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EFFECTS OF A CYMOTHOID ECTOPARASITE ON THE TURNING BEHAVIOR (LATERALIZATION) OF THE BRIDLED MONOCLE BREAM *SCOLOPSIS BILINEATA*

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Abstract

Lateralization, or behavioral asymmetry, is the tendency to favor one side of the body over the other, and exists in humans and animals including in mammals, birds, and fishes. It has been found to increase performance in certain behaviors such as escape from predators by lowering reation time. Lateralization has predominantly genetic bases, but can also be influenced by environmental factors. For example, lateralization has been observed to increase in populations of fish subject to high predation pressure as it decreases their response time to predatory attacks. Parasitism may also have important effects on lateralization. In particular, increased drag from large ectoparasitic isopods is thought to reduce swimming performance of fishes and increase vulnerability to predation. Here, we examined whether fish infected with an ectoparasite compensate for a potential decrease in their swimming performance by increasing their degree of lateralization. Specifically, we examined the bridled monocle bream (*Scolopsis bilineata*), which is parasitized by a large ectoparasitic cymothoid isopod, *Anilocra nemipteri*, on the Great Barrier Reef.

In order to gain insight into host-parasite interactions, we quantified the prevalence of infections in the population of *S. bilineata* at Lizard Island, on the Northern Great Barrier Reef, Australia. We then examined the effect of *A. nemipteri* on lateralization patterns in *S. bilineata* by comparing the turning behavior of unparasitized and parasitized individuals. We found no preference for right or left turns at the group level, but individuals were lateralized in all groups. Individuals were significantly more lateralized in the parasitized group than in the unparasitized group, and removing parasites from infected individuals decreased lateralization, suggesting that parasitism by

A. nemipteri has a significant effect on turning behavior. As lateralization has been shown to reduce reaction time in fish and increase the probability of escaping from predators, *S. bilineata* may compensate for lower fitness and swimming performance due to infection by *A. nemipteri* by increasing its turning preference to one side.

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1. Introduction

1.1 Ectoparasitism in Coral Reef Fishes

Cymothoid isopods are a widespread family of blood-feeding crustaceans that parasitize both marine and freshwater fishes in South America, Asia, Africa, and Australia (Trilles et al. 2011, Bunkley-Williams and Williams 1998). Cymothoids make up about 62% of isopods associated with fishes (Bunkley-Williams and Williams 1998). These abundant and relatively large (4.2 – 23.0 mm) ectoparasites either attach themselves to a fixed spot on their hosts using hooks located at the ends of their legs, or move around freely on the host's body (Bunkley-Williams and Williams 1998, Grutter 1994).

Isopod ectoparasites have a variety of negative effects on coral reef fishes. They are responsible for causing large wounds, stunted growth, and sometimes death in their hosts (Bunkley-Williams and Williams 1998). A study by Östlund-Nilsson et al. (2005) found that parasitized cardinal fish *Cheilodipterus quinquelineatus* had decreased aerobic swimming endurance and higher energy needs compared to unparasitized fish. The parasites also affected the stability of their host requiring them to expend more energy just to keep upright (Östlund-Nilsson et al. 2005). Similarly, a study by Grutter et al. (2011) found an overall decrease in the swimming performance of juvenile damselfish, *Pomacentrus amboinensis*, parasitized with gnathiid isopods. Specifically, parasitized individuals had a lower critical swimming speed than unparasitized fish, and a higher rate of oxygen consumption (indicative of a higher metabolic rate) in lab studies, and a lower rate of survival to adulthood in the wild.

These parasites were also found to stunt growth and increase mortality in another damselfish, *Chromis nitidia* (Adlard and Lester 1994) as well as in juveniles of three cardinal fishes (Fogelman and Grutter 2008). Parasitism by cymothoids has also been found to decrease fecundity in adults (Adlard and Lester 1994, Fogelman et al. 2009). Other sub-lethal effects include anemia (Adlard and Lester 1995) and tissue damage (Bunkley-Williams and Williams 1998) in hosts.

1.2 Background on Lateralization

Lateralization refers to the tendency of an individual to favor one side of the body over the other (Reebs 2008), and includes specialization in sensory, motor, and/or cognitive abilities. This "handedness" can occur at the level of the individual, where an individual shows a non-random preference for one side of its body over the other, or at the level of the population, when more than 50% of the individuals in a group show a non-random preference in the same direction (Bisazza et al. 1998*b*). The strength of lateralization at these two levels can be calculated using a lateralization index (Bisazza et al. 1998*a*, Dadda et al. 2010, Domenici et al. 2012). The relative lateralization index (L_R) quantifies the degree to which a particular direction is preferred, while the absolute lateralization index (L_A) quantifies the degree of lateralization irrespective of the direction preferred. A L_R that deviates significantly from 0 suggests that a population has a strong directional preference whereas high values of L_A suggest that the direction of preference is not important, but that individuals are likely to demonstrate highly lateralized behavior.

While early studies of lateralization often focus on sensory and cognitive abilities, behavioral asymmetries at the individual and population level have increasingly become of interest to researchers (Bisazza et al. 1998*b*). Lateralization affects a wide range of behaviors in numerous taxa, including birds (Rogers 2004, Zucca and Sovrano 2008), mammals (Ehret 1987, McGrew and Marchant 1999, Phillips et al. 2003, McGreevy and Rogers 2005), fishes (Bisazza et al. 1998*a*, De Santi et al. 2001, Bisazza and Dadda 2005, Bisazza et al. 2007, Brown et al. 2004, Brown et al. 2007, Dadda et al. 2010, Domenici et al. 2012), and invertebrates (Glovind and Blundon 1985). For example, quails showed a preference for using their right eye when viewing unfamiliar conspecifics and their left eye when viewing familiar companions (Zucca and Sovrano 2008). Similarly, chimpanzees demonstrate preferential hand use when termite fishing (McGrew and Marchant 1999).

