POPULATION DYNAMICS OF LAKE WHITEFISH IN LAKE PEND OREILLE, IDAHO

By

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ABSTRACT

To evaluate the biological potential of a commercial fishery for lake whitefish in Lake Pend Oreille, I estimated population attributes that regulate production and yield and constrain compensatory responses to exploitation. The length-frequency distribution based on trap netting in autumn 2005 was unimodal with a mean of 448 mm, whereas the length-frequency distribution based on gillnetting in spring 2006 was bimodal with a mean of 390 mm. The sex composition (proportion females) was skewed toward females (0.66; 95% CI = 0.63 – 0.70). The shape parameter of the weight-length equation (β = 3.363) was similar to other unexploited whitefish populations and indicated that whitefish grew plumper as length increased. The instantaneous growth coefficient for whitefish in Lake Pend Oreille (K = 0.12/year) was among the lowest recorded for unexploited whitefish across their range. Maturation occurred at an age (6 years, range = 4–12 years) and length (383 mm, 340–440 mm) that was relatively high for unexploited populations of whitefish. The instantaneous natural mortality rate (M = 0.167) was among the lowest observed among unexploited populations of the species. Population density of adult whitefish was low based on total surface area (1.35 fish/acre; 95% CI = 1.11–1.78 fish/acre), but average based on expected whitefish habitat ≤ 230 feet deep (4.07 fish/acre; 95% CI = 3.35–5.35 fish/acre). Density of immature and adult whitefish over expected whiteifish habitat (11.93 fish/acre; 95% CI = 8.42–17.53 fish/acre) was within the range observed for unexploited populations of the species. Natural mortality was low, growth was slow, and maturity was late for whitefish in Lake Pend Oreille, which indicate a high biological potential for yield to a commercial fishery.

To determine if subpopulations of whitefish were present in Lake Pend Oreille, Idaho, I compared population attributes and movement among putative subpopulations. To enable comparison, the population was divided into five putative subpopulations based on bathymetry and geographical separation. Mean length increased from north (445.3 mm) to south (459.2 mm) and size-structure differed significantly among putative subpopulations. Female proportion increased from north (0.59) to south (0.76). Body condition differed significantly among putative subpopulations and was highest in the south and lowest in the north. Length-at-age differed significantly among putative subpopulations, though the average maximum difference in length-at-age among putative subpopulations ranged from only 13 mm (SD = 5.2 mm) for the first 20 age classes to 19 mm (SD = 7.7 mm) for all age classes combined. Length- and age-at-50% maturity differed significantly among putative subpopulations, and increased from north (367.97 mm; 5.44 yr) to south (395.5 mm; 7.36 yr). Mortality rates did not differ significantly among putative subpopulations. Whitefish tended to be recaptured in the sampling area where they were tagged and overall fidelity was 81%. Recaptured fish tagged in the north, midwest, and mideast areas were predominantly recaptured (96.4%) within these three areas, and recaptures tagged in the mid-south were predominantly recaptured (85.1%) in the mid-south area, which suggests the presence of two discrete spawning subpopulations. Population attributes generally differed most from north to south, but were relativeily similar among north, midwest, and mideast areas, further suggesting the presence of at least two spawning subpopulations.

To provide harvest recommendations for optimizing yield of lake whitefish in Lake Pend Oreille, Idaho, I used a Beverton-Holt yield/recruit model to estimate yield for

each fully recruited whitefish, calculated catch rates of whitefish in trap nets spatially and temporally, and estimated annual yield based on yield/recruit results and an estimate of adult age-structured abundance. Maximum yield/recruit (YPR_{MAX}) was 111.37 g at an instantaneous fishing mortality rate of $F_{MAX} = 3.59$ (annual fishing mortality rate = 63.2%) and t_r = age 6. For $t_r \geq$ age 6, yield/recruit could not be maximized for reasonable values of fishing mortality. Increases in yield/recruit above age 4 were small and yield/recruit was similar for t_r = ages 4–8. Whitefish reached 50% sexual maturity between the ages of 6 and 8 years, and 95% of YPR_{MAX} was at $F = 0.50$ (105.4 g) for t_r = age 6, $F = 0.70$ for t_r = age 7 (105.1 g), and $F = 0.80$ for t_r = age 8 (101.1 g). Catch rate was highest at Sunnyside Bay (CPE = 69.7) in the north (CPE = 34.0) and lowest at Idlewilde Bay (CPE = 0.9) in the south (CPE = 1.8). Catch rate peaked during the weeks of 3 and 17 October, 14 November, and 12 December 2005. Harvesting fish older than age 7 at a fishing mortality rate of $F = 0.5$ would result in a 48.6% total annual mortality rate and an estimated annual yield of 86,512 lbs, similar to the annual commercial lake whitefish harvest from Red Lakes Minnesota (93,136 lbs). I conclude that the whitefish population in Lake Pend Oreille can sustain a commercial fishery if harvest is maintained within sustainable limits.

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Introduction

Knowledge of the dynamics of fish populations is necessary for developing management plans and evaluating management success. Population dynamics, in the context of fisheries management, includes estimation of changes in population composition, numbers, and biomass (Kohler and Hubert 1999). Population dynamics can be divided into two areas having different uses in the management of fisheries. One area, termed population assessment, focuses on quantifying biological attributes and parameters of fish populations and comparing those attributes to other populations or to the same population over time (Kohler and Hubert 1999). Biological attributes and parameter estimates quantified in a population assessment can be used directly or indirectly in fisheries management. For example, fish stocks of recreational and commercial value are typically managed with a goal of maintaining sustainable harvests through regulation of fishing mortality (Hilborn and Walters 2001; Pine et al. 2003). Achieving such a goal requires an accurate assessment of mortality rates (a direct use). The second area of population dynamics, the use of mathematical models in stock assessments, is an indirect application of a biological attribute or parameter estimate in fisheries management (Kohler and Hubert 1999; Hilborn and Walters 2001). Parameters estimated in a population assessment are applied to predictive mathematical models to predict future population trends. Important population attributes for effective fishery management include size and age structure, growth rates, mortality rates (harvest and natural), maturity schedules, sex ratio, and abundance.

Stock Identification

Population parameters, biological attributes, and tagging data have been used in prior studies, in the absence of genetic information, to identify discrete subpopulations of fish (Van Oosten and Deason 1939; Dryer 1962; Casselman et al. 1981; Ihssen et al. 1981; Ebener and Copes 1985; Koziol 1982; Walker 1993; Peck 1994). In such studies, a subpopulation is defined as a group of fish subject to similar rates of growth, mortality, and recruitment that return to the same spawning ground each year (Ebener and Copes 1985). The identification of discrete subpopulations permits management to proceed on a stock-by-stock basis, which is inherently more sustainable than managing for a single lake-wide population when multiple subpopulations exist (Larkin 1977; Walker et al. 1993). Commonly, tagging data, mortality rates, growth rates, weight-length relationships, size and age structures, and maturity data are compared among and between putative spawning subpopulations to identify discrete subpopulations. For example, based on mark-recapture data, differences in year-class abundance and mortality provided evidence that lake whitefish *Coregonus clupeaformis* (hereafter, termed whitefish) from North and Moonlight Bays (NMB) and Big Bay de Noc (BBN) were discrete stocks within Lake Michigan (Ebener and Copes 1985). Similarly, two discrete whitefish stocks were present in the south and north areas of Upper Entry in Michigan waters of Lake Superior, based on differences in age composition and back-calculated length-at-age (Peck 1994).

Unexploited Population Significance

Ricker (1949) described studies of unexploited populations as “prized rarities” in fisheries, because studies of fish populations typically begin only after a fishery has been in operation for many years. Unexploited populations of whitefish are rare, and mostly exist in small remote lakes in northern Canada (Healey 1975; Johnson 1976). Knowledge of size and age structure, growth rates, and other biological attributes of an unexploited population may be used to understand mechanisms of natural regulation in the population (Ricker 1949; Johnson 1972, 1976, 1983); Power 1978; Parker and Johnson 1991; Mills et al. 2004). Furthermore, a mortality rate estimated for an unexploited population can be used as an estimate of natural mortality under conditions of exploitation in the same or similar lakes (Ricker 1949, 1975).

