Environ Biol Fish (2006) 76:317–327
DOI 10.1007/s10641-006-9035-2

ORIGINAL PAPER

The biology of pygmy whitefish, *Prosopium coulterii*, in a closed sub-boreal lake: spatial distribution and diel movements

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Received: 8 August 2005 / Accepted: 20 March 2006 / Published online: 3 June 2006

Abstract Using gillnets and trap nets, we examined the spatial distribution, diel movements, and environmental tolerances of pygmy whitefish, *Prosopium coulterii*, in a small boreal lake in north-central British Columbia. Most gillnets were set below the thermocline but we also fished a shore net in the littoral zone. During the ice-free season (May to November) there was a strong diel onshore–offshore movement: during the day pygmy whitefish were offshore and below the thermocline (water temperatures of 4–6°C) but at night they were inshore and above the thermocline (water temperatures of 12–18°C). This onshore–offshore movement occurred close to the bottom and, regardless of where they were caught, most fish were < 4 m off the bottom. Oxygen concentrations in most of the hypolimnion dropped to < 5.0 mg l^{-1} in June and by late August to < 1.0 mg l^{-1}; indicating pygmy whitefish can tolerate low oxygen conditions. The catch of pygmy whitefish in gillnets set below the thermocline was highly skewed: 53% of the nets were empty, 37% caught 18 or less fish, and 10% caught 70% of the total catch (742 fish). Trap nets produced similarly skewed results: most trap net sets caught no pygmy whitefish but one set caught over 2,000 individuals. Our catch data suggest that in Dina Lake #1 some pygmy whitefish aggregate.

Keywords *Prosopium coulterii* · Whitefish · Environmental tolerances · Spatial distribution · Diel movements · Aggregation

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Introduction

The Peace/Williston Fish and Wildlife Compensation Program (PWFWCP) was created in 1988 to conserve and enhance fish, wildlife, and their habitats, within the Williston Reservoir Watershed. The reservoir was formed by the construction of the W.A.C. Bennett Dam on the upper Peace River, British Columbia. Originally, the PWFWCP concentrated its resources on recreational species. Recently, however, the major aquatic conservation concern of the electric utility industry has shifted from recreational fisheries to protecting biodiversity (Olmsted and Bolin 1996). Consequently, in 1998, the PWFWCP began a study of the indigenous non-game fishes in the Williston Watershed.

The pygmy whitefish, *Prosopium coulterii*, was the first species chosen for study. Although little is known about the biology of pygmy whitefish, they are generally viewed as glacial relicts inhabiting cold, deep lakes (Scott and Crossman 1973; Weisel et al. 1973; Becker 1983). While primarily a western North American species with populations scattered from Washington, Idaho, and Montana north to Alaska and the Yukon Territory, it also occurs east of the Continental Divide (e.g., Lake Superior, Lake Athabasca, Great Bear Lake, and Waterton Lake) and even on the Chukotsk Peninsula, Siberia (Chereshnev and Skopets 1992). This disjunct distribution not only reflects the vast geographic range the species inhabits but also raises interesting questions about the diversity of habitats it may occur in. Typically, they are caught in fine mesh (25 mm or less stretch mesh) gillnets or in otter trawls set in relatively deep water (45–70 m) and usually only a few individuals (up to 15) are caught in a single haul (Eschmeyer and Bailey 1955).

Although pygmy whitefish were known from the upper Peace River system before the construction of the W.A.C. Bennett Dam, nothing was known about their biology, and little about their distribution within the watershed. Thus, the purpose of our pygmy whitefish program was two fold—(1) to obtain any data relating to habitat use, feeding habits, age, growth, and reproduction of pygmy whitefish in Dina Lake #1, and then (2) apply this biological knowledge towards the design of an effective sampling schedule so we can determine the distribution of the species within the broader range of the Williston Watershed. Upon completion of the biology and distribution work, the ultimate goal of the program is to produce a management plan for this enigmatic species. To date, 17 lakes (out of approximately 360 surveyed) in the Williston Watershed are known to contain pygmy whitefish; however, the watershed is large (about 70,000 km^2) and many of its lakes are reachable only by air. In addition, many of the records on these lakes are dated and are questionable with regards to their accuracy on fish identification. Thus, we began our study on a relatively accessible lake (Dina Lake #1) that was known to contain pygmy whitefish. We reasoned that by testing different collecting techniques and investigating the spatial distribution of pygmy whitefish in Dina Lake #1, we could increase the probability that brief, basin-wide fly-in surveys would detect pygmy whitefish if they were present.

