

**Coarse woody habitat as a major source of benthic invertebrates for fishes
in Crampton Lake, WI**

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ABSTRACT

Lakeshores and surrounding watersheds are rapidly being developed for human use leading to loss of coarse woody habitat (CWH) in lakes, which is essential for inland fisheries. For example, CWH is needed for reproduction of certain fish species and provides refuge to prey fish from predators. Little attention, however, has been given to the possible contribution of benthic invertebrate production from CWH to prey fish diets. In this study, we found that prey fishes occupied CWH more frequently than exposed sites and that there was a greater probability that fish diets came from CWH. Contrary to our predictions, there was no significant difference in invertebrate biomass or abundance between habitat types, indicating that higher foraging by prey fishes in CWH may have masked the possibility of higher invertebrate production in CWH. Our findings suggest that CWH is a major source of food for prey fishes and thus contributes to the production of high order consumers such as common sport fishes. As anthropogenic removal of CWH for residential development, recreation, and aesthetics continues to rise, protecting CWH may be necessary for maintaining sustainable fish stocks and healthy lake ecosystems.

INTRODUCTION

Coarse woody habitat (CWH) in lake ecosystems is composed of trees, branches, roots, and wood fragments that have fallen into the littoral zone of a lake through natural or anthropogenic means and provide preferred habitat for fish and benthic invertebrates (Guyette and Cole 1992; Christensen *et al.* 1996). CWH may provide an important link between terrestrial and aquatic ecosystems and play a key role in lake food webs (Newbrey *et al.* 2005; Roth *et al.* 2007; Sass *et al.* 2012), particularly when the availability of other habitats is limited, such as in lakes that are either highly oligotrophic or eutrophic (France 1997; Mehner *et al.* 2005). Areas of aquatic CWH provide a substrate for primary and secondary production and tend to harbor a

greater abundance of benthic invertebrates because they provide refuge from fish predators and high food availability, potentially making CWH a major source of food for prey fishes (Angermerier and Karr 1984; Benke *et al.* 1984; Everett and Ruiz 1993; Storry *et al.* 2006).

Understanding the role of CWH in prey fish production is therefore important for maintaining healthy lake ecosystems and sustainable levels of piscivorous fishes, which are of high cultural and economic value (U.S. Fish and Wildlife Service 2011).

During the past couple of centuries, housing density has increased in the United States in rural areas and previously undisturbed ecosystems, including around lakes (Motzkin *et al.* 1996; Radeloff *et al.* 2001; Hansen *et al.* 2002; Schnaiberg *et al.* 2002). As such, anthropogenic activities including residential development and recreation may explain the negative correlation between density of cabins and CWH in Wisconsin and Michigan lakes (Christensen *et al.* 1996). Logging and land-clearing also reduce CWH in terrestrial and aquatic ecosystems, and create a lag in the recruitment of new, large, dead wood into ecosystems (Webster *et al.* 2007).

After CWH removal, yellow perch populations decline because yellow perch require submerged wood and vegetation to lay eggs (Hanchin *et al.* 2003). Decreases in CWH are also associated with declines in prey fishes, shifts in foraging behavior of piscivorous fishes, and declines in consumption rates of piscivorous fishes (Ahrenstorff *et al.* 2008). CWH thus serves a significant role in the life histories of fishes by providing protection for nesting sites, a spawning substrate, and an area of greater prey availability (Hjelm *et al.* 2000; Hunt & Annett 2002).

While much of the literature to date has focused on the influence of CWH on fish reproduction and refuge for prey fishes, limited research has been conducted on the contribution of benthic invertebrate production in CWH to fish diets. Benthic invertebrate production constitutes approximately 40% of whole lake invertebrate production and often constitutes a

large portion of the diets of many fish species such as bluegill, largemouth bass, and yellow perch in small, shallow lakes (Vadeboncoeur *et al.* 2002).

In this study, we examined the contribution of benthic invertebrates to fish diets in CWH in Crampton Lake, located in northern Wisconsin, USA. We hypothesized that CWH increases invertebrate production compared to exposed sites (*i.e.*, low abundance of CWH) and thus, we expected to find a greater biomass of benthic invertebrates in CWH. We also hypothesized that CWH is an optimal place for fish to forage, and thus expected fish catch rates to be greater in CWH. Finally, we hypothesized that benthic invertebrates from CWH constitute a greater portion of fish diets than invertebrates from exposed areas, expecting that there will be a greater probability of finding invertebrates from CWH in fish diets than finding invertebrates from exposed sites. These findings may help elucidate the role of CWH in the production of prey fishes.