Mechanisms of population regulation acting within unexploited fish populations are debateble within the fisheries community (Ricker 1949; Johnson 1972, 1976, 1983); Power 1978; Parker and Johnson 1991; and Mills et al. 2004). Johnson (1983) proposed that unexploited whitefish, lake trout, and arctic char populations exhibited a climax condition like the predominant tree species in a climax forest, and were therefore in a state of thermodynamic equilibrium with their environment (least energy loss). He hypothesized a complex growth mechanism with a highly sensitive intra-population control on recruitment to explain the long-term stability of northern fish populations (Johnson 1983). This regulatory mechanism accounted for unimodal or bimodal leptokurtic length-frequency distributions, and the prevalence of dome-shaped age structures of unexploited northern lake trout and whitefish populations (after ruling out gear selectivity). A second view, proposed by Power (1978) and supported by Mills et al. (2004), hypothesized that systematic errors in age estimation were responsible for the dome-shaped age structures observed by Johnson (1983). Power (1978) and Mills et al. (2004) argued that when age was estimated accurately, the complex regulatory mechanism involving variable growth rates theorized by Johnson (1976) was not needed. However, Power (1978) and Mills et al. (2004) failed to explain the occurrence of leptokurtic length-frequency distributions observed by Johnson (1976). Power (1978) proposed a model in which growth was relatively rapid until maturity, after which growth slowed through a life span that may exceed 50 years and mortality declined through early life and stabilized at a very low level. This combination of growth and mortality patterns produces a population containing many small, few intermediate, and many large fish.

Fishery Potential

Evaluating the biological potential of fish populations for commercial fishery development requires a detailed understanding of biological attributes that constrain production and yield. According to Healey (1975), such attributes include mortality, growth, age structure, and maturity, and vary greatly within exploited and unexploited populations of whitefish (Healey 1975; Jensen 1981; Jensen 1985; Taylor et al. 1992; Beauchamp et al. 2004; Mills et al. 2004). The scope of compensatory response to exploitation is equivalent to the difference between the observed estimate of the attribute and the theoretical limit of the attribute for a given species (Healey 1975). For example, populations with the greatest fishery potential would be those with low natural mortality and slow growth, because such populations could absorb a high rate of fishing mortality and have ample scope for increased growth to maintain fishable stock biomass (Healey 1975). Unexploited populations that mature at a relatively old age likely will mature at a younger age when exploited, because growth will increase as density declines and fish will therefore reach mature size at a younger age (Taylor et al. 1992; Beauchamp et al. 2004). A population with a low mortality rate and high growth rate would be of limited fishery potential, because population density is low and growth is high, possibly due to limited spawning habitat or very high egg and larval mortality (Healey 1975). Recruitment in such a population would be limited by factors unrelated to fishing, and because of a high growth rate, the population would have little scope for compensation. An unexploited population with the least fishery potential would have both a high natural mortality rate and growth rate, because such a population would have little scope for compensatory response to exploitation in either growth or recruitment.

Unexploited whitefish populations have significant potential for commercial fishery development. Slow growth rates, low rates of natural mortality, high density, age structure with greater than 20 age classes, and old age at maturity typify such populations (Ricker 1947; Healey 1975; Power 1978; Jensen 1981; Mills and Beamish 1980; Mills et al. 2004). Fecundity, growth rate, adult mortality, juvenile mortality, and age at maturity vary widely among whitefish populations (Jensen 1984). The level of harvest mortality that a population can sustain depends on the extent to which life history attributes are able to compensate for exploitation (Jensen 1981). The scope of density-dependent compensatory response to exploitation in growth, recruitment, and the age of sexual maturity for both exploited and unexploited whitefish populations are significant (Healey 1975; Healey 1978; Jensen 1981; Jensen 1984; Mills and Chalanchuk; Taylor et al. 1992; Beauchamp et al. 2004; Mills et al. 2004). The most powerful compensatory mechanisms of whitefish populations to exploitation have been studied through manipulative studies (Mills and Chalanchuk 1988; Mills et al. 2002), observational studies (Miller 1949; Healey 1978; Taylor et al. 1992; Beauchamp et al. 2004), and theoretical modeling (Jensen 1981; Jensen 1982; Jensen 1985). For example, Jensen (1981) reviewed the impacts of fishing on population size, age structure, and reproductive potential, and then used a theoretical modeling approach determined the changes in growth rate, sex ratio, fecundity, age at maturity, and egg and larval survival necessary to compensate (maintain constant recruitment) for different levels of exploitation. Change in fecundity, growth, and sex-ratio alone were not important compensatory mechanisms, while a decrease in age of maturity and an increase in egg and larval survival had the greatest potential for compensation (Jensen 1981).

Whitefish Biology and Significance

The whitefish is an ecologically and economically important freshwater fish species throughout its range, which extends from Newfoundland (introduced) through Nova Scotia, New Brunswick, New York, Quebec, Ontario, and northwest to Alaska (Lawler 1965). The southernmost occurrence of the whitefish is in Lake Erie. Whitefish are ecologically important because they comprise a substantial portion of total fish biomass throughout most of their range and are key components of benthic food webs (Johnson 1973, 1976; Nalepa et al. 2005). In arctic lakes, whitefish and lake trout together often account for 95% of total fish biomass (Johnson 1976; Power 1978). Larval and juvenile whitefish are largely planktivorous, whereas adults are primarily benthivorous and consume large numbers of aquatic insect larvae, amphipods, mollusks, and other invertebrates (Van Oosten and Deason 1939; Kennedy 1949; Bidgood 1973). For example, in Lake Champlain, invertebrates made up 99.1% of the diet and small mollusks made up 92.8% of all whitefish stomach contents (Van Oosten and Deason 1939). The whitefish is a terminal predator in benthic food chains and will eventually reach a size that is free from predation (Johnson 1976). In addition, whitefish consume fish eggs and small fishes (Van Oosten and Deason 1939; Bidgood 1973). Whitefish eggs were eaten by whitefish from October to January in Pigeon Lake, Minnesota, in contrast to most other diet studies that have not observed cannabilism (Bidgood 1973). Whitefish eggs, larvae, and juveniles are eaten by lake trout, northern pike, burbot, walleye, and other species (Carl and McGuiness 2006).

Ecologically, the whitefish is a cool-water species, restricted to freshwater in the south but found in marine and brackish waters in the north (Lawler 1965). From October through December, depending on water temperature, whitefish move from deeper water to littoral areas to broadcast their eggs in depths ranging 2–4.5 m over sand, gravel, flat stone, cobble, and boulder (Dumont and Fortin 1978; Fudge and Bodaly 1984; Nester and Poe 1984; Anras et al. 1999). Whitefish spawn at water temperatures of 40–50 F in Lake Ontario, and the peak of spawning occurred during 19–25 October at a water temperature of 43 F in Heming Lake, Manitoba (Lawler 1965). Similarly, peak spawning activity of whitefish occurred at temperatures of 36–43 F for 5–6 days during the 15-day spawning period that began in late October in Lake 226 of the Experimental Lakes Area, Canada (Begout Anras et al. 1999). In Lake Michigan, whitefish spawn during November and early December, where they concentrate in shallow water shallower than 5 m over stony or gravel substrate (Freeburg et al. 1990).

Historically, whitefish supported one of the most economically valuable freshwater fisheries in North America (Mills et al. 2004). The largest, most valuable fisheries for whitefish are still found in the Great Lakes. The whitefish is currently the most valuable commercial fish species in lakes Michigan, Huron, Ontario, and Superior, and in 2005, commercial harvest of whitefish in these four lakes was 8.5-million pounds valued at US$6.8-million (NMFS). In 2004, harvest of whitefish in Canada was 8.5-million pounds valued at CAN$10.8-million (Fisheries and Oceans Canada). Numerous smaller commercial whitefish fisheries occur in Canadian lakes.

Objectives

My first objective is to evaluate the biological potential for a commercial whitefish fishery in Lake Pend Oreille by estimating population parameters and vital statistics that regulate production and yield and constrain compensatory responses to exploitation. In chapter one, I estimate size structure, age structure, body condition, growth, age and size at maturity, total annual mortality, density, and biomass. I then infer the compensatory scope of the population to exploitation by comparing population parameters and vital statistics of whitefish in Lake Pend Oreille to unexploited and exploited populations throughout the species' range. I expect to find that the whiteifish population in Lake Pend Oreille exhibits signs of density-dependent population regulation typical of unexploited populations, including slow growth, old age and large size at maturity, poor body condition, low mortality, and high density (both numbers and biomass), which would indicate a substantial potential to compensate for exploitation.

My second objective is to determine if multiple discrete whitefish spawning subpopulations exist in Lake Pend Oreille. If multiple subpopulations of whitefish are found to exist, management may proceed to manage individual stocks, which has been found to improve fishery sustainability and optimize yield (Larkin, 1977; Walker et al. 1993). In chapter two, I compare biological attributes and parameters estimated as part of my first objective among putative spawning stocks within Lake Pend Oreille, and evaluate mark-recapture movement data of whitefish sampled prior to and during the spawning period. If biological statistics differ significantly and meaningfully among putative spawning stocks within the lake, then I will conclude that the whitefish population is segregated into multiple discrete spawning stocks in Lake Pend Oreille, and my findings may provide insight into approximate geographic regions of discrete stocks. Mark-recapture data will be used to assess movement of marked fish between sites of tagging and recapture. If fish disperse randomly throughout the lake after marking, I would expect to observe a random distribution of recaptures relative to location of tagging. Deviation from a random distribution of tag returns relative to tagging location will measure the strength of fidelity to a particular spawning location and will be useful for confirming or refuting subpopulation identification based on differences in biological attributes.