Methods

Study site

Our study lake (Dina Lake #1, UTM: 10.4806.61539) is 25 km north-northwest of Mackenzie, British Columbia (Fig. 1). The lake has no surface outlet but has a permanent inlet stream that drains into the lake from Dina Lake #2 (UTM: 10.4715.61544). There are no inlet streams to Dina Lake #2 and the lake contains no pygmy whitefish. Dina Lake #1 (henceforth referred to as Dina Lake) has a surface area of 158 ha and a complex shoreline consisting of two major basins (Fig. 2). A 5 m sill separates the northern and southern basins. The lake is mesotrophic and has a shoreline length of 14,800 m and a maximum depth of 27 m. At the start of the project we did not know how abundant pygmy whitefish were in Dina Lake. Since we wanted to test different sampling methods but did not want to deplete the population, we confined our sampling to only the

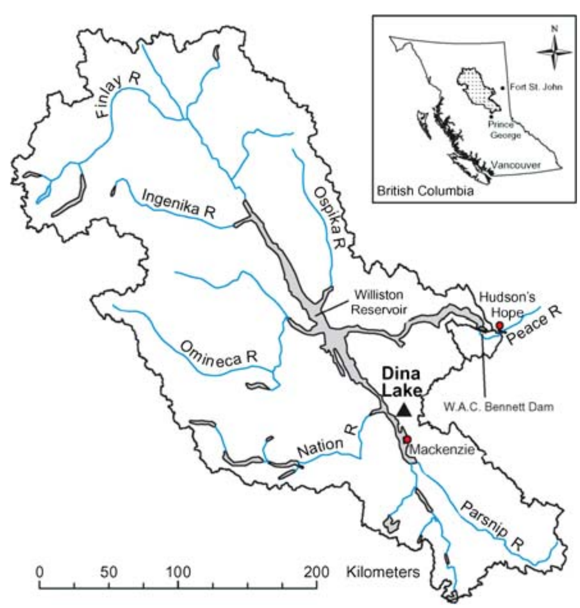

Fig. 1 Location of Dina Lake in the Williston Watershed located in north-central BC

northern basin and left the southern basin as a refuge.

The northern basin consists of a large central basin that is up to 27 m deep and two shallower sub-basins (the eastern and western sub-basins; Fig. 2). The eastern sub-basin has a maximum depth of 9 m and is connected to the central basin by a 5 m sill. In contrast, the western sub-basin has a maximum depth of 14 m and is connected to the central basin by a 3 m sill. Thus, limnologically, the eastern sub-basin remains part of the central basin throughout the summer while the hypolimnion in the western sub-basin is isolated from the central basin for much of the summer.

Typically, Dina Lake becomes ice-free in late May and the lake turns over shortly after the ice leaves (Fig. 3A). As spring progresses the surface waters warm and the lake stratifies. By mid-summer there is a strong epi-, and hypolimnion (Fig. 3B). Early in the season the epilimnion is about 4 m deep but as summer progresses it deepens to about 7 m. Just before freeze-up in late November the lake again becomes isothermal (Fig. 3C). During the summer, oxygen concentrations are relatively high in the epilimnion (about 8–9 mg l^{-1}) but oxygen concentrations in the hypolimnion decline and by late August there is almost no oxygen (0–4 mg l^{-1}) below 18 m (Fig. 3B).

Dina Lake is unusual in that it is a relatively small, shallow lake, which is atypical for pygmy whitefish to inhabit. In addition, it is the only known lake in the Watershed not to contain any

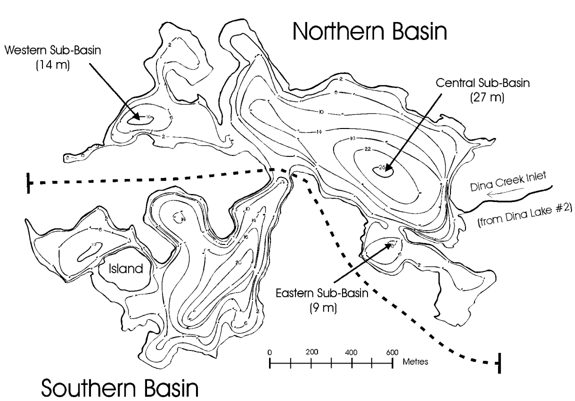

Fig. 2 Bathymetric map for Dina Lake. Depth isobaths are in meters

other whitefish species and that the original fish fauna consisted of only three species: lake chub, *Couesius plumbeus*, longnose sucker, *Catostomus catostomus*, and pygmy whitefish. None of these species are piscivorous. However, in the 1980s, to increase recreational angling opportunities, rainbow trout, *Oncorhynchus mykiss*, and brook trout, *Salvelinus fontinalis*, were introduced into the lake.

Sampling

Once we knew more about the biology of pygmy whitefish in Dina Lake, our secondary objective of the study was to utilize a simple collecting method that would increase our probability of detecting pygmy whitefish during brief fly-in surveys. We tried a variety of collecting methods—beach seines, minnow traps, light traps, trawling, gillnets, and trap nets—as well as acoustical surveys. The most successful method of this 2 year study would then be tested on two fly-in lakes (Quentin and Weissener lakes) in 2003. If successful, additional sampling would be conducted on other lakes in 2004 and 2005 to learn more about the distribution of the species within the vast watershed. Also, the only a priori information we had about habitat use by pygmy whitefish is that, outside the spawning season, they are usually collected in deep water. Consequently, we scattered our sampling effort in Dina Lake over a variety of times (day and night), habitats (littoral, benthic, limnetic), depths (surface to bottom), and sites (bays, exposed shoreline, and sub-basins). Numerous nets were also set over a 24 h period and were checked regularly. Night time was determined when field notes could no longer be taken without the aid of a flashlight. Additionally, day time was determined when field notes could be taken without the aid of additional light sources.