It can be argued that lateralization has some disadvantages, as relevant stimuli have an equal chance of occurring on either side of the body (Vallortigara and Rogers 2005). However, many studies have found that lateralized individuals show superior performance in a variety of behaviors. In fishes, lateralization has been found to improve schooling performance (Bisazza and Dadda 2005), multitasking (Dadda and Bisazza 2006), and escape performance (Dadda et al. 2010). Lateralization is known to have a genetic basis (Bisazza et al. 2007, Brown et al. 2007). However, environmental factors such as high predation (Brown et al. 2007) have also been shown to promote lateralization.

1.3 Justification for Current Study

Although coral reef fishes are known to be affected by cymothoid isopod ectoparasites (Adlard and Lester 1994, Adlard and Lester 1995, Bunkley-Williams and Williams 1998, Fogelman and Grutter 2008, Östlund-Nilsson et al. 2005, Grutter et al. 2011), and to exhibit lateralization in turning direction (Domenici et al. 2012), the effects of parasitism on lateralization behavior has never been studied.

The bridled monocle bream (*Scolopsis bilineata*) is a ubiquitous member of coral reef communities on the Great Barrier Reef (Boaden 2011), and can be parasitized by a large cymothoid isopod *Anilocra nemipteri*. However, the effects of parasitism on this species are only just beginning to be studied (Binning and Roche in prep), and current quantification of the prevalence of parasitism by *A. nemipteri* in populations of *S. bilineata* in the Great Barrier Reef is lacking. Apart from the novelty of studying parasitism in *Scolopsis bilineata*, we chose to study this species because of the size, survivability, and ease of manipulation of its parasite, *Anilocra nemipteri*.

In this study, we estimated the prevalence of parasitism in a population of *S. bilineata* around Lizard Island, northern Great Barrier Reef, Australia. We also investigated the effects of parasitism on lateralization in *S. bilineata* by comparing the turning behavior unparasitized and parasitized individuals. Predation has been shown to cause increased lateralization in fish (Brown et al. 2004, Brown et al. 2007). As another costly environmental pressure, we expected parasitism to have an effect on lateralization as well. Lateralization has been shown to help lower reaction time and improve escape performance in fish (Dadda et al. 2010). Thus, we hypothesized that parasitized individuals are more lateralized, as lateralization may help improve the escape abilities of infected fish who may suffer from decreased swimming performance.

2. Methods

2.1 Animal Collection and Care

Parasitized and unparasitized *Scolopsis bilineata* were collected from various reefs in the Lagoon at Lizard Island, Queensland, Australia, between the middle of March and the end of April 2012 (Figure 1).

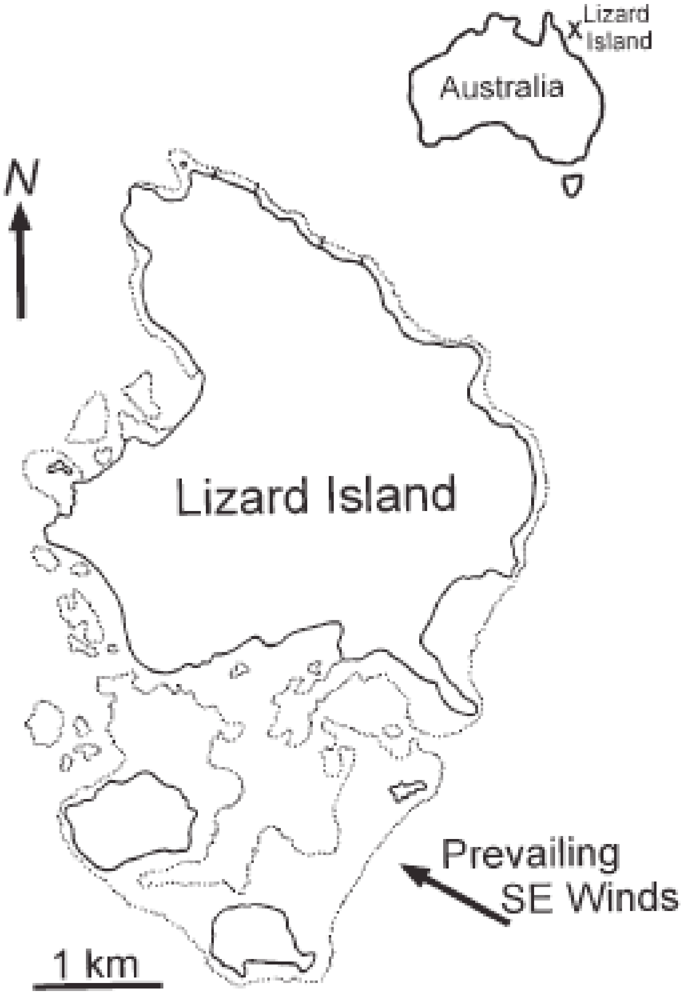

Figure 1. Map of Lizard Island, northern Great Barrier Reef, Australia.

2.2.1 Abundance Transects

To estimate the prevalence of cymothoid ectoparasites in populations of *S. bilineata*, data on the size and condition of individuals was recorded on snorkel along 50 x 4 m belt transects (n = 3 to 7 per site) on 12 different reefs around Lizard Island. Data was collected by two observers swimming at a constant speed holding a tape between them, each looking within 2 m on either side of the transect tape. Four variables were recorded for each individual observed: size (total length), color phase (juvenile or adult), condition (unparasitized, parasitized, scarred from past parasite), and side of attachment (left or right for parasitized or scarred individuals) (Figure 2).