METHODS

Study site

This study was conducted in Crampton Lake, located on the University of Notre Dame Environmental Research Center property in northern Wisconsin. For nearly a century, the lake has seen minimal anthropogenic disturbance (“History of UNDERC” 2015), and thus allows us to examine the contribution of CWH to fish diets in an ecosystem without significant development.

Site selection and sediment sampling for invertebrates

CWH and exposed sampling sites were selected based on visual judgment of the “woodiness” of a site. At each site, the number of pieces of wood and number of branch sites present along a transect 1 meter perpendicular to the lakeshore were recorded as a means of

quantifying its “woodiness.” We compared the number of pieces of wood using a one-way ANOVA, and the number of branch sites using a Wilcoxon rank-sum test with continuity correction to ensure that CWH and exposed sites were indeed significantly different in “woodiness.”

Twelve CWH and twelve exposed sites along the entire lakeshore of Crampton Lake were selected. At each of the 24 sites, we sampled benthic invertebrates in the sub-surface sediment using a sediment corer, and invertebrates from the disturbed surface sediment using a D-net. Per site, we collected five core samples at a water depth of 1.0 meter and two D-net samples at a depth of 0.5 meter.

Determining catch rates and sampling fish diets

We determined fish catch rates by setting minnow traps at eleven CWH and nine exposed sites along the entire lakeshore, chosen independently from the sediment sample sites. Although we intended to sample ten sites of each habitat type, we later judged one of the exposed sites to be CWH instead, due to its relatively high number of mostly decomposed wood fragments. We set the traps in the morning and checked them for minnows in the afternoon. All traps were set for a relatively equal amount of time around the same time of day, from late morning to mid afternoon. To determine the minnow catch per unit effort (CPUE) rate between CWH and exposed sites, we used equation (1) and statistically compared CPUE rates using a one-way ANOVA.

$$(1) \quad \text{CPUE} = \frac{\# \text{ of minnows caught}}{\text{unit effort (hrs)}}$$

We used a gastric lavage technique as described by Seaburg (1957) to sample the stomach contents of fishes caught in the traps. We did not statistically compare fish diets between habitat

types because the few fishes that we caught in exposed sites did not have any invertebrates we could identify in their diets; their diets were mostly digested.

Invertebrate biomass and taxa abundance in the sediment and fish diets

We characterized the benthic invertebrate community in CWH and exposed sites by calculating the abundance and dry weight of oven-dried invertebrate samples, and by identifying the taxa of benthic invertebrates to order. The invertebrate abundance and biomass were compared between habitat types using a one-way ANOVA, respectively. Fish diets were characterized by abundance of invertebrates by taxa. We also constructed a frequency distribution of the invertebrate orders present in CWH, exposed sites, and fish diets, respectively. Because dipterans were the most abundant order in each sampling type, we compared the abundance and biomass of dipterans between CWH and exposed sites using a one-way ANOVA. We believed this could provide more information on the foraging behavior of fish.

Calculating probabilities of fish diet origin

We used the abundance of benthic invertebrate taxa in CWH and exposed sites to determine the relative importance of CWH for fish food production. Our metric of relative importance of CWH versus exposed sites for fish food production was the probability that all diet items came from CWH alone and the probability that all items came from exposed sites alone. Equation (2) was used to calculate the probability that all the invertebrate orders (order x, y, z...) in a given fish's diet came from CWH. The resulting probability is a weighted probability that uses the CPUE data to account for the possibility that fish may spend more time foraging in one habitat type than the other.

$$(2) P_{CWH} = \left[\left(\frac{\# \text{ of inverts. of order } x \text{ in all CWH}}{\# \text{ of inverts. of order } x \text{ in all sites}} \right) \left(\frac{\# \text{ of inverts. of order } y \text{ in all CWH}}{\# \text{ inverts. of order } y \text{ in all sites}} \right) \cdots \right] \left(\frac{CPUE \text{ in CWH}}{\text{total CPUE}} \right)$$

$$(3) P_{exp.} = \left[\left(\frac{\# \text{ of inverts. of order } x \text{ in all exp.}}{\# \text{ of inverts. of order } x \text{ in all sites}} \right) \left(\frac{\# \text{ of inverts. of order } y \text{ in all exp.}}{\# \text{ inverts. of order } y \text{ in all sites}} \right) \dots \right] \left(\frac{CPUE \text{ in exp.}}{\text{total CPUE}} \right)$$

Equation (3) was used to calculate the probability that all the invertebrate orders in each fish's diet came from exposed sites. The probabilities calculated from equation (2) were then statistically compared to those from equation (3) using a Wilcoxon rank-sum test with continuity correction to determine if there was a higher probability that fishes' diets came from CWH or exposed sites.