Each year we conducted five 1-week sampling trips over the period from May to November. We used sinking gillnets (stretch mesh of 10, 14, 19, 25, 32, and 40 mm) and, initially, set them horizontally along the bottom at a variety of depths. The only mesh sizes that caught pygmy whitefish were the 10, 14, 19, and 25 mm nets. The 10 mm net was used to catch young-of-the-year (YOY)

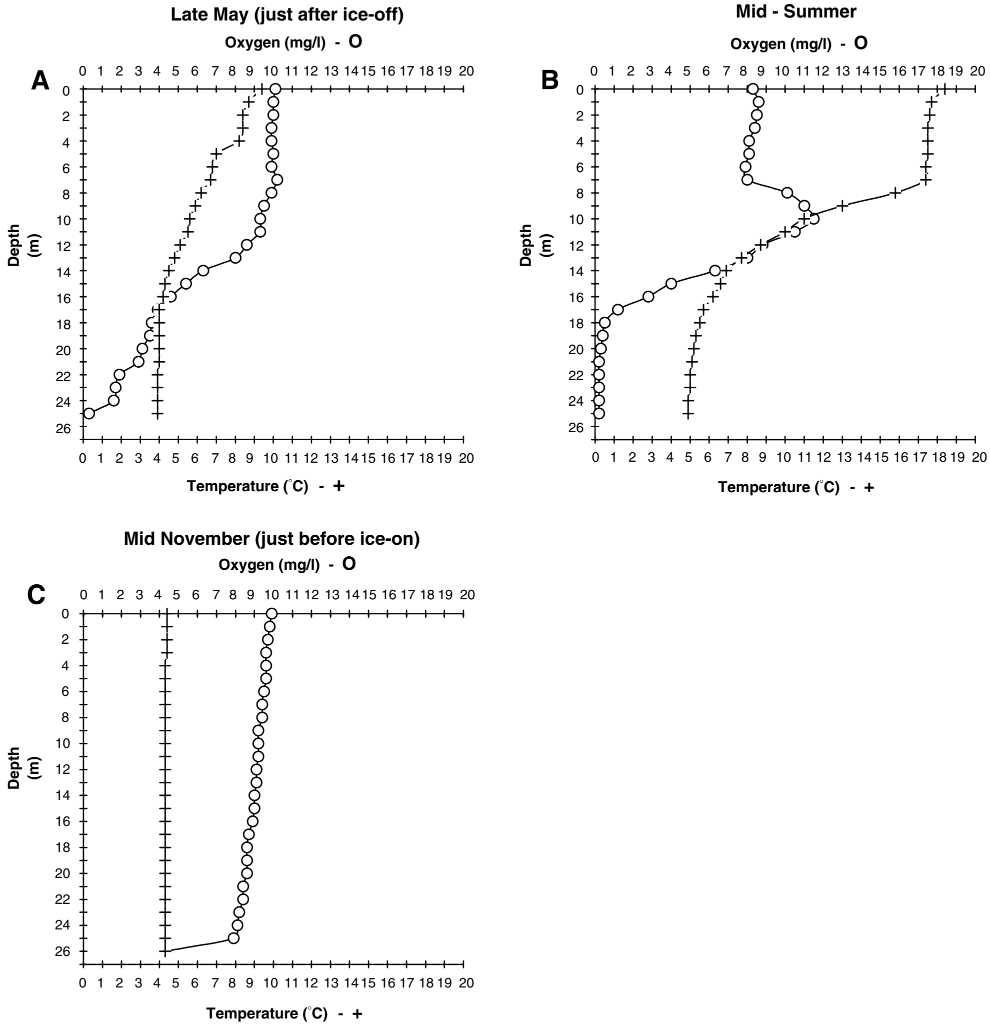

Fig. 3 Representative spring, summer, and fall temperature/oxygen profiles for Dina Lake

sized fish. The 32 and 40 mm nets were set to establish the maximum size of pygmy whitefish in Dina Lake. The maximum length recorded for the pygmy whitefish species is 26 cm (McCart 1965) but in Dina Lake the maximum length is around 13 cm and our two largest meshes failed to catch pygmy whitefish. Later, in an attempt to determine if pygmy whitefish move up in the water column at night, we set four different sized net panels (10, 14, 19, and 25 mm) vertically so they fished from the surface to the bottom. Then in 2001, to further determine if there was an upward movement at night, we also fished horizontally set gillnets suspended at different depths above the bottom. For all gillnet sets we recorded the catch, the duration of the set, and position of each fish in the net-panel.