Figure 2. Conditions of *Scolopsis bilineata* recorded in the field: *a)* unparasitized adult color phase, *b)* juvenile color phase, *c)* parasitized, *d)* scarred from past parasite.

Observers practiced estimating fish lengths to the nearest 1 cm prior to collecting the data.

2.2.2 Data analysis

I calculated the relative frequency distributions of *S. bilineata* lengths for unparasitized, parasitized, and formerly parasitized, as well as all three groups combined using histograms with bin sizes of 3 cm. Mean (± SE), median, and mode of fish length was calculated for each group to compare the size of fishes in each group (unparasitized, parasitized, formerly parasitized). The total number of unparasitized, parasitized, and formerly parasitized individuals out of all the *S. bilineata* observed in the study was determined, both as the number of individuals and as a percentage of all *S. bilineata*, and separately for adults only and juveniles only.

2.3 Measurements of Experimental Fish

Information was recorded on the total length, standard length, body depth, body width, and mass for all fish tested. For the parasitized fish, the length and width of the parasite was also recorded. Measurements were taken by sealing the fish in a plastic bag with enough water to breathe, but little enough that the fish lay flat on its side. The fish (and parasite) were then measured to the nearest tenth of a mm using calipers or a ruler to the nearest mm if the fish was too long for the calipers. Mass was measured by emptying the water from the plastic bag, quickly weighing the fish in the bag, then replacing the fish in water and weighing the bag alone. The mass of the fish was then calculated as the difference between these two measurements.

2.4.1 Detour Test

In order to test for lateralization in parasitized and unparasitized *S. bilineata*, the fish were subjected to a detour test (Bisazza et al. 1998*a*, Bisazza and Dadda 2005, Dadda et al. 2010, Domenici et al. 2012). The apparatus consisted of an opaque white tank (102 cm x 51 cm x 50 cm, length x width x height) with a runway in the middle (70 cm x 15 cm, length x width). An opaque white barrier (25 cm x 16.5 cm, length x height) was positioned 12 cm from the end of the runway, oriented perpendicular to the runway (Figure 3).

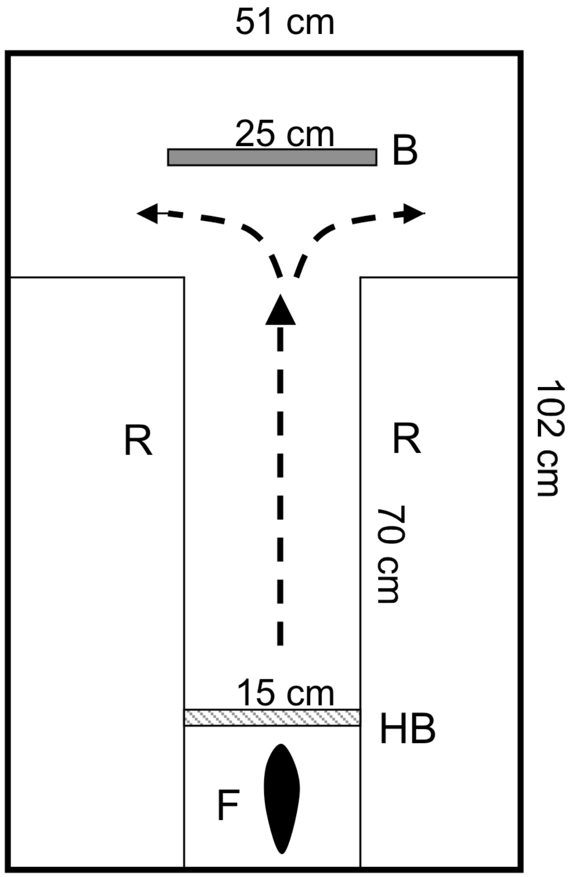

Figure 3. Schematic representation of the apparatus used for the detour test. During each trial, the holding barrier (HB) was raised, allowing the fish (F) to swim down the runway (R). At the end of the runway the fish faced a barrier (B), which the fish would turn either left or right to get around. The direction chosen was recorded.

Water height in the tank was maintained at 13 cm. To avoid bias in the maze, different orientations of the maze were tested prior to beginning the detour tests. The orientation used in the experiment was determined when there was no difference in the turning behavior of a trial individual regardless of the orientation of the maze.

Prior to each test, a single fish was introduced into the starting point of the runway and held there with an opaque barrier. The fish was left for at least 10 minutes to adjust to the environment. During each trial, the holding barrier was raised and the fish was gently guided down the runway using a plastic paddle. At the end of the runway the fish faced the barrier and had to decide to turn right or left to get around the barrier. Once the fish made a choice, and turned, the direction chosen was recorded on a slate. The fish was then guided back to the starting position of the runway and the holding barrier was lowered. The fish was given at least 2 minutes rest between trials. Ten trials were conducted per fish. A total of 41 *S. bilineata* were tested (n = 25 unparasitized, n = 16 parasitized).

In order to test whether the turning behavior of parasitized *S. bilineata* changed when the parasite was removed, we removed the parasites from all the parasitized fish. To remove the parasite, a fish was put in a plastic bag with water and, holding the fish in one hand, forceps were used to grasp the tail of the parasite and pull it gently towards the head of the fish. The forceps were then used to unhook the legs of the parasite from the fish tissue, detaching the parasite from the fish. The fish were then retested in the detour maze after giving them 24 hours to adjust to the absence of the parasite (n = 16 parasite removed).