RESULTS

Greater woodiness in CWH than exposed sites

The CWH sites we chose based on visual observations had a significantly greater number of branch sites and pieces of wood than the exposed sites, $W = 135$, $p < 0.001$, and $F(1, 22) = 23.82$, $p < 0.0001$, respectively (Fig. 1).

Fish catch rates greater in CWH

The CPUE rate in CWH was significantly greater than in exposed sites, $F(1, 18) = 4.56$, $p < 0.05$ (Fig. 2). No fishes were caught in five out of the eleven CWH sites and eight out of the nine exposed sites. At sites in which fishes were caught, fishes tended to be in groups of five or more and included bluegill and yellow perch species. The mean time that minnow traps were set was 4.7 ± 0.9 hours (mean \pm standard deviation).

Invertebrate frequency distribution between site types and in fish diets

Although we did not perform a statistical test on the frequency distributions within or among site types and fish diets, we observed that *Diptera* was the most abundant order in CWH, exposed sites, and fish diets, respectively (Fig. 3). Other prevalent orders included *Odonata*, *Trichoptera*, and *Veneroida*.

No difference in invertebrate biomass or abundance between habitat types

No significant difference in benthic invertebrate biomass or abundance existed between CWH and exposed sites, $F(1, 20) = 0.83, p > 0.05$; $F(1, 18) = 0.04, p > 0.05$ (Figs. 4 and 5).

Greater Diptera biomass and abundance in exposed sites

A significantly greater biomass and abundance of dipterans were observed in exposed sites, $F(1, 21) = 10.62, p < 0.01$; $F(1, 22) = 5.223, p < 0.05$ (Figs. 6 and 7). Most of the dipterans were the larvae of midges belonging to the family *Chironomidae*, informally known as chironomids.

Greater probability of fish diets coming from CWH

There was a significantly greater probability that all the benthic invertebrates in any given fish's diet came from CWH than from exposed sites, $W = 961, p < 0.0001$ (Fig. 8).

DISCUSSION

Our results supported our prediction that CWH would have a greater CPUE rate than exposed sites, indicating that prey fishes prefer to occupy CWH. CWH may offer greater invertebrate availability, a refuge from predators, or both to prey fishes. Benke *et al.* (1985) found that the stomach contents of three of four *Lepomis* species and of pirate perch (*Aphredoderus sayanus*) consisted of at least 60% of taxa associated with CWH, with the rest coming from more exposed areas such as the mud or sand. Our findings that there was a higher catch rate in CWH and a greater probability that fish diets came from CWH are consistent with the literature and suggest that CWH provides a significant source of invertebrates for prey fishes.

Because aquatic invertebrates use coarse woody debris as a substratum for egg deposition, a direct food source, and protection from predators, one would expect to find greater taxonomic diversity and increased biomass in CWH (Angermeier and Karr 1984; Benke *et al.*

1984; Wallace 1993; Vander Zanden and Vadeboncoeur 2002). We found no significant difference in invertebrate biomass and abundance between the two habitat sites, however. Thus, our result initially appeared not to be supported by the scientific literature. It is possible, however, that the high density of fishes occupying and foraging in CWH relative to exposed sites masked the greater rate of invertebrate production in CWH and was responsible for the insignificant difference in invertebrate biomass and abundance between habitat types.

Our findings that dipterans were both more abundant and had a greater biomass in exposed sites were also inconsistent with the literature. In stream ecosystems, dipterans have been found to be present in greater densities in CWH (Phillips and Kilambi 1994). In our study, although *Diptera* the most abundant order in fish diets, dipterans were much more abundant in exposed sites than in CWH. Combined with our CPUE data and diet origin probabilities, this finding suggests that greater consumption of dipterans by fish in CWH led to the lower abundance of dipterans observed in CWH compared to exposed sites. Because of this phenomenon, we should interpret the probabilities of fish diet origin with caution; the actual probabilities may be higher or lower.

