* **16**: 89–98.
- Rainey, P.B., Buckling, A., Kassen, R. & Travisano, M. 2000. The emergence and maintenance of diversity: insights from experimental bacterial populations. *TREE* **15**: 243–247.
- Raymond, M., Pontier, D., Dufour, A. & Møller, A.P. 1996. Frequency-dependent maintenance of left handedness in humans. *Proc. R. Soc. Lond. B.* **263**: 1627–1633.
- Reimchen, T.E. 1995. Predator-induced cyclical changes in lateral plate frequencies of *Gasterosteus*. *Behaviour* **132**: 1079–1094.
- Robinson, B.W. & Wilson, D.S. 1994. Character release and displacement in fishes: a neglected literature. *Am. Nat.* **144**: 596–627.
- Rolan-Alvarez, E., Johannesson, K. & Erlandsson, J. 1997. The maintenance of a cline in the marine snail *Littorina saxatilis*: the role of home site advantage and hybrid fitness. *Evolution* **51**: 1838–1847.
- Ruzzante, D.E., Walde, S.J., Cussac, V.E., Macchi, P.J., Alonso, M.F. & Battini, M. 2003. Resource polymorphism in a Patagonian fish *Percichthys trucha* (Percichthyidae): phenotypic evidence for interlake pattern variation. *Biol. J. Linn. Soc.* **78**: 497–515.
- Sandoval, C.P. 1994. Differential visual predation on morphs of *Timema cristinae* (Phasmatodeae: Timemidae) and its consequences for host range. *Biol. J. Linn. Soc.* **52**: 341–356.
- Shigemiya, Y. 2003. Does the handedness of the pebble crab *Eriphia smithii* influence its attack success on two dextral snail species? *J. Zool.* **260**: 259–265.
- Shine, R., Ambariyanto, Harlow, P.S. & Mumpuni. 1998. Ecological divergence among sympatric colour morphs in blood pythons, *Python brongersmai*. *Oecologia* **116**: 113–119.
- Sinervo, B. & Lively, C.M. 1996. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* **380**: 240–243.
- Sinervo, B. & Svensson, E. 2002. Correlational selection and the evolution of genomic architecture. *Heredity* **89**: 329–338.
- Smith, T.B. 1993. Disruptive selection and the genetic basis of bill size polymorphism in the African finch *Pyrenestes*. *Nature* **363**: 618–620.
- Smith, T.B. & Skúlason, S. 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annu. Rev. Ecol. Syst.* **27**: 111–133.
- Svensson, E., Sinervo, B. & Comendant, T. 2001. Condition, genotype-by-environment interaction, and correlational selection in lizard life-history morphs. *Evolution* **55**: 2053–2069.
- Taylor, E.B. & McPhail, J.D. 1985. Variation in burst and prolonged swimming performance among British Columbia populations of coho salmon, *Oncorhynchus kisutch*. *Can. J. Fish. Aquat. Sci.* **42**: 2029–2033.
- Taylor, E.B. & McPhail, J.D. 1986. Prolonged and burst swimming in anadromous and freshwater threespine sticklebacks, *Gasterosteus aculeatus*. *Can. J. Zool.* **64**: 416–420.
- Vamosi, S.M. & Schluter, D. 2004. Character shifts in the defensive armor of sympatric sticklebacks. *Evolution* **58**: 376–385.
- Wainwright, P. & Richard, B.A. 1995. Predicting patterns of prey use from morphology of fishes. *Environ. Biol. Fishes* **44**: 97–113.
- Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. *Am. Zool.* **24**: 107–120.
- Windig, J.J. & Nylin, S. 1999. Adaptive wing asymmetry in males of the speckled wood butterfly (*Pararge aegeria*)? *Proc. R. Soc. Lond. B* **266**: 1413–1418.

Supplementary Material

The following supplementary material is available for this article:

Appendix S1. Population frequencies of sinistral fish and mean values of morphological traits.

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/full/10.1111/j.1420-9101.2006.01290.x>

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

Received 16 October 2006; revised 7 November 2006; accepted 7 November 2006