In order to compare fish in their right-left preference, we calculated a relative lateralization index (L_R) according to the following formula (Bisazza et al. 1998*a*, Dadda et al. 2010, Domenici et al. 2012):

[(Turns to the right – Turns to the left)/(Turns to the right + Turns to the Left)]*100

The L_R index classified the turning preference of the fish between the extremes of 100 (10 out of 10 turns to the right) and -100 (10 out of 10 turns to the left), with a L_R index of 0 indicating equal turns to the left and right.

To compare the lateralization of the fish irrespective of the direction of preference, an absolute lateralization index (L_A) was calculated as the absolute value of the L_R (Dadda et al. 2010). Thus, a L_A of 100 corresponds to 10 out of 10 turns in a particular direction (but does not indicate whether the fish showed preference for turning right or left), and a L_A of 0 corresponds to equal turns to the right and left. We considered fish with $L_A \geq 60$ (corresponding to at least 8 out of 10 turns in one direction) to be highly lateralized (Brown et al. 2007). The distributions of all three treatment groups (unparasitized, parasitized, and parasite removed) were compared to a theoretical random binomial distribution with $n = 25$, $p = 0.5$, and $q = 0.5$ (a 50% probability of turning left or right) (Domenici et al. 2012).

2.4.2 Data analysis

All analyses were done using R v2.11.1 (R Development Core Team).

2.4.2.i. Data Analysis for L_R

The lateralization data for unparasitized, parasitized, and parasite removed groups was checked for significant departures from normality using a Shapiro-Wilk test. Since L_R data was not normally distributed, L_R of unparasitized, parasitized, and parasite removed groups were compared using Wilcoxon signed-rank tests (non-parametric t-tests). These tests were used for all groups for consistency even though the parasite removed group had a normal distribution. Kruskal-Wallis tests (non-parametric analysis of variance) were used to test for differences in L_R between the test groups (unparasitized, parasitized, and parasite removed) and the random binomial simulation.

2.4.2.ii Data Analysis for L_A

Absolute indices of lateralization (L_A) were compared between unparasitized, parasitized, and random binomial simulation groups using a Kruskal-Wallis test. L_A of individual groups were compared to the L_A of the random binomial simulation using Wilcoxon signed rank tests. A paired Wilcoxon signed rank test was used to compare the L_As of the parasitized and parasite removed groups due to the repeated measures of testing the same individuals under two treatments (parasitized and parasite removed).

2.4.2.iii Other Data Analysis

Chi-squared tests of independence were used to determine if parasitized fish were lateralized to the same side as their parasites, both among all parasitized fish (n = 16) and only among fish considered heavily parasitized ($L_A \geq 60$, n = 13).

3. Results

3.1 Parasite Abundance

Transect surveys covered a total surface area of 79,300 m^2. The average density of *S. bilineata* around Lizard Island is 0.005 fish/m^2. Transect surveys revealed that the majority of *S. bilineata* observed were unparasitized (Table 1).

Table 1. Abundance of unparasitized, parasitized, and formerly parasitized *S. bilineata* across 12 reefs at Lizard Island, Australia.

		Number of Individuals [% of Population]		
	Number of Individuals Observed	Unparasitized	Parasitized	Parasite Removed
All Fish	427	363 [85.0]	17 [4.0]	47 [11.0]
Adults Only	383	324 [84.6]	12 [3.1]	47 [12.3]
Juveniles Only	44	39 [88.6]	5 [11.4]	0 [0.0]

Parasitized *S. bilineata* tended to be smaller (median length: 12 cm, mode length: 12 cm) than unparasitized (median length: 15 cm, mode length: 16 cm) and formerly parasitized fish (median length: 15 cm, mode length: 15 cm) (Figure 4).