There still remains the question of whether CWH is more important as a refuge for prey fishes or as a source of invertebrates. Czarnecka *et al.* (2014) suggested that the answer depends on a variety of factors and thus, may vary from one lake ecosystem to another. Some studies have indicated that CWH is more important as an area of refuge than greater prey availability for prey fishes and that prey fishes seeking refuge in CWH from predators contribute to the increased foraging observed (Angermeier and Karr 1984; Roth *et al.* 2007). To better understand the role CWH plays in the production of prey fishes, future studies should examine fish foraging

and refuge behavior as well as benthic invertebrate density and diversity in the presence and absence of piscivorous fishes.

Our study indicated that CWH contributes significantly to the sustainability of fish stocks in lake ecosystems through the production of fish prey by providing them with increased invertebrate availability. With rising lakeshore development and human activities that remove CWH, lake food webs and piscivorous fishes may suffer. Understanding the mechanisms by which CWH affects aquatic food webs can inform projects to restore lake ecosystems. Studies have shown that the addition of CWH may improve reproduction of fishes in lakes where CWH is lacking or has been removed (Hunt and Annett 2002; Lawson *et al.* 2011; Weis and Sass 2011). Others have indicated that adding CWH cannot quickly reverse the negative effects on fish populations of reducing CWH (Sass *et al.* 2012). Thus, a comprehensive understanding of the dynamics in a given lake, and regulations that protect CWH are vital for maintaining resilient lake ecosystems in the face of increasing lakeshore residential development.

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Figures

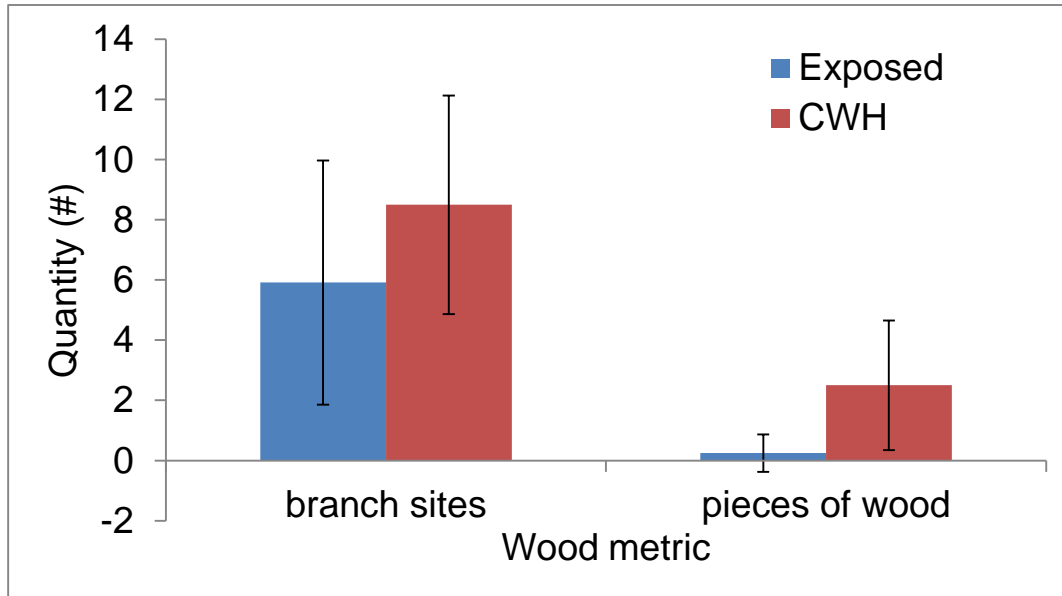


Fig. 1 Number of branch sites and pieces of wood between habitat types. CWH had a significantly greater number of branch sites (5.9 ± 4.1 ; $p < 0.001$) and pieces of wood (8.5 ± 3.6 ; $p < 0.0001$) than exposed sites (0.3 ± 0.6 and 2.5 ± 2.2 , respectively).