My third objective is to provide harvest recommendations that would optimize the commercial yield of whitefish in Lake Pend Oreille. In chapter three, I use growth and mortality rates estimated as part of my first objective in a Beverton-Holt yield-per-recruit model to estimate the fishery yield for each fully recruited whitefish in Lake Pend Oreille. Yield-per-recruit results will be useful for identifying mortality rates and ages at harvest that would maximize yield of whitefish in Lake Pend Oreille, if a commercial fishery were implemented for the species. I then evaluate catch-per-effort statistics to reveal locations and areas of highest relative whitefish abundance. Finally, I evaluate the potential ecological impacts of harvesting whitefish from Lake Pend Oreille.

Chapter 1:

Biological Potential of a Fishery for Lake Whitefish in Lake Pend Oreille

Abstract – To evaluate the biological potential of a commercial fishery for lake whitefish in Lake Pend Oreille, I estimated population attributes that regulate production and yield and constrain compensatory responses to exploitation. The length-frequency distribution based on trap netting in autumn 2005 was unimodal with a mean of 448 mm, whereas the length-frequency distribution based on gillnetting in spring 2006 was bimodal with a mean of 390 mm. The sex composition (proportion females) was skewed toward females (0.66; 95% CI = 0.63 – 0.70). The shape parameter of the weight-length equation ($\beta = 3.363$) was similar to other unexploited whitefish populations and indicated that whitefish grew plumper as length increased. The instantaneous growth coefficient for whitefish in Lake Pend Oreille ($K = 0.12$/year) was among the lowest recorded for unexploited whitefish across their range. Maturation occurred at an age (6 years, range = 4–12 years) and length (383 mm, 340–440 mm) that was relatively high for unexploited populations of whitefish. The instantaneous natural mortality rate ($M = 0.167$) was among the lowest observed among unexploited populations of the species. Population density of adult whitefish was low based on total surface area (1.35 fish/acre; 95% CI = 1.11–1.78 fish/acre), but average based on expected whitefish habitat ≤ 230 feet deep (4.07 fish/acre; 95% CI = 3.35–5.35 fish/acre). Density of immature and adult whitefish over expected whiteifish habitat (11.93 fish/acre; 95% CI = 8.42–17.53 fish/acre) was within the range observed for unexploited populations of the species. Natural mortality was low, growth was slow, and maturity was late for whitefish in Lake Pend Oreille, which indicate a high biological potential for yield to a commercial fishery.

Introduction

Population assessments are used in fisheries management to provide biological information on a population necessary for management (Kohler and Hubert 1999). Such information may include size and age structure, body condition, fishing and natural mortality rates, growth rate, age and size at maturity, and abundance. For an unstudied population of fish, population assessments provide initial biological information and estimates of life history parameters that are necessary to evaluate the populations' recreational or commercial fishery potential (Healey 1975; Bruce 1984).

Unexploited populations of fish of recreational or commercial value are rare and are therefore of great scientific and management importance (Ricker 1947). Typically, the study of a fish population begins only after a fishery has been in operation for a number of years, which results in a lost opportunity to study the population in its primitive state (Ricker 1947). The primitive (unexploited) state of a population provides a research opportunity to explore mechanisms of population regulation without the confounding influences of harvest mortality (Ricker 1947; Healey 1975; Johnson 1972, 1972; Power 1978). In addition, baseline biological data collected during population assessment of an unexploited fish population may be compared to data collected during exploitation to help understand how exploitation affects population dynamics. Further, the rate of natural mortality estimated from the primitive state of the population may be used as an estimate of natural mortality rate under exploitation (Ricker 1947).

My first objective was to evaluate the biological potential of a commercial fishery for lake whitefish *Coregonus clupeaformis* (hereafter, termed whitefish) in Lake Pend Oreille by quantifing population parameters and vital statistics that regulate production and yield and constrain compensatory responses to exploitation. To quantify biological attributes, trap nets similar to those used by commercial fishermen in the Great Lakes were fished throughout the lake from early October to mid-December 2005 to sample whitefish from Lake Pend Oreille for collection of biological data and to facilitate a mark-recapture population estimate. Gill nets were fished from mid-February to early April 2006 to complete the single-census population estimate. Biological attributes were compared between genders, and if significantly different, biological attributes were estimated for each gender. I then compared biological attributes of the whitefish population in Lake Pend Oreille to exploited and unexploited populations of whitefish elsewhere and to biological criteria for evaluating whitefish commercial fishery potential estabilished by Healey 1975, to evaluate the potential responses and compensatory scope of the population to commercial harvest.

Methods

Study Area

Lake Pend Oreille, a temperate, oligotrophic lake located in the northern panhandle of Idaho, is the state's largest natural lake with 85,960 surface acres and a shoreline length of 111 miles. The lake basin is deep and steep-sided with a maximum depth of 351 m and a mean depth of 164 m. The lake is in the Pend Oreille drainage basin. The Clark Fork River is the largest tributary to the lake and the outflow from the lake forms the Pend Oreille River, which flows into the Upper Columbia River. Thermal stratification occurs from late June to September. Operation of the Albeni Falls Dam on the Pend Oreille River keeps the lake level high and stable at 628.7 m during summer (June–September), followed by reduced lake levels of 625.1–626.4 m during fall and winter (Maiolie et al. 2002). Lake Pend Oreille is a temperate, oligotrophic lake. Summer water temperature (May–October) averages about 9 C in the upper 45 m (Rieman 1977; Bowles et al. 1987, 1988, 1989). Surface temperatures are as high as 24 C in hot summers. Thermal stratification occurs from late June to September, and the thermocline typically lies between 10 and 24 m. Littoral areas are limited and mostly characterized by having a steep bottom slope, although some littoral areas have gradually or moderately sloping bottoms (mostly in the northern end of lake and in bays). Most fish habitat occurs in the pelagic area of the lake.

The fish assemblage in Lake Pend Oreille is composed of a mix of native and exotic species. Native fish species include bull trout *Salvelinus confluentus*, westslope cutthroat trout *Oncorhynchus clarkia lewisi*, mountain whitefish *Prosopium williamsoni*, pygmy whitefish *Prosopium coulterii*, five cyprinids, two castastomids, and one sculpin. Historically, bull trout and northern pikeminnow *Ptychocheilus oregonensis* were the top native predators in Lake Pend Oreille (Hoelscher 1992). Non-native fish species include kokanee salmon *Oncorhynchus nerka*, Gerrard-strain rainbow trout *Oncorhynchus mykiss*, lake trout *Salvelinus namaycush*, and several other cold-, cool-, and warm-water species in low numbers including northern pike *Esox lucius*, brown trout *Salmo trutta*, cutthroat trout, smallmouth bass *Micropterus dolomieu*, largemouth bass *Micropterus salmoides*, and walleye *Sander vitreus* (Maiolie et al. 2002). Kokanee colonized the lake from Flathead Lake, Montana, during the winter flood of 1933, and became abundant by the 1940s. Presently, kokanee are the principal prey of rainbow trout, lake trout, and bull trout (Vidergar 2000). Northern pikeminnow use kokanee for about half of their total consumed food items (Vidergar 2000). The Gerrard-strain rainbow trout was introduced from Kootenay Lake, British Columbia in 1941–1942 and has supported a trophy fishery ever since. The lake trout was introduced into Lake Pend Oreille by the U.S. Fish Commission in 1925, but the population only recently began to increase in abundance, for reasons that remain unclear (Hansen et al. 2007). The opossum shrimp *Mysis relicta* was introduced in the mid 1960s to increase the food supply for kokanee salmon and was well established by the mid-1970s.

A virtually unexploited population of whitefish resides within Lake Pend Oreille. This population was introduced in 1889 by the U.S. Fish Commission (IDFG Fishery Management Plan). Presently, no commercial fishery exists for whitefish on Lake Pend Oreille and the sustainability of such a fishery is unknown. In addition, despite the predominance of whitefish in the fish assemblage of Lake Pend Oreille, little is known about whitefish population dynamics. The role whitefish play in the ecology of Lake Pend Oreille is unknown, but may be significant. Therefore, a study of basic population characteristics of whitefish is needed in Lake Pend Oreille. Such information is vital for effective management of fishery resources in Lake Pend Oreille, and will be useful for understanding the ecological role of whitefish in other aquatic systems of Idaho and the Western United States. Such information is also essential for modeling population dynamics of whitefish in Lake Pend Oreille under prospective management actions.