In addition, to detect any onshore–offshore movements, we fished a 19 mm gillnet perpendicular to the shore in shallow water (1.5–4.1 m). This shore net was set three times in October 2000 and four times in 2001. Each sample trip contained at least one 24 h net set. One additional net was set but was only fished for a short time and is not included in our analysis. Temperature recorders (Stowaways), programmed to record every 2 h, were placed at each end of the inshore net.

Trap nets were our only successful live capture method. These nets were 4.1 m long (0.9 by 0.9 m at the mouth) with 6.1 m side wings and a 30.5 m centre wing. The mesh size was 3.1 mm. The trap nets were set on the bottom at a number of depths and fished for 24 h. Because of time constraints, the trap nets were checked only once a day. Consequently, although they sometimes caught large numbers of pygmy whitefish, the trap nets provided little information on diel movements.

Data analyses

Since we had no prior information on the abundance or spatial distribution of pygmy whitefish in Dina Lake, our gillnet sites were scattered throughout the north basin. For analysis, we pooled the 2000 and 2001 data but grouped the sets by time (day vs. night), type of set (benthic vs. pelagic), and, when fish were caught, recorded their distance above the bottom. Although the thermocline descended during the summer, its top was never more than 7 m deep and its bottom was stable at about 14 m. Consequently, fish caught above 7 m were assumed to be in the epilimnion and fish taken at, or below, 14 m were assumed to be in the hypolimnion.

Because catch frequencies were contagiously distributed (the variances were much greater than the mean catches), we compared the fish capture/hour during day versus night using: (1) a Mann–Whitney U-test for all gillnet sets, and (2) a Sign test for those sets which sampled both day and night periods. The null hypothesis was no difference between groups. We did not include catches from the suspended gillnets and trap nets in the analysis because they are not comparable to the rest of the gillnet sets; however, information from the suspended and trap nets are included in the discussion while the shore net data are analyzed separately.

Results

Over the two summers (2000 and 2001), the only gear types that caught, or detected pygmy whitefish were gillnets and trap nets. Consequently, only data obtained by these methods are reported below.

Gillnets

A total of 88 gillnet sets were made over two summers—41 horizontal bottom sets, 35 vertical (surface to bottom) sets, 8 shoreline sets, 3 suspended horizontal sets, and 1 surface floating net. Combined the gillnet sets (a total of 1,265 h) caught 742 pygmy whitefish, of which 90 were caught during the day, and 652 caught during the night. Two-thirds of this sampling effort (842 h) occurred during the day. The 14 and 19 mm nets caught juveniles and adults; whereas, the 25 mm mesh caught only adults (mostly females) and the 10 mm mesh caught only young-of-the-year (Table 1).

With the exception of the shore net, all the pygmy whitefish caught in gillnets were taken deeper than 7 m from the surface. Below the epilimnion, catches varied from zero to 174 fish. These catch data are highly skewed (the variance of 489.7 is about 60 times greater than the arithmetic mean of 8.4). Most sets (53%) caught no whitefish (Fig. 4) and, of the nets that caught fish, 10% of the sets caught 70% of the total fish.

Fish also appeared to move more at night than during the day. Our mean catch rate during the day was 0.1 fish per hour, whereas, the night catches were 1.5 fish per hour. The Mann–Whitney U-test showed a significant difference between day (n_1 = 85, R_1 = 4,624.5) and night (n_2 = 46,

Table 1 Fish fork lengths (mm) captured by each size of gillnet in 2000 and 2001

Net size (mm)	2000 Samples				2001 Samples			
	Sample number	Min.	Mean	Max.	Sample number	Min.	Mean	Max.
10	–	–	–	–	8	52	55	59
14	114	62	82	118	8	65	76	109
19	79	92	103	122	149	70	101	120
25	116	101	117	130	75	92	114	132

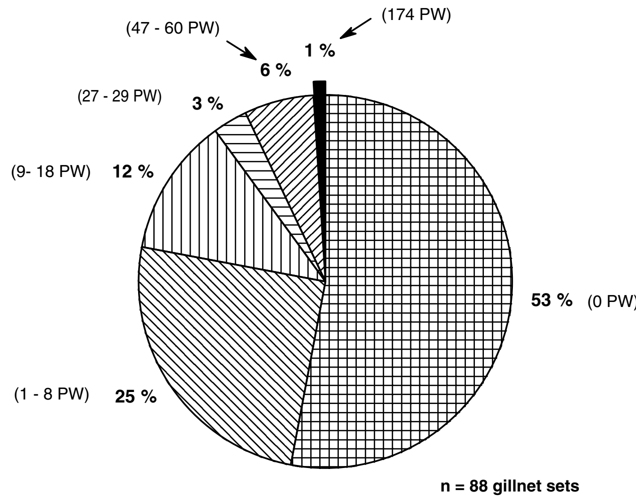

Fig. 4 Gillnet frequency distribution results. Eighty-eight gillnet sets captured 742 pygmy whitefish (PW). The range in numbers of fish captured per individual net set are shown in parenthesis. The most common capture result was zero fish

R_2 = 4,021.5) catches (U = 969.5; Z = −4.75, $P \ll 0.01$). The Sign test on paired catch rates also showed differences between day and night catches. Every catch per unit effort at night was larger than its paired day catch per unit effort (non-ties = 28, Z = 5.1, $P < 0.00$).