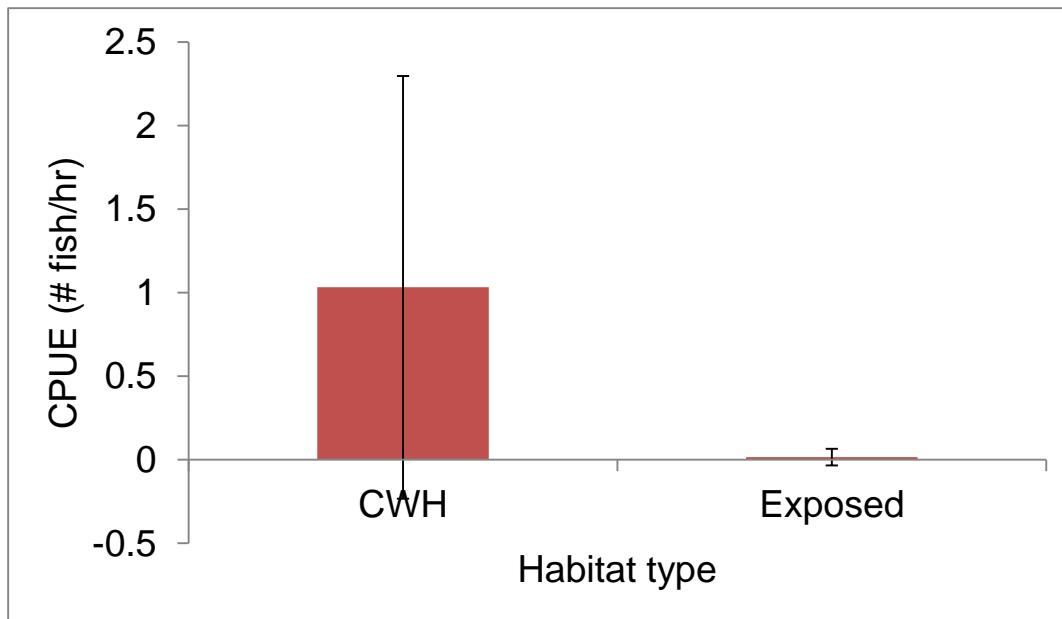


Fig. 2 Fish catch rates between habitat types. There was a significantly greater CPUE in CWH (1.03 ± 1.26 fish/hr) than exposed sites (0.02 ± 0.05 fish/hr) ($p < 0.05$).

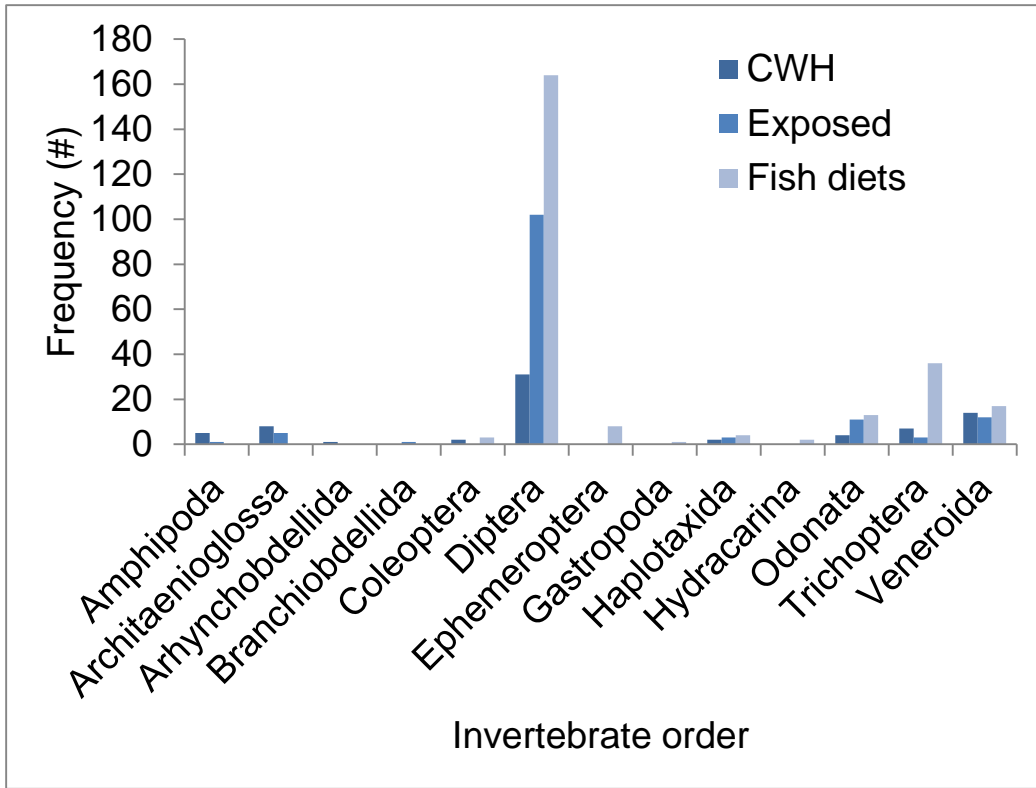


Fig. 3 Invertebrate order frequency between habitat types and in fish diets. Diptera was the most abundant order in CWH, exposed sites, and fish diets, respectively. (No statistical tests performed.)