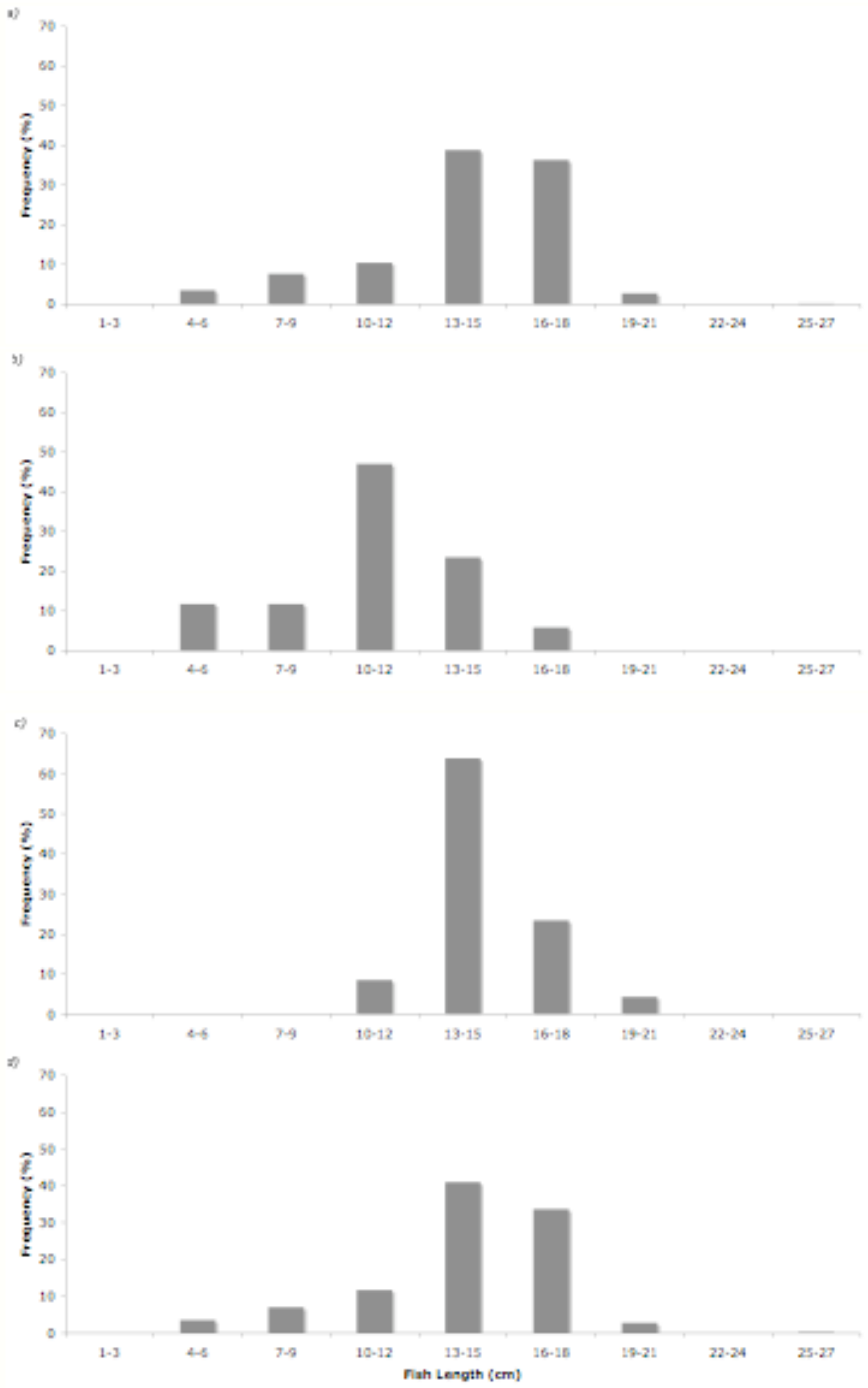

Figure 4. Relative frequency distribution (% of population surveyed) of *S. bilineata* size in *(a)* unparasitized, *(b)* parasitized, *(c)* formerly parasitized, and *(d)* all fish.

The mean lengths (cm) ± SE of *S. bilineata* were 14.11 ± 0.17, 10.7 ± 0.74, 14.89 ± 0.25, and 14.06 ± 0.16 for unparasitized, parasitized, formerly parasitized, and all fish, respectively.

3.2 Lengths of Fish and Parasites Tested

The average total lengths (cm ± SE) of the unparasitized and parasitized fish tested were 14.73 ± 0.3 and 11.85 ± 0.57, respectively. The average parasite length (cm ± SE) was 1.99 ± 0.15. On average, the parasites were 16.4% the total length of the fish.

3.3 Lateralization

We found no preference for right or left turns at the group level in any of the three groups of *S. bilineata* tested (Wilcoxon signed-rank test: unparasitized, $p = 0.446$; parasitized, $p = 0.444$; parasite removed, $p = 0.252$; random simulation, $p =0.70$). There was also no significant difference in L_R between the *S. bilineata* groups and the random binomial simulation (Kruskall-Wallis test: chi-squared = 2.6488, df = 3, $p = 0.449$). Mean L_R values ± SE were -10.4 ± 13.47 (unparasitized), 11.25 ± 21.68 (parasitized), 16.25 ± 14.29 (parasite removed), and -6.4 ± 6.9 (random simulation) (Figure 5).

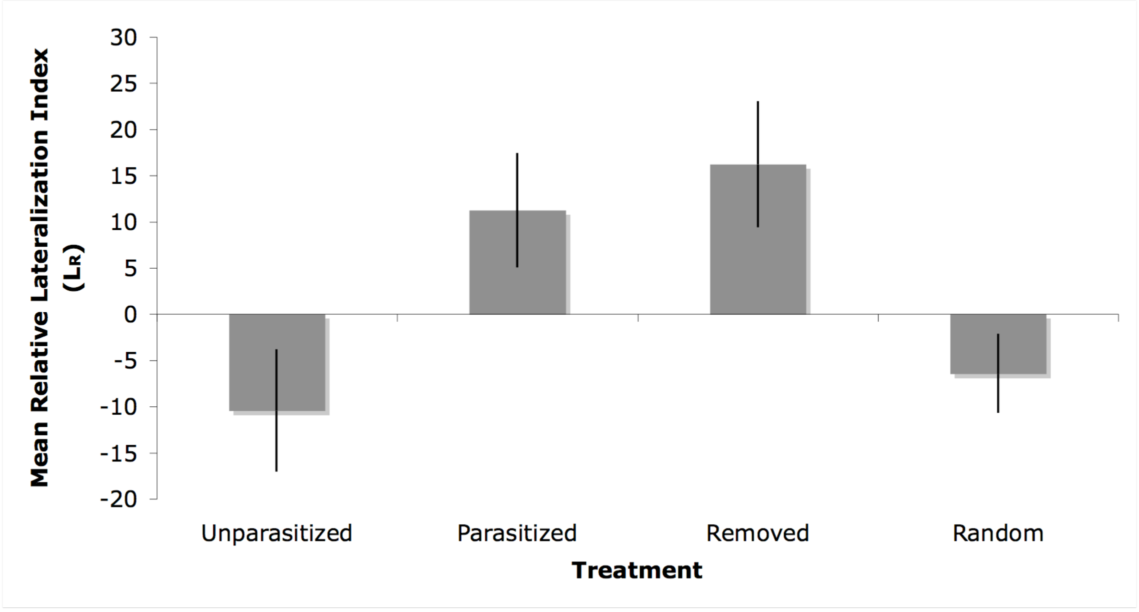

Figure 5. Relative lateralization index (L_R, mean ± SE) in unparasitized (Unparasitized; n=25), parasitized (Parasitized; n=16), and parasite removed (Removed; n=16) *Scolopsis bilineata*, and a random simulation (Random; n=25) based on 10 detour test trials per fish with a 0.5 probability of turning left or right. Positive values indicate preference for right turns, and negative values indicate a preference for left turns. Extreme values of -100 or 100 indicate 10 out of 10 turns in the same direction.