Field Sampling and Laboratory Analysis

During autumn 2005, trap nets were used to sample whitefish for estimating abundance and movement by means of a mark-recapture study, and to obtain biological data from a length-stratified sub-sample of the population. Up to nine trap nets were fished simultaneously (Figure 1). The lake trout was the target species for the mark-recapture study, so trap nets were fished in areas that yielded the largest number of adult lake trout. Some nets were moved during the course of field sampling to increase catches of lake trout. In 2005, most trap nets were soaked between lifts for three or seven nights, with some nets soaked for up to 16 nights (Figure 2).

The target population for my study included all whitefish present in Lake Pend Oreille. A sample was treated as a net catch of whitefish from a particular sampling location in Lake Pend Oreille on a particular date. The target population may have included discrete sub-populations, so the population may have been a meta-population of multiple subpopulations. The number of sub-populations was unknown, but was likely fewer than the number of net locations, so net locations were arbitrarily aggregated into five sample areas for initial consideration as "stock" areas for determining the number of sub-samples to be collected (Table 1). Stock areas were therefore defined as North (Sunrise Bay and Sunnyside Bay), Mid-West (Warren Island and Pearl Island), Mid-East (Thompson Point and Sheepherder Point), Mid-South (Garfield Bay and Whiskey Bay), and South (Idlewilde Bay and Cape Horn).

A sub-sample was defined to include all whitefish from a sample area that were collected for biological data. A stratified sub-sampling approach for determining age composition of the population was used (Ketchen 1949). The practice of sampling a population of individual fish, grouping the fish into length-groups, and then selecting a random sample from each group is formally termed double sampling for stratification (Bettoli and Miranda 2001**)**. Two different methods of double sampling are commonly used for stratification. The first method sub-samples a fixed number of fish from each length-group (fixed-age sub-sampling) and the second method sub-samples in proportion to the number of fish in each length-group (random-age sub-sampling). Random-age sub-sampling is statistically more valid and yields more representative results than fixed-age sub-sampling Kimura (1977), but age proportions in the smallest and largest length-groups are often poorly estimated (Ketchen 1949). Fixed-age sub-sampling ensures over-sampling of the smallest and largest length-groups, each of which likely will contain several age classes, and therefore ensures that younger and older (rarer) fish are adequately represented in the sub-sample (Bettoli and Miranda 2001). Fixed-age sub-sampling is logistically simpler to conduct in the field, so was used in this study.

All fish captured were measured in total length and the first five fish captured in each 10-mm length class were sub-sampled for measurement of weight, collection of age-estimation tissues (scales and otoliths), and determination of gender, maturity status, and stage of maturity. For length classes with five or fewer fish, all biological attributes were measured, collected, or determined, whereas for length classes with more than five fish, all biological attributes were recorded only for the first five randomly-selected fish in each 10-mm length class. Total length was measured to the nearest mm, wet-weight was measured to the nearest gram, and 10–20 scales were removed from each fish from below the anterior region of the dorsal fin above the lateral line and then placed in an envelope labeled with a unique identification number, capture date, and net location. Scales were scraped free of excess slime prior to storage in envelopes. Sagittal otoliths were extracted from the fish by laying the fish on its side and cutting back the gill arches to expose the spine. The spine was then cut and cracked open by bending the head back while holding the body still to expose the otoliths. Sagittal otoliths were removed with forceps and cleaned of membrane and fluids prior to being placed into a labeled scale envelope. Gender was determined by direct inspection of the gonads. If gender could not be determined, the fish was classified as unknown gender.

Fish maturity status was classified as mature, immature, or resting. Mature male whitefish had testes that contained at least some milt upon dissection, or gave the appearance that milt was about to form by being developed in thickness and length and mostly white in coloration. Mature female whitefish had ovaries filled with eggs that were medium to large in size, opaque or clear orange, and extended from one-half to two-thirds of the distance from the anterior portion of the body cavity to the vent. Female whitefish that were not obviously mature or immature based on these attributes were subjectively classified based on whether a given female whitefish was capable of completing the maturation process between the time of capture and the end of the spawning season (mid-late December). Photographs of such fish and descriptions of their ovaries were recorded. Female whitefish in a resting state had ovaries that were fully developed in a continuous strand of tissue exceeding half of the body cavity length, but occupied only half of the body cavity volume, because eggs were small and not fully developed. Male whitefish in a resting state were nearly impossible to discern from mature, spent males. Misclassified fish were likely labeled as immature. Mature fish were classified as green if their gonads were mature but sexual products did not expel from the vent under gentle abdominal pressure, ripe if their gonads were mature and sexual products expelled readily from the vent under gentle abdominal pressure, or spent if their gonads were mature but sexual products did not expel from the vent under gentle abdominal pressure because sexual products were mostly expended.

All fish in good condition (active, submerged, and uninjured) and not killed for sub-sampling were double-marked by insertion of a uniquely numbered Floy T-bar anchor tag as the primary mark and adipose fin removal as the secondary mark**.** Double marking was used to estimate tag loss. The adipose fin was chosen for removal because it is the least harmful fin to remove on a fish (Murphy and Willis 1996). Tags were inserted into the muscle tissue that lies below the anterior-central region of the dorsal fin, and then rotated 90 degrees while withdrawing the tagging gun to secure the tag between the bones supporting the fin rays**.** Tagging guns and needles were cleaned between sampling days to lessen the risk of spreading pathogens among tagged fish. Tagged fish were released at the site of capture. Substantial numbers of whitefish were not in suitable condition for tagging (primarily, distended gas bladders). For these fish, lengths were recorded and they were then either sub-sampled, or submerged and released into the lake. Tag numbers and lengths of previously-tagged or fin-clipped fish caught during the marking period were recorded, along with the date and location of capture. Substantial numbers of whitefish that had been tagged prior to 2005 were recaptured, and for these fish, tag numbers and total lengths were recorded, and each fish was then considered a newly tagged fish. Recaptured fish therefore included fish that were tagged during the 2005 marking period and the 2003–2004 marking periods. Tagged fish caught during the study period were released at the location of recapture if they were submerged, active, and uninjured. Recaptured fish that were dead, floating, or injured were kept for additional biological data and their tag numbers were recorded.

The original tagging protocol anticipated marking and releasing 25,000 whitefish, based on available funding and a need to obtain a precise estimate of abundance. I reasoned that Lake Pend Oreille may contain as many as 238,833 whitefish based on: (1) a mark-recapture estimate of 6,376 lake trout in 2003; (2) a ratio of 41,204 whitefish to 1,100 lake trout caught in 2003; and (3) an assumption that lake trout and whitefish were equally vulnerable to capture in trap nets (equal catchability). Given this initial estimate of population abundance, I selected a combination of numbers of fish to be tagged and numbers of fish to be examined for recaptures that would produce an abundance estimate with a specified level of precision. Because the recapture method (gill nets) was less likely to yield as large a sample as the marking method (trap nets), a range of numbers of fish to be checked for marks was examined (250–1,000). If the true abundance of whitefish was 250,000 fish and 25,000 fish were marked, then examining 1,000 fish would produce an estimate with a coefficient of variation (CV) of ± 9.5% of the estimate. A 10% marking rate generally leads to estimates with relatively high precision (Seber 1982). Declining numbers of fish examined for marks would result in progressively less precise estimates of abundance. A CV of ± 25% is often considered adequate for management purposes (Robson and Regier 1964).

Beginning on 12 February 2006, gill nets were fished to provide a random sample of the proportion of marked fish in the population to overcome the potential weakness of trap nets that were fished in a limited number of non-randomly selected locations. Gill nets could be set in areas unsuitable for trap nets, thereby sampling the entire area occupied by whitefish in Lake Pend Oreille. Further, gill nets were fished in a season (spring) when mature and immature whitefish were intermingled, which enabled the capture of whitefish too small to be caught during trap netting. Gill nets were 305-m long, 3-m high, and of multiple panels of different stretch measure (2.0, 2.5, 3.0, 3.5, 4.0, 4.5, and 5.5 inch), which reduced the effect of size selectivity of individual mesh sizes (Ricker 1975). Gill net sampling locations were randomly selected from a 0.5-km grid in the (shallow) northern section of the lake and 0.5-km distances along shore in the deep central and southern sections of the lake. Each net was soaked for one night.

Age was estimated for all sub-sampled fish from scales and otoliths. Otoliths are the preferred structure for estimating age of older fish because otoliths continue to grow and record cyclic seasonal growth and age through periods of reduced or negligible somatic growth, whereas scales of older fish fail to grow or record annuli and may reabsorb or erode (Casselman 1990; Campana and Thorrold 2001; Moritta and Matsuisihi 2001). Otoliths were glued to glass microscope slides with Crystalbond 509 adhesive. After drying for 2 hr, a ~500-µm section was cut from the region containing the nucleus with a low-speed saw and diamond-coated blade. Each slide was heated to the flow temperature of the adhesive and the loosened section was removed and adhered back onto the slide and allowed to dry for 2 hr. The sections were ground and polished using 500–600 grit wet-dry sandpaper to a thickness of ~300 µm, viewed under a dissecting scope with immersion oil, and photographed for back-calculation of growth history. Image Pro Plus software was used to measure annular radii. Scales were cleaned of dried slime and examined under a microfiche projector. Annuli were characterized by a distinct change in the spacing and continuity of circuli in the posterior and lateral portions of the scale that extended through the anterior and lateral fields, and by cutting over of circuli in lateral fields. For each fish, 4–6 clean dry scales were placed between two microscope slides and taped together for age estimation.