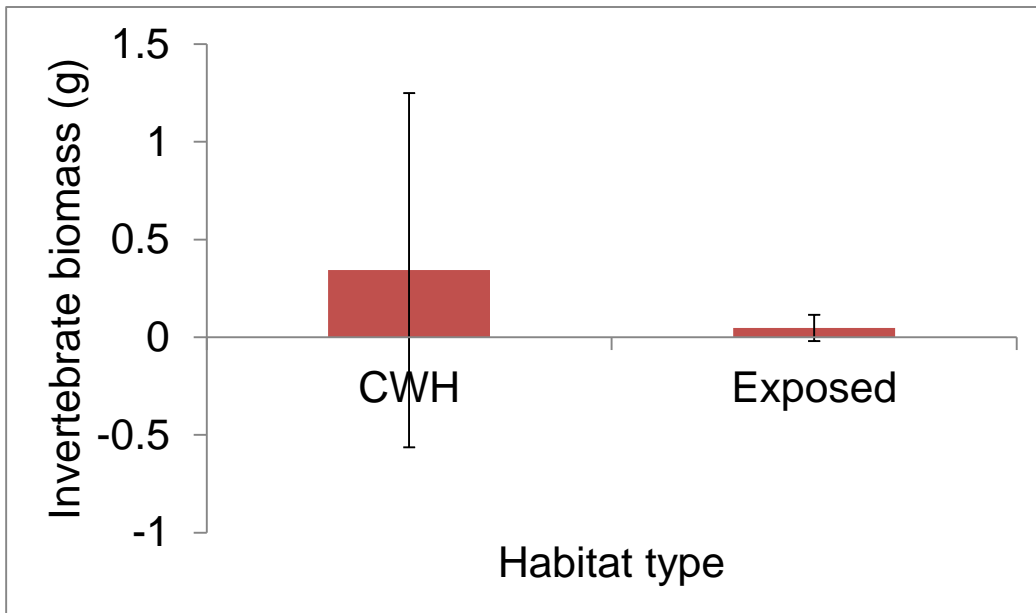


Fig. 4 Invertebrate biomass between habitat types. There was no significant difference in biomass of all invertebrate orders combined between CWH (0.34 ± 0.91 g) and exposed sites (0.05 ± 0.07 g) ($p > 0.05$).