The distribution of L_R was non-normal for the unparasitized (Shapiro-Wilk test: p = 0.029) and parasitized (Shapiro-Wilk test: p = 0.002) groups, and normal for the parasite removed group (Shapiro-Wilk test: p = 0.254) and the random binomial simulation (p = 0.5) (Figure 6).

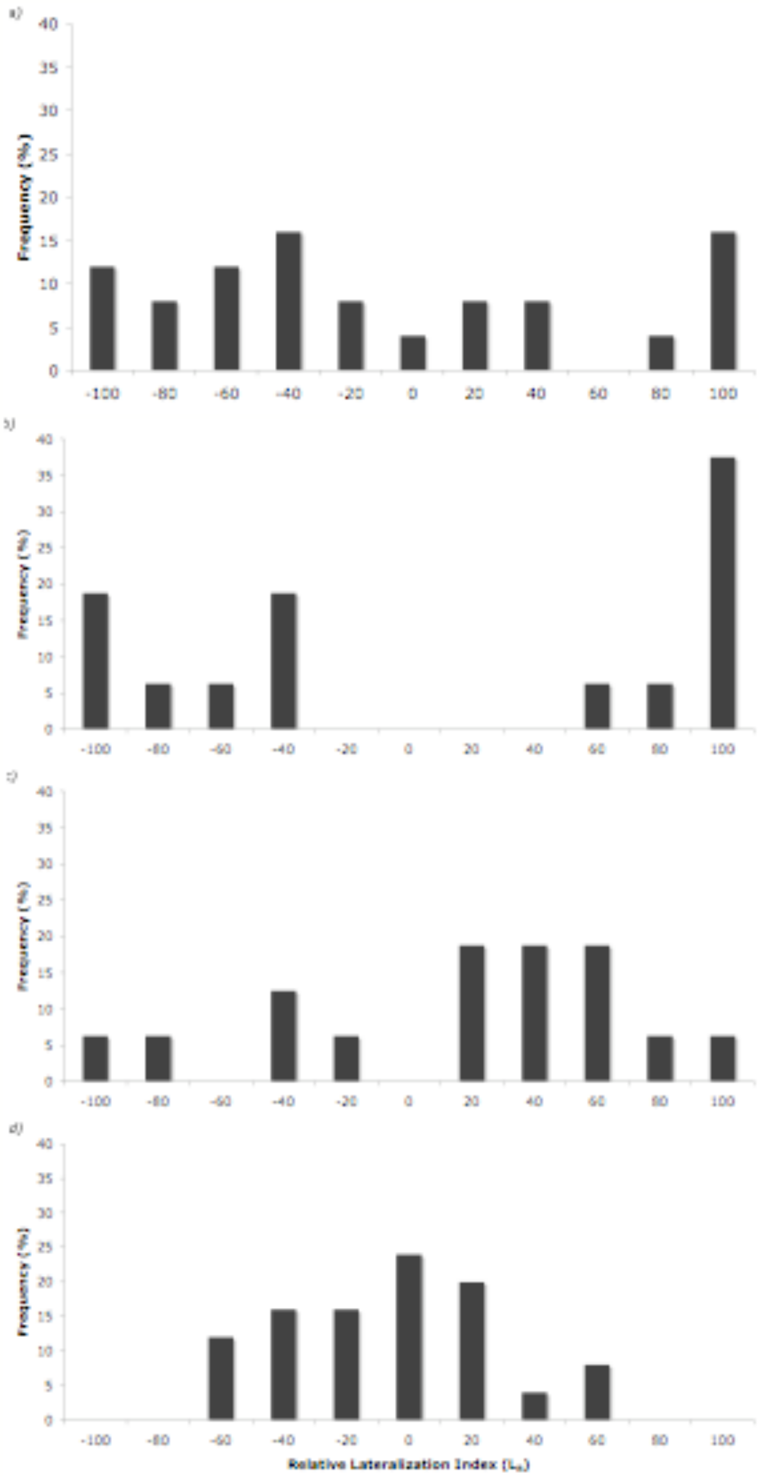

Figure 6. Relative frequency distribution (% of population tested) for L_R in *(a)* unparasitized, *(b)* parasitized, and *(c)* parasite removed *Scolopsis*, and *(d)* a random simulation for fish with equal chances of turning left and right. Positive and negative values indicate prevalence of right and left turns, respectively, with extreme values of |100| indicating 10 out of 10 turns in the same direction.

We found significant differences in the absolute lateralization index (L_A) among groups (Kruskall-Wallis test: $x^2 = 24.997$, df = 2, $p = 3.732e-06$) (Figure 7).