Bottom nets

Initially, it was thought that pygmy whitefish generally inhabit the deeper part of lakes. Without knowing where pygmy whitefish inhabit Dina Lake, we felt this was a good starting point as fishing in this deeper zone of the lake would also lessen the bi-catch and unnecessary harming of other fish species within the lake. Our horizontal bottom gillnets fished a wide variety of depths (ranging from 4.5 to 26.0 m). Sampling effort averaged 8.7 h per net set. Pygmy whitefish catches varied from as little as 1 fish at a time to as many as 60 fish in a single set. All bottom netting effort mainly focused in both the thermocline and hypolimnion. Clearly, night time sets were more successful (quantity) but day time captures were not rare. No specific depth was more successful in either day or night. Catches ranged from 8.0 to 26.0 m, even when oxygen levels were suspect (2.6 mg l^{-1}) at the deeper locations. In addition, no differences in catch was detected by season as we obtained our sample quota (minimum of 30 fish) during each individual sample trip.

Vertical nets

In an attempt to determine if pygmy whitefish inhabit the pelagic zone of the lake, we set some vertical gillnets. These nets fished the entire water column (from the surface to 15 m deep). Overall, the 33 vertical nets showed little evidence of upward movement—one fish was caught as much as 7 m from the bottom but 134 of the 136 fish caught in vertical nets were captured within 4 m of the bottom (Fig. 5). While samples were obtained in the vertical nets during each month, July produced the highest concentration of fish (n = 104). This large quantity does not correspond with the species fall spawning migration. Some other factor must be involved with this peak capture during the summer. Results from these vertically set nets do confirm our findings in the horizontally bottom net sets.

Shore nets

Usually, lacustrine pygmy whitefish are characterized as a deep-water species. In order to determine if the shoreline habitat was utilized at some point in time throughout the ice free season, we used a shore net to fish in the epilimnion. The shore net was set perpendicular to the shoreline for a 24-h period and was checked regularly. The small net (19 mm) fished for a total of 132 h, of which 97 h were in the day and 35 h were at night. The total catch was 104 pygmy whitefish. Of

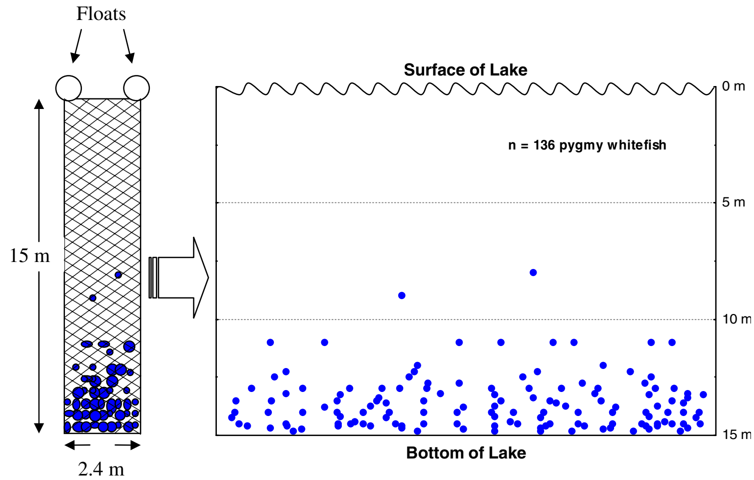

Fig. 5 Representation of the pygmy whitefish capture locations in the vertical net sets. When combined, 33 sets captured 136 fish. Approximately 99% of all fish captured in these nets were within 4 m of the bottom indicating the pelagic zone of the lake is rarely utilized

these, only one fish was caught during the day and 103 were caught at night.

Initially (October 2000), it was not clear if this movement to the littoral zone was a foraging or a reproductive migration. Consequently, during all of our sampling trips in the second year (2001), we set and obtained pygmy whitefish in the shore net. October provided the largest catch with 57 individuals obtained. Usually, the temperature recorders showed similar (0.5°C or less) water temperatures at both ends of the shore net and temperature may not be a factor once in the epilimnion on depth distribution. Regardless of which season obtained the most fish, the shore net clearly established that pygmy whitefish move onshore at night and offshore during the day.