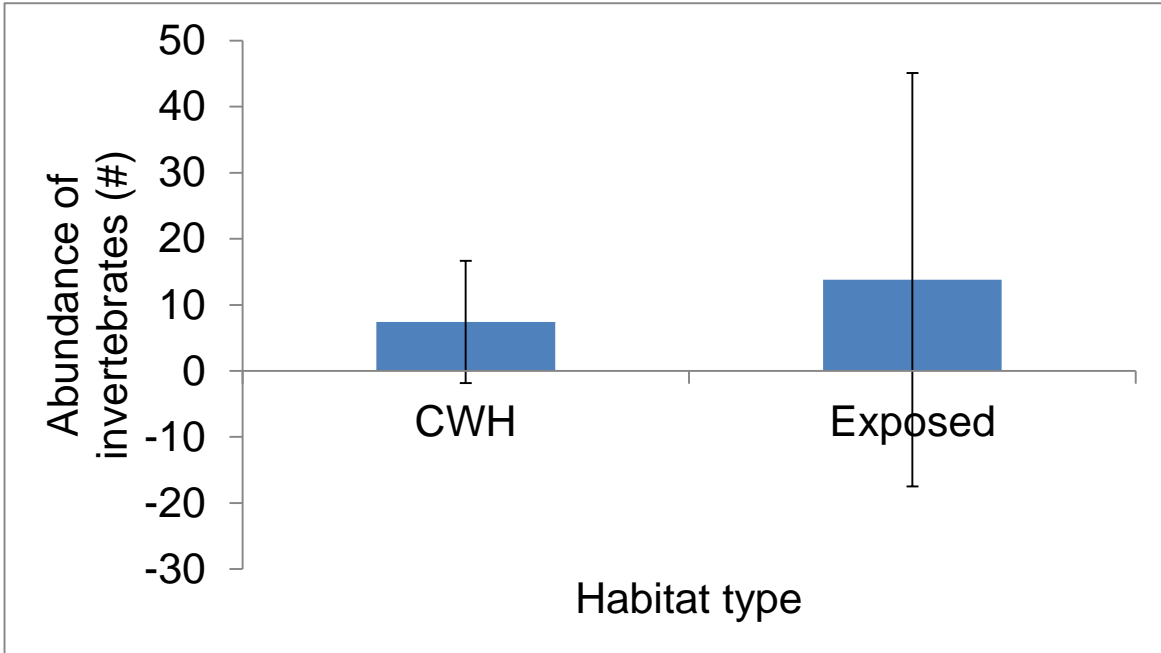


Fig. 5 Abundance of invertebrates between habitat types. There was no significant difference in abundance of invertebrates between CWH (7.4 ± 9.3 g) and exposed sites (13.8 ± 31.3 g) ($p > 0.05$).

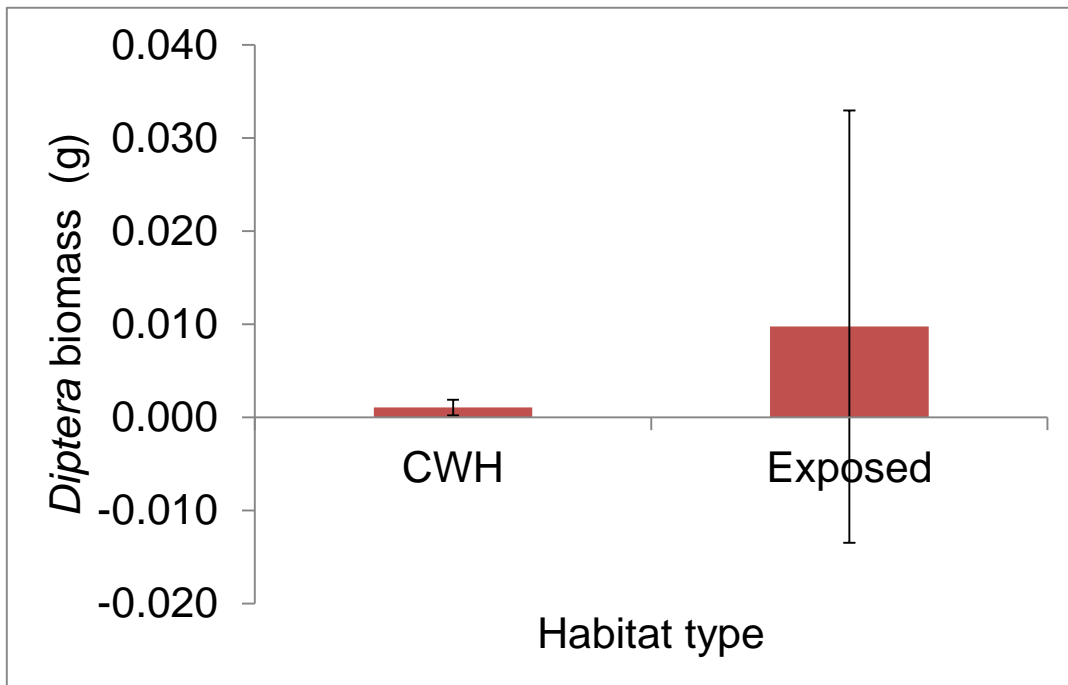


Fig. 6 Diptera biomass between habitat types. There was a significantly greater *Diptera* biomass in exposed sites (0.100 ± 0.023 g) than in CWH (0.001 ± 0.001 g) ($p < 0.01$).