To determine the age and length of fish for which scales failed to accrue additional discernable annuli, an age-bias plot was constructed with otolith age on the X-axis and scale age on the Y-axis (Campana et al. 1995). For age-bias plots, I assumed that otoliths provide unbiased estimates of true age (hence, their use on the X-axis), because Mills and Chalanchuk (2004) validated otoliths as estimators of true age for whitefish from unexploited arctic populations. If scales failed to reveal additional discernable annuli above a particular age relative to otoliths, age of fish younger than the cutoff age may be estimated from scales, whereas age of fish older than the cutoff age must be estimated from otoliths. This would ensure that an optimal combination of efficiency and accuracy for age estimation is used for future studies of this population. The average length of fish at the cutoff age will be used to inform fishery managers of which structure to use for age estimation of individual whitefish.

Data Analysis

Size Structure.—Population size structure was estimated with length-frequency histograms and summary statistics of the sample data. Length-frequency histograms were constructed from sample data from 2005 trap netting and 2006 gillnetting. I assumed that the trap-netting sample from autumn 2005 primarily represented the adult spawning portion of the whitefish population, whereas the gillnetting sample from spring 2006 better represented the size-structure of the entire (sub-adult and adult) population. Normality of size-structure was tested using symmetry and kurtosis measures (Zar 1999).

Sex Composition.—The proportion of female whitefish in Lake Pend Oreille was estimated for mature, immature, and all fish combined, and for each week of sampling during fall trap-netting. Whitefish whose gender could not be determined were excluded from the analysis. I calculated 95% confidence intervals for the proportion of females using formulae for exact 95% confidence limits for a binomial proportion (Zar 1999).

Body Condition.—Body condition was estimated using a power function for describing the rate at which weight increases with length:

$$W_i = \alpha L_i^{\beta} e^{\varepsilon_i} .$$

In the power function, W_i = weight of the ith fish, α = condition factor, L_i = length of the ith fish, β = the shape parameter, and ε_i = multiplicative process error. The weight-length relationship was fit from weight-length data of individual fish, so model parameters were estimated for the multiplicative-error model with linear regression on the $\log_{10}$-transformed model:

$$\log_{10}(W_i) = \log_{10}(\alpha) + \beta \log_{10}(L_i) + \varepsilon_i .$$

The multiplicative error model assumes that logarithms of the residuals are equally distributed at all lengths, and that variability in weight is an increasing function of length. This model is appropriate for data on weight and length of individual fish. I examined residual plots to determine if residuals were equally distributed at all lengths.

To determine if body condition differed between male and female whitefish, I compared weight-length relationships between genders using a general linear model (GLM):

$$\log_{10}(W_i) = \log_{10}(\alpha) + \beta \log_{10}(L_i) + b_1 X + b_2 (X * \log_{10}(L_i)) + \varepsilon_i .$$

In the GLM, X = gender (the main effect), $\log_{10}(L_i)$ = the base-10 logarithm of the length of the ith fish, and other terms are as defined for the power function. I tested for homogeneity of slopes between genders using the interaction between the main effect and the covariate. If the interaction term b_2 was significant ($P \leq 0.05$), separate weight-length models were constructed for each gender. If the interaction term was not significant, then the interaction term was dropped and the reduced model provided a test of homogeneity of mean body condition between genders. If male and female whitefish had similar shape parameters β and mean condition factors α, then male and female data were combined and a single weight-length model was estimated. If either parameter differed between genders, then separate weight-length models were fitted to each gender.

Growth.—Fish lengths at annulus formation were back calculated for each sub-sampled fish from otolith cross sections to increase the total amount of length-age data for growth analyses and to provide length-age data for lengths of fish that were too small to be sampled (Campana 1990; Francis 1990, 1995; Moritata and Matsuishi 2001). To address the potential bias in back-calculated lengths at age and associated absolute growth rates resulting from a lack of proportionality between fish and otolith growth rates, I applied the back-calculation model of Morita and Matsuishi (2001). This model is a scale-proportional model that is modified to account for age effects in which the otolith increases in size continuously, even though somatic growth slows to zero (Secor and Dean 1992; Holmgren 1996; and Morita and Matsuishi 2001). The basis for this model is the hypothesis that many back-calculation models overestimate fish somatic growth rates for slow-growing fish because the otolith increases in size, despite little somatic growth, coupled with the fact that many back-calculation models assume that fish growth is proportional to otolith growth. The Morita-Matsuishi back-calculation model incorporates fish age into the otolith-fish length regression:

$$O = \alpha + \beta L + \gamma t + \varepsilon_i .$$

In the otolith-fish regression model, O = otolith length, L = fish body length, t = fish age, α, β, and γ = parameters estimated using multiple-linear regression, and ε_i = additive additive process error. If multiple regression analysis indicated that the age effect, λ, was significant ($P \leq 0.05$), I used the full back-calculation model:

$$L_t = -\frac{\alpha}{\beta} + \left(L_T + \frac{\alpha}{\beta} + \frac{\gamma}{\beta} T \right) \frac{O_t}{O_T} - \frac{\gamma}{\beta} t + \varepsilon_i .$$

In the back-calculation model, L_t = back-calculated fish body length at age t, L_T = fish body length at time of capture T, O_t = otolith length at annulus (age) t, O_T = otolith length at time of capture T, α, β, and γ = parameters estimated for the multiple-linear regression model, and ε_i = additive additive process error.

The Morita-Matsuishi model accounts for the common observation that otolith growth is a conservative process in which otoliths continuously increase in size during periods of starvation or negative somatic growth. The model assumes that otoliths increase in length with increasing fish body length and age, and the deviation of otolith length for a fish from the average for that fish length and age is relatively the same throughout the life of a fish (scale-proportional hypothesis; Morita and Matsuishi 2001).

Back-calculated lengths at age were used to test for presence of Rosa Lee's phenomenon in an unexploited population. Lee's phenomenon occurs whenever back-calculated lengths-at-age differ significantly from observed lengths-at-age in the sampled population. Causes of Lee's phenomenon include: (1) use of an incorrect scale-body relationship in growth back-calculation; (2) biased sampling where fish of different sizes are not represented in samples of scales or otoliths in proportion to their abundance; and (3) selective mortality where the mortality rate among larger fish of an age group differs from that of smaller fish (Ricker 1969). False Lee's phenomenon is caused by back-calculation error that is typically associated with an incorrect regression intercept. Biased sampling, where the larger or smaller individuals of a given age are disproportionately represented in the sample, can only result in positive Lee's phenomenon, where back-calculated length-at-age for a given age decreases with increasing fish age (Ricker 1969). This is in direct contrast to the effect of selective mortality, which produces positive Lee's phenomenon only when mortality increases with length within age groups, and produces negative Lee's phenomenon when mortality decreases with length because vulnerability decreases with length within an age group (Ricker 1969). Negative Lee's phenomenon occurs when smaller individuals of an age class are more vulnerable to predators or parasites than larger individuals, so mean length of surviving individuals of an age class is greater than actual mean-length of the age class (observed as a progressive increase in back-calculated length at each annulus with increasing age; Ricker 1969). If detected, negative Lee's phenomenon will likely be found for the first few years of life. True positive Lee's phenomenon occurs when larger fish within a year class are more vulnerable to fishing or natural mortality than smaller fish within a year class, thereby leaving survivors that are subsequently sampled whose back-calculated lengths-at-age are smaller than corresponding observed length-at-age in the population (the magnitude of which increases with increasing age of captured fish; Ricker 1975).

Negative Lee's phenomenon is due to size-selective mortality, whereas positive Lee's phenomenon may be due to biased sampling or size-selective mortality. To test for

Lee's phenomenon, I compared age of capture to mean back-calculated length at age for the first ten annuli. Simple linear regression was used to determine whether mean back-calculated length was related to estimated age at capture (for age classes represented by $\geq$10 fish) for the first five annuli. A significant decline in mean back-calculated length for a particular annulus with increasing age-at-capture would indicate positive Lee's phenomenon, whereas the opposite would indicate negative Lee's phenomenon. I would expect biased sampling or size-selective mortality to affect primarily the youngest age classes, so restricting the analysis to the first five annuli would likely be sufficient to determine the presence of Lee's phenomenon. The presence of Lee's phenomenon may provide insight into mechanisms of whitefish population regulation in Lake Pend Oreille.