Suspended nets

We also suspended three nets at various depths throughout the water column (Fig. 6). The vertical net sets provided very little evidence of upward movement and we suspended these nets in a final attempt in October 2001 to understand if pygmy whitefish migrate off the bottom and into more pelagic waters. A 19 mm gillnet (2.4 m deep) was set horizontally and suspended in the water column at three depths: 0, 5, and 10 m from the surface. Three separate days were used to fish each selected depth. The surface net set (#1) captured no fish during either the day or overnight. The net set in the middle of the water column (#2) captured no fish during the day but

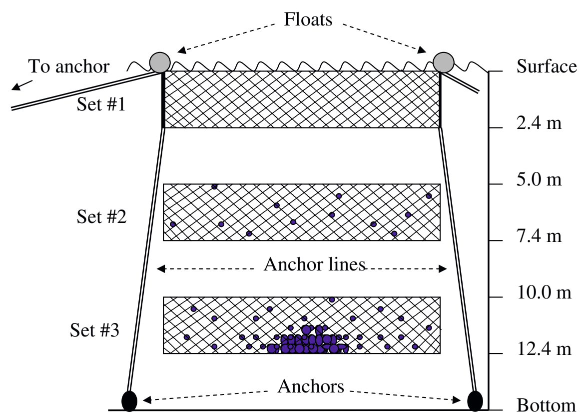

Fig. 6 Representation of the pygmy whitefish capture locations in the three suspended horizontal net sets. Illustration shows only net set #1 with anchor lines used to prevent the net from collapsing in on itself. Net set #2 and #3 also contained similar anchor lines. Together these data argue that, although some pygmy whitefish probably move as individuals, others appear to move in large aggregations, especially near the bottom

captured 12 pygmy whitefish overnight. One fish was observed as much as 10 m above the bottom. These fish were equally scattered throughout the net. The net set nearest to, but not on the bottom (#3), captured no fish during the day but 174 pygmy whitefish over night. Most of these (85%) were 0.5 m from the lead line, or about 2.5–3.0 m off the bottom. This catch was also concentrated near the middle of the net (very few were located at the ends of the net). These findings indicate that after dark, some pygmy whitefish aggregate near the bottom and move around the lake.

Trap nets

Our horizontal bottom gillnets proved to be a successful capture technique during the 2000 sample year for pygmy whitefish. Consequently, we used trap nets set on the bottom overnight the following year as a live capture technique to look for YOY sized fish and to understand if pygmy whitefish ‘‘school’’. We primarily experimented in the epilimnion and thermocline, up to 15 m deep, during August and October. Little effort was put forth in the hypolimnion as there was too far of a risk of setting them in an anoxic zone (Fig. 3B) and we already verified their presence in this zone. We presume pygmy whitefish can tolerate low oxygen conditions, at least for a short period of time, but did not want to keep them trapped for a longer period of time (e.g., overnight). Except for one set at 7.3 m, no specific depth proved to be more successful as catches ranged from as shallow as 1.75 m to as deep as 10.0 m at the mouth.

The trap nets were only set in 2001. Unlike the gillnets, the trap net catches also contained YOY as well as juveniles and adults. These net catches were variable: 20 sets fished for a total of 651 h and caught about 2,214 fish. Typically, our trap nets caught relatively small numbers of fish; however, occasionally we caught unusually large numbers in a single net. Again, the catch distribution is highly skewed with zero the most common catch (45%). Even deleting a set that caught over 2,000 fish, the variance is still greater than the arithmetic mean (mean = 7.8; variance = 153.7). This large capture (~2,065) was obtained in August near the separation point between the North and South Basins in 7.3 m of water. While it is unknown what time of day these fish entered the trap, it appears based on the orientation of the trap that these fish were migrating from the deeper part of the north basin up into the shallows.

Discussion

Relatively little is known about the habitat use or environmental tolerances of pygmy whitefish. Over most of their geographic distribution they are assumed to be glacial relicts inhabiting deep, cold lakes. Certainly, east of the Continental Divide, and at the northern edge of their range (Alaska), they are often associated with large, oligitrophic lakes (e.g., Lake Superior, Lake Athabasca, Great Bear Lake, and Illiamna, Chignik, Naknek, and Aleknegick lakes). In the Rocky Mountain region, however, they also occur in smaller lakes and glacier-fed rivers. In Idaho, inter-mountain Montana, and Washington, they are associated with either glaciated areas or the southern margins of glaciation. In southern British Columbia, they also occur in large lakes (e.g., Kootenay and Okanagan lakes) and glacial rivers; however, in central and northern B.C. pygmy whitefish are found in a wide size range of lakes and rivers. This pattern of habitation is consistent with the hypothesis that, in the centre of their North American distribution, pygmy whitefish tolerate a wider range of environmental conditions than at the periphery of their distribution. Nonetheless, in the Williston Watershed, 15 of the 17 lakes known to contain pygmy whitefish are deep, cold lakes while two lakes are almost as shallow as Dina Lake but contain a more diverse fish fauna (including other whitefish species). By local measures, Dina Lake is not a typical pygmy whitefish lake—it is small, relatively shallow, develops a strong thermocline and an anoxic bottom layer during the summer, and it contains no other whitefish species. Yet, in spite of its atypical nature, Dina Lake supports a population of pygmy whitefish.