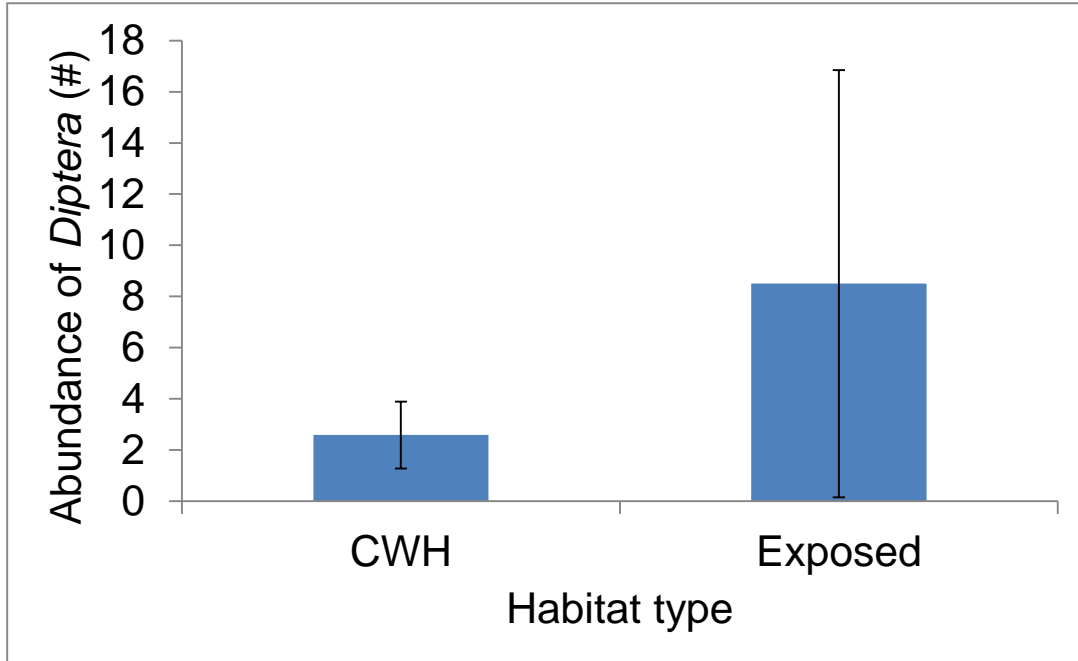


Fig. 7 Abundance of *Diptera* between habitat types. There was a significantly greater abundance of *Diptera* in exposed sites (8.5 ± 8.4) than in CWH (2.6 ± 1.3) ($p < 0.05$).

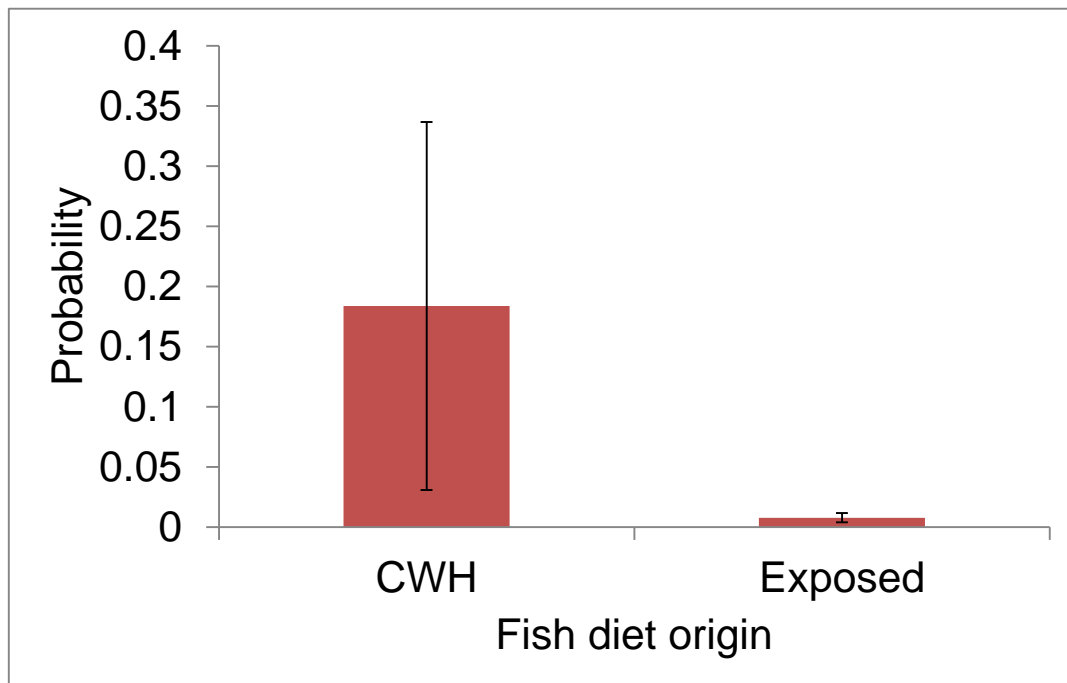


Fig. 8 Probability of fish diets coming from CWH versus exposed sites. There was a significantly greater probability that fish diets came from CWH (0.184 ± 0.153) than from exposed sites (0.007 ± 0.004) ($p < 0.0001$).