I estimated true growth rates from back-calculated length-age data and population growth rates from observed length-age data, because the true growth rate of fish differs from the apparent or population growth rate when either size-selective mortality within a year-class or size-selective sampling occurs (Ricker 1969). Back-calculation of length-at-age provided length at age data of fish too small to be sampled by trap nets. Back-calculated growth rates pertain to surviving members of year classes that were caught by the trap-net sampling gear.

Growth was modeled separately from data summarized as mean length at age using the Von Bertalanaffy length-age additive-error model:

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) + \varepsilon_i .$$

In the length-age model, L_∞ = average asymptotic length, K = the instantaneous rate at which an average fish grows from L_t to L_∞, t_0 = the hypothetical age at which length is zero, and ε_i = additive process error (Ricker 1975). Parameters were estimated with nonlinear least squares methods. To ensure that residuals were equally distributed at all values of age, residual were plotted against age.

Likelihood-ratio tests were used to compare growth curves between genders for the lake-wide whitefish population. Parameters of the Von Bertalanffy model were estimated separately for each gender (full model) and for both genders combined (reduced model). I then compared residual sums-of-squares for the full and reduced models in a likelihood-ratio test. I accepted the full model if the residual sum-of-squares was significantly lower for the full model than for the reduced model (i.e. separate growth curves for male and female fish). I accepted the reduced model if the residual sum-of-squares was not significantly lower for the full model than for the reduced model (i.e. a single growth curve for both sexes).

Absolute- and relative growth rates were calculated for age-1-and-older whitefish, for which back-calculated length-at-age data were available from Lake Pend Oreille. Absolute growth rate G_a was calculated as the difference in length l between adjacent ages 1 and 2:

$$G_a = l_2 - l_1;$$

Relative (proportional) growth rate G_r was calculated as:

$$G_r = \frac{l_2 - l_1}{l_1};$$

In models for both absolute and relative growth rate, l_1 and l_2 = mean back-calculated lengths at age 1 and age 2, respectively. Other terms are equivalent between the two models.

Calculation of absolute growth rates enabled direct comparisons of growth rates among populations for which length-age data were not used to fit the Von Bertlanffy growth model. Relative growth rate provided an intuitive description of growth rate useful for conceptualizing the relationship between growth rate and age of whitefish in Lake Pend Oreille.

Growth in weight was modeled with mean weight-age data using the Von Bertlanaffy additive error weight-age model:

$$W_t = W_\infty \left(1 - e^{-K(t_i - t_0)}\right)^\beta + \varepsilon_i .$$

In the weight-age model, W_∞ = average asymptotic maximum weight, K = instantaneous rate at which W_t approaches W_∞, and t_0 = the hypothetical age when W_t = zero, β = the exponent of the weight-length relationship, and ε_i = additive process error. Absolute and relative growth rates were also calculated with mean weight-at-age data and model-derived estimates of weight-at-age from the Von Bertlanaffy weight-age model.

Maturity.—Maturity of whitefish was modeled as a logistic function of age and size. The proportion of mature fish of each gender was related to each 10-mm length class and to each age class using a logistic (nonlinear) regression model:

$$M_x = \frac{1}{1 + e^{-r(X - X_m)}} \varepsilon_i .$$

In the maturity model, M_x = the proportion of mature fish at each age or length X, r = instantaneous rate at which the proportion of mature fish reaches 1.0, X_m = the length or age at which 50% of the fish sampled were mature, and ε_i = multiplicative process error (Quinn and Deriso 1999).

Likelihood-ratio tests were used to compare age and size at maturity models between genders. Parameters of the logistic models were estimated separately for each gender (full model) and for both genders combined (reduced model). I then compared residual sums-of-squares for the full and reduced models in a likelihood-ratio test. I accepted the full model if the residual sum-of-squares was significantly lower for the full model than for the reduced model (i.e. separate logistic curves for male and female fish). I accepted the reduced model if the residual sum-of-squares was not significantly lower for the full model than for the reduced model (i.e. a single logistic curve for both sexes).

Mortality.—Age structure was estimated by extrapolating an age-length key estimated from sub-sample data to sample length-frequency data. The statistically valid way of treating such data is to extrapolate the sub-sample to the sample and then estimate parameters based on all fish in the sample (Bettoli and Miranda 2001).

Mortality rates were estimated using catch-curve analysis. A catch-curve is a graph of log-number against age, thereby enabling estimation of survival and mortality rates from a sample of a single population. Catch-curve analysis is based on the concept that a decline in the frequency of individuals present from one age group to the next reflects the combined effect of mortality and difference in initial year-class strength (recruitment) for the two age groups (Robson and Chapman 1961). If the population experiences recruitment and mortality that does not trend upwards or downwards through time for fully recruited ages, then the number present in each fully recruited age class would decline exponentially with age (Haddon 2001):

$$N_t = N_0 e^{-Zt} e^{\varepsilon} .$$

In the catch-curve model, N_t = number present at age t, N_0 = average annual recruitment, Z = instantaneous total mortality rate, t = age for fully recruited ages, and ε_i = multiplicative process error. The first fully recruited age of whitefish caught during autumn in trap nets was estimated by visually examining the dome and descending limb of the catch curve, because Ricker (1975) showed that the modal age in the catch lies close to the first year in which recruitment is complete. The multiplicative-error model was $\log_e$-transformed to estimate Z using linear regression of $\log_e(N_t)$ against age t beginning with the first fully recruited age:

$$\log_e(N_t) = \log_e(N_0) - Zt + \varepsilon .$$

The slope of the model is the instantaneous total mortality rate (Z) and its 95% confidence interval. The intercept, $\log_e(N_0)$, when back-transformed, provides an estimate of average recruitment to the fishery for fully-recruited ages. The coefficient of determination (r^2) describes relative variation in recruitment. Positive residuals indicate relatively strong year classes and negative residuals indicate relatively weak year classes.

Similarity of mortality rates and average recruitment were compared between genders in a GLM:

$$\log_e(N_t) = \log_e(N_0) - Zt + b_1 X + b_2 (X * t) + \varepsilon .$$

In the GLM, X = gender (the main effect) and t = age (the covariate). I tested for homogeneity of mortality rates (Z) between genders using the interaction term (b_2) between the main effect and the covariate. If the interaction term was significant ($P \leq 0.05$), I estimated separate catch curves for each gender. If the interaction term was not significant ($P > 0.05$), I dropped the interaction term and tested for homogeneity of mean recruitment (N_0). A significant main effect indicated that mean recruitment differed between genders, whereas a non-significant main effect indicated that genders shared a common mortality rate and an average recruitment.

Assumptions of catch-curve analysis include: (1) recruitment does not trend upward or downward through time; (2) fishing and natural mortality do not trend upward or downward through time; and (3) vulnerability to fishing gear is constant for all fully recruited ages (Hilborn and Walters, 2001). Younger fish are less vulnerable to capture, but become increasingly vulnerable to capture, as they grow older, until they are fully recruited to the fishery at a certain age. For fish older than the age of full recruitment, catch at age is assumed proportional to the abundance of an age class (fish do not become less vulnerable with age). When vulnerability increases with age up to the age of full vulnerability, the catch curve is dome shaped with ages of increasing vulnerability to capture (ascending limb and dome), followed by ages of full vulnerability that experience an exponential decline in numbers with age (descending limb).

Abundance, Density, Biomass.—Abundance of whitefish in Lake Pend Oreille was estimated using single-census (Petersen) and multiple-census (Schnabel and Schumacher-Eschmeyer) mark-recapture models. I estimated total abundance of whitefish in Lake Pend Oreille from trap-net catches in autumn and gillnet catches in spring using Chapman's modification of the Petersen estimator:

$$\hat{N} = \frac{(M+1)(C+1)}{(R+1)} - 1 .$$

In the Chapman model, M = the number of fish marked during fall 2005 trap netting, C = the number of fish caught during spring 2006 gill netting, and R = the number of marked fish recaptured during spring 2006 gill netting. Chapman's estimator is appropriate when sampling is without replacement, so individual fish cannot be observed more than once during a recapture event (Ricker 1975). Single-census mark-recapture models, such as the Chapman estimator, are nearly unbiased if the number of recaptures exceeds seven (Ricker 1975). I estimated 95% confidence limits for estimated abundance from 95% confidence limits for the number of recaptures from the Poisson distribution (Zar 1999):

$$L_1 = \frac{\chi^2_{\left(1-\frac{\alpha}{2}\right),V}}{2} \text{ and } L_2 = \frac{\chi^2_{\left(\frac{\alpha}{2}\right),V'}}{2} .$$

For confidence limits on R, L_1 = the lower 95% confidence limit for R, $V = 2(R)$, L_2 = the upper confidence limit for R, and $V' = 2(R + 1)$. I then inserted 95% confidence limits for R into the Chapman model to estimate 95% confidence limits for abundance:

$$\begin{aligned} LL(\hat{N}) &= \frac{(M+1)(C+1)}{(L_2+1)} - 1 \\ UL(\hat{N}) &= \frac{(M+1)(C+1)}{(L_1+1)} - 1 \end{aligned} .$$

For confidence limits on $\hat{N}$, $\alpha = 0.05$ and $LL(\hat{N})$ and $UL(\hat{N})$ = lower and upper 95% confidence limits for the estimate of abundance, respectively.