One of our secondary study goals was to increase the probability of detecting pygmy whitefish during brief fly-in surveys. Gillnets proved to be a successful capture technique for this goal. However, given the unusual environment (at least for pygmy whitefish), caution should be used when extrapolating our spatio-temporal findings in Dina Lake to sampling programs in cold, deep lakes. Still, the Dina Lake netting program provides useful information on the environmental tolerances of pygmy whitefish.

During two summers, gillnet sets caught 638 pygmy whitefish from below the epilimnion. In the limnetic zone of the lake, we only captured 104 pygmy whitefish. The temperature in this shallow zone ranged from 12°C (early June) to almost 18°C (late August) and, during the day, we caught only one pygmy whitefish above the thermocline. This finding is consistent with the notion that pygmy whitefish are a coldwater species. Surprisingly, however, at night throughout the summer our shore net regularly caught pygmy whitefish in shallow water (2.5–4.1 m). The summer temperatures in this inshore littoral area were the same as those in the epilimnion (12–18°C). Temperature probably remains as the ultimate causal factor but proximate factors such as food come into play at night and drive short-term behavior. In addition, our inshore trap nets retained pygmy whitefish in shallow water for almost 24 h and the fish showed no obvious signs of thermal stress. Thus, pygmy whitefish can tolerate temperatures up to 18°C for at least a day and this suggests that something other than temperature is involved in their apparent daytime avoidance of shallow water. For example, Levy (1987) and Neverman and Wurtsbaugh (1994) reported that diel migrations between foraging and digesting habitats result in a net energy gain in fish undertaking these movements because the growth efficiency of the animal is greater at the lower temperatures but feeding rates and feeding efficiency are greater at higher temperatures. According to this differential growth-feeding hypothesis, it is advantageous to feed at the higher temperatures for a short time and digest and grow at the lower temperatures. Although, two-thirds of our gillnet sampling occurred during the day, and we only captured 90 fish. If the netting effort was standardized for both day and night, one would expect to only catch 45 pygmy whitefish during the night. Yet, our night results, with only one-third of our total effort, caught more than 14 times (652) of the expected catch. One possible explanation is that pygmy whitefish see and avoid the nets during the day. However, this is an unlikely explanation for the lack of day time catches in the littoral zone since the monofilament gillnets caught all the other fish species during the day, and we almost never observed pygmy whitefish in the littoral zone during the day.

Since this onshore–offshore movement occurs throughout the summer and fall months, we concluded it is a foraging migration rather than a reproductive migration. The onshore movement was associated with the onset of darkness and, since throughout the summer only one pygmy whitefish was caught inshore with a gillnet during the day, we assume that there is an offshore movement into deeper water at dawn. These fish may move inshore to exploit food items that are unavailable near the bottom in deep water where they spend most of their summer daytime hours.

Another explanation for their movements towards the littoral zone at the onset of darkness is that pygmy whitefish are negatively phototropic (e.g., they avoid lighted areas). Regulation of light as it enters the eye and adaptation to light or dark are accomplished by several means. The relative size of the eye for pygmy whitefish is quite large in comparison to the length of its head which may suggest it is a sight-feeding fish (Bond 1979). Although, the adaptations of the eye to light for pygmy whitefish have yet to be researched. If they are primarily a deep-water species, and in one lake during a 2003 brief fly-in survey (Weissener Lake) we gillnetted pygmy whitefish at 92 m, their vision may be adapted to low light conditions (Breder and Rasquin 1950).

Interestingly, in another deep, cold lake in our catchment (Quentin Lake) we gillnetted pygmy whitefish (also in 2003) at the shoreline during the day; however, Quentin Lake is glacial and has a Secchi disc reading of only 20 cm. Under these turbid conditions pygmy whitefish appear to use inshore areas during the day. This pattern of daytime use of inshore areas in turbid lakes and avoidance of these areas in clear lakes is consistent with the hypothesis that daytime habitat use is governed by responses to light.

Although, with the onset of darkness, pygmy whitefish in Dina Lake move inshore, there is no evidence of a nocturnal upward movement in the water column. Instead, at the onset of darkness, the fish appear to move inshore along the bottom. This explains the observation that more fish are caught in the horizontal than in the vertical nets—the horizontal nets (15 m panels) were set lengthwise on the bottom while the vertical nets fished the entire water column in a 2.4 m swath. Because of this difference in the length of net fishing near the bottom, horizontal nets are more likely than vertical nets to intercept fish moving close to the bottom. Still, of the 136 fish caught by the vertical nets, 134 (about 99%) were captured within 4 m of the bottom. This finding argues that pygmy whitefish rarely move up in the water column during the night.