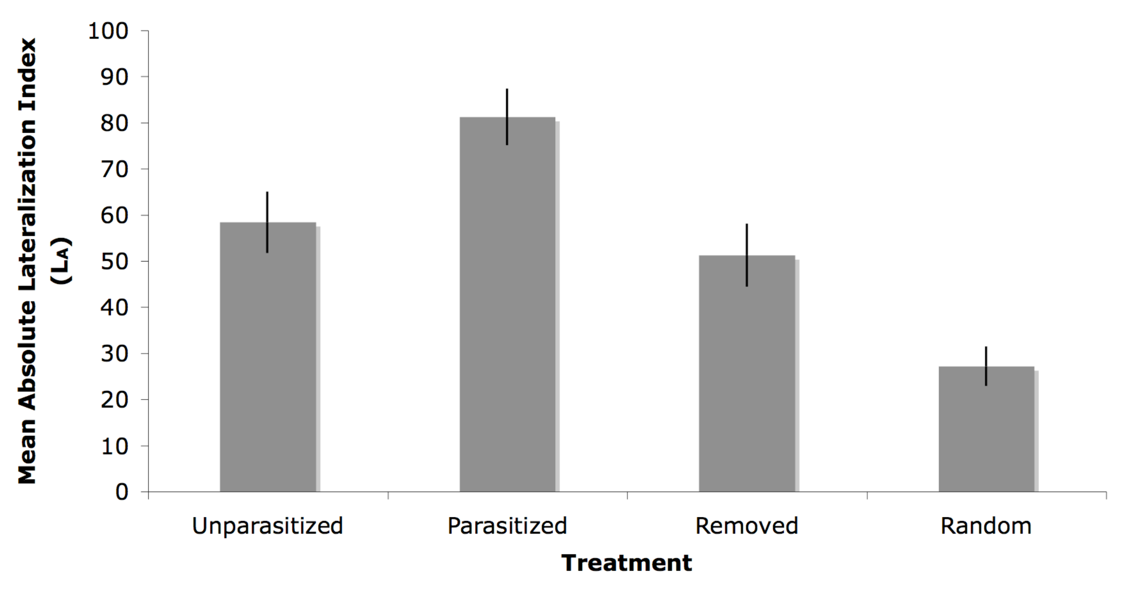

Figure 7. Absolute lateralization index (L_A, mean ± SE) in unparasitized (Unparasitized; n=25), parasitized (Parasitized; n=16), and parasite removed (Removed; n=16) *Scolopsis bilineata*, and a random simulation (Random; n=25) based on 10 detour test trials per fish with a 0.5 probability of turning left or right. L_A calculated as $|L_R|$, thus indicating the degree of lateralization irrespective of the direction preferred.

L_A of the parasitized and unparasitized groups were significantly higher than the L_A of the random binomial simulation (Wilcoxon signed rank test: $p < 0.01$ and $p < 0.01$, respectively). Additionally, L_A was higher in the parasitized group than the unparasitized group (Wilcoxon signed rank test: $p = 0.026$). We did not adjust for multiple tests when comparing the unparasitized group, parasitized group, and random binomial simulation because there were only three comparisons. When we compared L_A between the parasitized and parasite removed groups, the L_A of the parasitized group was higher than that of the same individuals when the parasites were removed (paired Wilcoxon signed rank test: $p = 0.01$). The L_A of the parasitized group and the parasite removed group were also both higher than the random binomial simulation (Wilcoxon signed rank test: $p = 0.008$ and $p = 2.834e\text{-}06$ respectively).

Parasitized *S. bilineata* showed no preference for turning in the direction of their parasite (chi-squared test of independence: $\chi^2 = 0.254$, df = 1, $p > 0.1$), even if the fish were highly lateralized ($L_A \geq 60$, n = 13; chi-squared test of independence: $\chi^2 = 0.008$, df = 1, $p > 0.5$).

4. Discussion

4.1 Abundance and Distribution of Cymothoid Parasites in S. bilineata

Parasitism by *Anilocra nemipteri* appears to be fairly rare in *S. bilineata*, affecting only about 4% of the fish population. A study by Grutter (1994) quantified the abundance of different types of parasites in seven different fish species at Lizard Island, including *S. bilineata*. Of the 13 parasite categories observed in *S. bilineata*, isopods such as *A. nemipteri* were the least common, at less than one parasite per fish on average (Grutter 1994). Isopod parasites were also the least common parasite group to infect the six other fish species studied, with less than one parasite per fish (Grutter 1994). The isopods were also by far the largest of all the parasites observed by Grutter (1994) around Lizard Island. Due to the relatively low occurrence of these parasites on *S. bilineata* and other fishes found by Grutter (1994), and the low prevalence quantified in this study, it is likely that *Anilocra nemipteri* parasites carry a very high cost to the host, and thus only a small number of fish are able to sustain the parasitism. This has implications for the role of these parasites in the ecology of *S. bilineata*, as the high cost of parasitism would select for strong individuals that can survive despite the costs of parasitism. Further quantification of parasite prevalence in other coral reef fish species as has been done in this study would provide important comparisons among parasites and their relative costs to their hosts.

The size distribution of parasititzed individuals relative to unparasitized individuals in the field suggests that the parasites rarely attach to full-grown adults. Rather, it seems that the parasites prefer to attach to young fish and that the parasite and fish grow together. This is supported by prevalence of larger individuals with scars from previous parasitism, as well as the higher frequency of parasitism (11.4%) in juvenile *S. bilineata* compared to adults (3.1%).

The higher infection rates in juveniles compared to adults also suggests that the parasites may contribute to some mortality in juvenile fish. Grutter et al. (201!) studied the effects of a gnathiid ectoparasite, another isopod ectoparasite, on the damselfish *Pomacentrus amboinensis* and found that parasitized juveniles had a lower rate of survival to adulthood than unparasitized fish in the wild, most likely due to decreased swimming performance which made them more susceptible to predatation (Grutter et al. 2011). This study and ours suggest an ecologically important role of parasitism in the survivorship of young coral reef fishes. By placing an extra selective pressure on juvenile fish, these ectoparasites may influence the future fitness of the host species by selecting for strong individuals that can survive to adulthood despite the costs of being parasitized.