I estimated the abundance of spawning (sexually mature) whitefish vulnerable to capture in trap nets during the autumn spawning period using Schnabel and Schumacher-Eschmeyer estimators. The Schnabel and Schumacher-Eschmeyer models relied on data from the trap-netting period that occurred during the autumn and early winter spawning period of whitefish, so I assumed that the estimates of abundance from both models primarily estimated the abundance of sexually mature fish. The Schnabel estimator treats multiple recapture samples as a weighted average of repeated single-census estimates:

$$\hat{N} = \frac{\sum (C_t M_t)}{\sum R_t + 1}.$$

I used the normal approximation to estimate 95% confidence intervals for $1/\hat{N}$:

$$CI = \frac{1}{\hat{N}} \pm t_{\alpha, s-1} \sqrt{V\left(\frac{1}{\hat{N}}\right)}$$

$$V\left(\frac{1}{\hat{N}}\right) = \frac{\sum_{t=1}^{s} R_t}{\left(\sum_{t=1}^{s} C_t M_t\right)^2}.$$

The 95% confidence limits for $1/\hat{N}$ were then inverted into 95% confidence limits for $\hat{N}$. The Schumacher-Eschmeyer estimator treats multiple samples as a linear regression of R_t/C_t against M_t, with slope $1/N$:

$$\hat{N} = \frac{\sum_{t=1}^{s} (C_t M_t^2)}{\sum_{t=1}^{s} (R_t M_t)};$$

I estimated 95% confidence limits for $1/N$ from the variance V of $1/N$ and then inverted the confidence limits into 95% confidence limits for $\hat{N}$:

$$CI = \frac{1}{N} \pm t_{\alpha,s-1}\sqrt{\frac{V\left(\frac{1}{\hat{N}}\right)}{\sum_{t=1}^{s}\left(C_t M_t^2\right)}}$$

;

$$V\left(\frac{1}{\hat{N}}\right) = \frac{\sum_{t=1}^{s}\left(\frac{R_t^2}{C_t}\right) - \left[\frac{\left(\sum_{t=1}^{s} R_t M_t\right)^2}{\sum_{t=1}^{s} C_t M_t^2}\right]}{s-1}$$

Because trap nets are size selective, particularly for smaller fish (Latta 1959: Hamley and Howley 1975), I evaluated size selectivity by plotting *R/M* against 2-cm length-classes. Size-selectivity was likely if *R/M* varied systematically with length. If so, I estimated corrected adult whitefish abundance by the capture probability method (Latta 1959). If corrected abundance did not differ significantly from the Schanbel and Schumacher-Eschmeyer estimates, I concluded that size-selectivity did not affect the multiple-census estimates.

I assessed the accuracy of multiple-census and single-census estimates of whitefish abundance by comparison to estimates of lake trout abundance derived from the same sampling. First, I assumed that whitefish and lake trout were equally vulnerable to trap netting in autumn 2005 and gillnetting in spring 2006, so that the ratios of catches for the two species reflected their relative abundance. Next, I multiplied abundance estimates for lake trout that were vulnerable to trap netting in autumn 2005 (average of Schnabel and Schumacher-Eschmeyer estimates) and gill netting in spring 2006 (Chapman estimate; Hansen et al. 2007) by the ratios of catch-per-effort (whitefish to lake trout) in both capture methods. Last, I estimated 95% confidence intervals for the resulting estimates of whitefish vulnerable to trap netting in autumn 2005 and gillnetting in spring 2006 by multiplying 95% confidence intervals for each estimate of lake trout abundance by the ratios of catch-per-effort in each capture method.

Density of whitefish in Lake Pend Oreille was estimated by dividing the estimated abundance of whitefish by lake surface area, and by the area of the lake covering depths ≤ 230 ft (28,585 acres) to estimate abundance over the depth range that whitefish occupy in Lake Superior, a bathymetrically similar lake (Dryer 1966). Density was estimated for mark-recapture estimates of adult whitefish based on trap netting in autumn 2005 and immature and mature whitefish based on gillnetting in spring 2006, and for catch/effort ratio estimates of adult whitefish based on trap netting in autumn 2005 and immature and mature whitefish based on gillnetting in spring 2006.

Biomass was estimated by multiplying estimated numbers in each 10-mm length class by the mean weight of each length class predicted by the weight-length relationship and then summing across length classes. First, I estimated abundance in each 10-mm length class from the trap-net length-frequency and the average of the Schnabel and Schumacher-Eschmeyer estimates. Next, I used the weight-length model to estimate the average weight of fish in each length bin, which I multiplied by the estimated number of whitefish in each length bin, and then summed across all length bins to estimate total biomass of mature whitefish in autumn 2005. Upper and lower 95% confidence limits were calculated by repeating the above analysis with the averages of the Schnabel and Schumacher-Eschmeyer upper and lower 95% confidence limits. Biomass of whitefish vulnerable to gillnets in spring 2006 was estimated using the same method, but with the Chapman abundance estimate. I also estimated biomass from the product of the ratio of catch-per-net-night of whitefish to lake trout in gill nets and the Chapman estimate of total lake trout abundance in the same period (35,801 lake trout; 95% CI = 25,270–52,634; Hansen et al. 2007).

Results

Size Structure

The length-frequency distribution based on trap netting in autumn 2005 (n = 12,594) was strongly unimodal (Figure 3) with a mean of 448 mm and a mode of 450 mm (Table 2) whereas the length-frequency distribution based on gillnetting in spring 2006 (n = 886) was distinctly bimodal (Figure 3) with a mean of 390 mm (Table 3). The length frequency of whitefish caught during autumn trap netting was normally distributed (χ^2 = 3.204; df = 2; P = 0.201). For the gillnet length-frequency, the length of the first mode was 330 mm, the length of the second mode was 430 mm, and the two modes were represented by two overlapping normal length-frequency distributions. The average length of whitefish caught in gill nets increased steadily with mesh size from 315 mm in the 2-inch mesh to 455 mm in the 4.5-inch mesh (Figure 4). A length-frequency was not constructed for the 5.5-inch mesh, which caught only two whitefish.

Sex Composition

The sex composition (proportion females) of whitefish was skewed toward females (0.66; 95% CI = 0.63 – 0.70) in Lake Pend Oreille. The sex composition of mature fish (65% of all fish caught) was more strongly skewed toward females (0.70; 95% CI = 0.66 – 0.74) than for immature fish (0.54; 95% CI = 0.48 – 0.60). The proportion of females ranged from 0.27 during the week of 21 November 2005 to 0.83 during the week of 5 December 2005 (Table 4).

Body Condition

Male and female whitefish changed in shape similarly because shape parameters β of their weight-length relations did not differ significantly ($F_{1,\,600} = 1.28$; $P = 0.258$), whereas mean condition factor α differed significantly between genders ($F_{1,\,601} = 6.56$; $P = 0.011$). Therefore, separate weight-length relationships were used for male and female whitefish (Figure 5). Females had a smaller shape parameter and a larger condition factor than males (Table 5). The shape parameter ($\beta = 3.363$) indicated that whitefish grew plumper as length increased. The allometric weight-length model explained 97% of the variation in weight as a function of length (Figure 5).

Growth

The age-bias plot indicated that scales substantially undersestimated true age beginning at age 9 (Figure 6), so back calculation of growth history was restricted to otolith cross sections, and all age-related analyses relied on otolith age estimates. The Morita-Matsuishi back-calculation model:

$$O = 130.780 + 1.426L + 22.868t;$$

About 89% of the variation in otolith radius was attributed to variation in length ($t_{618} = 15.29$; $P < 0.001$) and age ($t_{618} = 26.83$; $P < 0.001$). The back-calculation model was:

$$L_t = -91.711 + \left(L_T + 91.711 + 16.036T\right)\frac{O_t}{O_T} - 16.036t;$$

The back-calculation model assumption of continual otolith growth with age was verified (Figure 7). Otolith growth rate declined from annulus 1 to annulus 15 and then stabilized at a constant rate for the remainder of the lifespan (Table 6).

Von Bertlanaffy growth models differed significantly between genders ($F_{3, 71} = 15.41$; $P < 0.001$), so separate models were used for each gender (Figure 8). Female whitefish reached a larger asymptotic length ($L_\infty = 532$ mm) than male whitefish ($L_\infty = 495$ mm), grew slower toward their asymptotic length ($K = 0.125$/year) than male whitefish ($K = 0.153$/year), and were younger at zero length ($t_0 = –3.012$ years) than male whitefish ($t_0 = –2.441$ years; Table 7). Confidence intervals for mean back-calculated lengths at age were small for all ages represented by at least 10 fish (Table 8; Figure 8, bottom panel). For ages represented by fewer than four fish, confidence intervals were not included because of large variance associated with small sample size.