This propensity of pygmy whitefish to remain close to the bottom in Dina Lake raises questions about their tolerance of low oxygen conditions. In Dina Lake, during the summer, the bottom water in the hypolimnion becomes progressively anoxic. By early June, oxygen concentrations in the upper part of the hypolimnion are <5.0 mg l^{-1} and by late August oxygen concentrations in most of the hypolimnion are <1.0 mg l^{-1}. By October or November there is no detectable oxygen below 18 m (Fig. 3C). Yet, even in the hypolimnion, we caught fish throughout the summer and into the fall. Although the spatial scale of our netting was not fine enough to resolve whether pygmy whitefish actually resided in anoxic water, it seems that they can tolerate lower oxygen concentrations than most whitefish. For example, the lake whitefish, *Coregonus clupeaformis*, appears to seek higher oxygen areas when oxygen concentrations in August deteriorate (below 2.0 mg l^{-1}) in the hypolimnion (Hartman 1973; Kenyon 1978). Davis (1975) reviewed the minimum oxygen requirements for Canadian aquatic organisms (including salmonids) and concluded that prolonged exposure to concentrations below 4.25 mg l^{-1} poses a risk for most species. Nonetheless, in Dina Lake, pygmy whitefish are exposed—at least diurnally—to low (<4.25 mg l^{-1}) oxygen concentrations throughout the summer.

Utilizing the horizontal bottom gillnetting technique on other lakes within the watershed also proved to be very successful in 2004 and 2005. The Dina Lake sampling program unequivocally demonstrated that pygmy whitefish inhabit the bottom of the lake. We tested this technique on Williston Reservoir (Fig. 1) and six other presumed pygmy whitefish lakes during this 2 year time frame. The lakes, ranging in size from 216 to 591 ha, were assessed with respect to their bathymetry and limnology prior to sampling. A gang of three gillnets of various sizes (14, 19, and 25 mm) were set during the summer months (June and July) in the hypolimnion and above the anoxic zone ($\gtrsim$5.0 mg l^{-1}). Initially, 3 or 4 gangs were set during daylight hours and then reset overnight if no fish were obtained throughout the day. If no fish were captured overnight, then the nets were gradually moved to shallower water until pygmy whitefish were obtained. On all surveys, we obtained pygmy whitefish located on the bottom and at various depths (including all three vertical zones) after only a few days of netting. The probability of catching pygmy whitefish during future surveys in remote, unknown lakes based on this specific sampling technique appears to be favorable if they are present.

Finally, based on our data we also suggest that the behavior of pygmy whitefish, rather than their abundance, may contribute to their rarity in faunal surveys. Specifically, our highly skewed catch data are consistent with schooling or aggregating behavior in pygmy whitefish. So far, the evidence is circumstantial; still, the numbers of fish caught by each net set are suggestive. Over two summers, 88 gillnet sets caught 742 pygmy whitefish—47 of the nets (53%) came up empty, 32 nets (37%) caught 18 or less fish, and 9 nets (10%) caught 522 fish (70% of the total catch). The nets that caught large numbers of fish were set at different months and at geographically scattered sites in the northern basin. Also, some of these sites were fished more than once but only made one large catch. This highly skewed catch-pattern (variance much greater than the mean) was repeated for the trap nets. This property of natural populations, to show some degree of aggregation, is commonly thought to be highly specific. For example, Taylor (1961) pointed out that many quadrant counts for insects could be summarized because the variance of the counts was related to the mean (high-density populations had high variances, and low-density populations had low variances). Additionally, on several occasions, over 40 pygmy whitefish were tightly grouped in a small part of a gillnet with no fish elsewhere in the net. Together these data argue that, although some pygmy whitefish probably move as individuals or small aggregations, others appear to move in large aggregations. Consequently, the probability of intercepting a few individuals or a school in a single net set is low even in a relatively small lake containing a large population of pygmy whitefish.

We do not know how long Dina Lake has been isolated from the rest of the upper Peace River system; however, the fish fauna is impoverished (three species and no native salmonines—coregonids are in the salmonid family) relative to nearby lakes. The fishes (e.g., northern pikeminnow, *Ptychocheilus oregonensis*, and redside shiner, *Richardsonius balteatus*) that are absent from Dina Lake are postglacial immigrants from the Columbia River system. Consequently, the isolation of Dina Lake probably occurred before the faunal exchange between the Fraser and Peace rivers (Lindsey 1956). Given long isolation, and the absence of predaceous fishes, selection may have fine-tuned some aspects of the biology of pygmy whitefish to specific conditions in Dina Lake. Our results from Dina Lake should be applied cautiously when designing sampling programs for pygmy whitefish in other lakes until a broader understanding of their biology and behavior has been determined.

Acknowledgments The Peace/Williston Fish and Wildlife Compensation Program supported this study with financial assistance from BC Hydro. Ray Pillipow and, especially Arne Langston helped with the field work. Additional thanks to Cynthia Powell and Ted Zimmerman for reviewing earlier drafts of this manuscript.

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