4.2 Effect of Parasitism on Lateralization

4.2.1 Relative Lateralization Index (L_R)

Although we found no preference for left or right turning at the population level, there was lateralization at the individual level in all test groups of *S. bilineata.* This was consistent with a study by Domenici et al. (2012), which found no group-level preference for left or right turning in another coral reef fish, *Neopomacentrus azysron*. Thus a lack of right or left turning preference at the group level in *S. bilineata* is most likely a genuine characteristic of the species and not the result of experimental error.

4.2.2 Absolute Lateralization Index (L_A)

Both the unparasitized and parasitized fish groups had mean absolute lateralization indices (L_As) significantly higher than the random binomial simulation, indicating the occurrence of lateralization in both groups. However, the parasitized group had a mean L_A significantly higher than the unparasitized group, indicating that the parasitized fish were more highly lateralized than their unparasitized conspecifics.

Further, when the parasitized fish were retested after having their parasites removed, the mean L_A was significantly lower than when those same individuals had parasites. The group remained lateralized after the parasites were removed, but there was a significant decrease in laterality with the loss of the parasite, such that these individuals were no longer different from the unparasitized fish. Because the parasitized group had the highest L_A of any of the test groups, and the L_A decreased when the parasites were removed, it appears that the parasitism causes an increase in lateralization.

The higher degree of laterality in parasitized *S. bilineata* could arise as a way to help the fish compensate for the decreases in fitness caused by the parasite. Studies on parasitism in other fish species have found many negative effects of parasitism on fish fitness, including lower critical swimming speed (Grutter et al. 2011), reduced swimming endurance and stability (Östlund-Nilsson et al. 2005), and increased metabolic rate (Grutter et al. 2011, Östlund-Nilsson et al. 2005) which results in higher energy demands. A recent study found that in *S. bilineata*, parasitized individuals have lower critical swimming speeds, higher resting metabolic rates, and lower aerobic swimming capacities than unparasitized individuals (Binning and Roche in prep.). All of these negative effects make parasitized individuals both more vulnerable to and less able to escape predators.

Lateralization has been shown to improve quick decision making (Vallortigara and Rogers 2005) and escape performance in fishes (Dadda et al. 2010). These advantages of lateralization could help parasitized fish to escape predators despite slower swimming speeds by allowing the fish to respond more quickly to threatening stimuli. This is supported by a study in which wild-caught poeciliid fish from a high-predation environment was found to be more highly lateralized than fish from a low-predation environment (Brown et al. 2004, Brown et al. 2007).

While our results show that parasitized *S. bilineata* are more highly lateralized on average than unparasitized individuals, the mechanism by which the parasite promotes lateralization remains unclear. We initially hypothesized that the relatively large size of the parasite in comparison to the fish would influence the turning preference of individuals. In this study, the parasite lengths were on average 16.4% the length of the fish, and a recent study of critical swimming speed in *S. bilineata* has shown that drag created by the parasite has an important effect on individual swimming performance (Binning and Roche in prep). We hypothesized that the asymmetrical drag created by the parasite would pull the fish to one side, making them prefer to turn in the direction of the parasite. However, our results did not support this hypothesis. It may be that the parasite somehow causes physiological changes that lead to increased lateralization, but that cannot be supported by the data collected in the present study.

4.3 Problems and Limitations of the Current Study

4.3.1 Abundance Transects

Potential for biases in our methodology while conducting abundance transects include the possibility for error in estimating fish sizes under the water. There also may have been inconsistencies in estimating fish sizes due to a number of different observers contributing to the data. To minimize these biases, all observers spent time practicing estimating fish length and checking estimates against sketches of fish with known lengths held underwater against the reef. Observers also practiced size estimates together and compared estimates to ensure consistency between observers before beginning to collect data.

4.3.2 Lateralization Study

Due to time constraints, the sample sizes of fish tested were small, particularly for parasitized fish. For logistical reasons, mainly the rarity of parasitized fish, we were limited by how many we could find and catch and did the best we could under the circumstances. The results seem reliable despite the low sample size, though the data may be supplemented in the future.

4.4 Further Studies

In order to investigate the mechanism through which parasitism causes increased lateralization, it would be interesting to attach fake parasites of similar size and weight as the actual parasites to unparasitized *S. bilineata* and run the detour test. This would determine whether the increased lateralization is caused solely by the drag created by the parasite, or if there is some physiological effect of the parasite which promotes lateralization.

To test whether parasitized *S. bilineata* really do have advantages in their responsiveness to stimuli, presumably due to higher lateralization, the fast-start performance behavior of parasitized fish could be compared to unparasitized fish. Traits such as reaction time, maximum escape speed, and rate of acceleration could be compared to examine whether parasitized fish appear to have a higher ability to escape from predators.

4.6 Conclusions

Infection by *A. nemipteri* is fairly rare on *S. bilineata* around Lizard Island, indicating that this parasitism carries a high cost to the host fish, and thus cannot be sustained except by exceptionally strong individuals. The parasites are also more common in juvenile and small adult *S. bilineata*, indicating that these parasites prefer to parasitize young fish rather than fully grown adults. The high cost of parasitism and early stage at which *S. bilineata* seems to be parasitized indicate an ecologically important role of *A. nemipteri* in adding selective pressure on *S. bilineata*. Lateralization in turning behavior was increased in parasitized fish, and decreased when parasites were removed such that the lateralization of the formerly parasitized fish was no different from fish that were never parasitized. Thus it seems that parasitism leads to an increase in lateralization in *S. bilineata*. This increase in lateralization may arise as a mechanism by which infected fish can compensate for the decrease in swimming performance caused by the parasitism to be able to better escape predators.

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