Growth curves differed between observed mean length-age and back-calculated length-age models. Asymptotic length was smaller for the observed mean length-age model ($L_\infty = 527$ mm) than for the mean back-calculated length-age model ($L_\infty = 538$ mm). Instantaneous growth rates were larger for the observed mean length-age model ($K = 0.129$/year) than for the mean back-calculated length-age model ($K = 0.125$/year). Age at zero length was younger for the observed length-age model ($t_0 = –4.014$ years) than for the mean back-calculated length-age model ($t_0 = –2.907$ years).

Sampling error of absolute and relative growth rates was substantial for ages with fewer than four fish. Absolute growth rates declined quickly with age and became mostly negative for ages 28 and older (Figure 9; Table 8). Relative growth rate declined rapidly from age 1 (~46%) to age 2 (~18%), and then declined at a steadily decreasing rate thereafter (Figure 9; Table 8). Relative growth rate was mostly constant for ages 15–27, and became predominantly negative for ages 28 and older.

The age range of sampled whitefish within 10-mm length groups was highest for the 500–510 mm length group with 18 age classes, and lowest for the 270–280 mm length group with one age class (Table 9). Within age classes, total length range increased with age and was greatest for age 30 (419–670 mm; Table 10).

Absolute growth in weight (grams per year) for whitefish of ages 2–36 using mean weight-age data for ages 1–41 and estimates of weight-at-age from the Von Bertalanffy weight-age model ($W_\infty = 1{,}436.96$ g, $K = 0.154$/year, $t_0 = -2.928$ years, and $\beta = 3.363$) increased erratically to 140 grams/year at age 6 and then declined (Table 11). Absolute growth rate increased to a maximum of 95.6 g at age 4 and then declined to a minimum of 2 g at age 35 (Figure 10). Relative growth rate was highest at age 2 and declined thereafter (Figure 10). Observed weight increased erratically with age because of high variability in observed weight at age for whitefish of age 15 and older (Figure 11). Small sample size was a problem for fish of age 18 and older ($n < 20$; Table 10).

Positive Lee's phenomenon was evident for the regression of mean back-calculated length against ages 2–31 for annuli 2–5 ($P \leq 0.05$), but was not evident for annulus 1 ($F_{1,\,28} = 3.77$; $P = 0.062$; Figure 12). When the regression for annulus 1 was limited to ages 2–20, the regression was significant ($F_{1,\,17} = 9.36$; $P = 0.007$). The amount of positive Lee's phenomenon for annuli 1–5 and ages 2–31 was small (Figure 12) and increased with annular age (Table 11). Small fluctuations in back-calculated length at age among year classes were evident (Figure 12).

Maturity

Male and female whitefish differed significantly in mean length at maturity ($F_{2, 55}$ = 35.31; $P < 0.001$). Male whitefish first matured at 340 mm, reached 50% maturity (X_m) at 378 mm, and reached 100% maturity at 430 mm at an instantaneous rate (r) of 0.186 (Table 13). Female whitefish first matured at 350 mm, reached 50% maturity (X_m) at 390 mm, and reached 100% maturity at 440 mm at an instantaneous rate (r) of 0.0605 (Table 13). For both genders combined, whitefish first matured at 340 mm, reached 50% maturity (X_m) at 383 mm, and reached full maturity at 440 mm at an instantaneous rate (r) of 0.074 (Table 13).

Male and female whitefish differed significantly in age at maturity ($F_{2, 57}$ = 8.89; $P < 0.001$). Male whitefish first matured at age 4, reached 50% maturity (X_m) at age 6, and reached 100% maturity at age 11 at an instantaneous rate (r) of 1.842 (Table 13). Female whitefish first matured at age 5, reached 50% maturity (X_m) at age 6.5, and reached 100% at age 12 at an instantaneous rate (r) of 1.1235 (Table 13). For both genders combined, whitefish first matured at age 4, reached 50% maturity (X_m) at age 6.2, and reached 100% maturity at age 12 at an instantaneous rate (r) of 1.277 (Table 13).

Mortality

The age structure from trap netting was comprised of 37 age classes and the oldest fish was age 42 (Figure 15). The age structure was strongly skewed to the right with numerous well-represented age classes. The modal age was age 11, which was used as the first fully vulnerable age class to estimate instantaneous natural mortality (Figure 15). The descending limb of the log-transformed catch-curve was linear with only a negligible amount of convexity present among the oldest age classes. The instantaneous natural mortality rate M (total instantaneous mortality rate Z) across ages 11–42 was 0.167, equivalent to an annual survival rate of 85%. The average sample age was 14 years from trap-net samples and 7.8 years from gillnet samples.

Male and female whitefish suffered similar mortality rates because the interaction between gender and age was not significant ($F_{1,42} = 1.78$; $P = 0.189$), whereas mean recruitment differed significantly between genders because the main effect for gender was significant ($F_{1,43} = 62.67$; $P < 0.001$). Age structures were similar between male and female whitefish of ages 5–29 (Figure 15). A larger proportion of males than females were age 5 and younger and no males older than age 35 were observed (Figure 15).

Abundance

Density of adult whitefish was 1.35 fish per acre (1.11 – 1.78 fish per acre) over the entire surface area and 4.07 fish per acre (3.35 – 5.35 fish per acre) over depths shallower than 230 feet in Lake Pend Oreille in autumn 2005. Of 13,384 whitefish that were caught, 8,313 were marked, and 447 were later recaptured during trap netting in autumn 2005. The rate of tag loss during fall trapnetting was zero, because all recaptured fish had attached tags. Abundance of sexually mature whitefish vulnerable to trap netting in autumn 2005 was 105,274 fish (95,258 – 117,645 fish) based on the Schnabel model and 127,525 fish (96,401 – 188,329 fish) based on the Schumacher-Eschmeyer model. The recapture rate increased to a high of 5.5% during the week of 14–21 November 2003, when 4,305 fish had been marked and released, and then fell to 3%, before increasing again through the last sampling week (Figure 16). The Schnabel abundance estimate increased steadily until the week of 14 November 2005, then declined temporarily, and increased linearly again through the end of sampling (Figure 17).

Trap nets sampled whitefish selectively based on length (Figure 18). The *R*/*M* ratio increased linearly with length from 360 mm to 440 mm, decreased to 480 mm, increased to a peak of 9.5% at 520 mm, and decreased to zero for length classes greater than 520 mm. Small sample size may have affected *R*/*M* ratios for fish longer than 500 mm. Corrected abundance was 102,317 adult whitefish, which was within the confidence limits of both multiple-census estimates.

Density of immature and adult whitefish was 38.12 fish per acre (23.69 – 60.12 fish per acre) over the entire surface area and 114.3 fish per acre (71.25 – 180.78 fish per acre) over depths shallower than 230 feet in Lake Pend Oreille in spring 2006. Of 6,305 whitefish that were caught during gillnetting in spring 2006, 15 were recaptures of previously marked fish. The rate of tag loss during spring gillnetting was zero, because all recaptured fish had attached tags. Abundance of whitefish vulnerable to gillnetting in spring 2006 was 3,276,754 fish (2,036,754 – 5,167,678 fish). Gillnetting effort in spring 2006 was 136 net-nights, where each net-night was ~20.6 hours and total effort was 2,796 hours. The average inside depth of all gillnets was 84 feet and the average outside depth of all gillnets was 136 feet.

The abundance of adult whitefish derived from the ratio of catch rates of adult whitefish to lake trout and the estimated abundance of adult lake trout in autumn 2005 was similar to Schnabel and Schumacher-Eschmeyer estimates of adult whitefish abundance. The estimated abundance of adult whitefish was 98,268 fish (83,034 – 118,068 fish) and density was 1.14 fish per acre (0.97 – 1.37 fish per acre) in autumn 2005, based on an estimated lake trout abundance of 10,824 adult fish (9,146 – 13,005 fish; Hansen et al. 2007) and a ratio of 9 whitefish per lake trout in trap nets in autumn

2005. Density of adult whitefish in waters shallower than 230 ft deep was 3.44 fish per acre (2.90– 4.13 fish per acre). During autumn 2005, trap netting caught 9 times more whitefish (Catch = 13,384 fish; Effort = 642 net-days; CPE = 20.8 fish/net-day) than lake trout (Catch = 1,798 fish; Effort = 783 net-days; CPE = 2.3 fish/net-day).

The abundance of total whitefish derived from the ratio of catch rates of total whitefish to lake trout and the estimated abundance of lake trout in spring 2006 was much lower than the Chapman estimate of total whitefish abundance. The estimated abundance of whitefish was 340,975 fish (240,676 – 501,295) and density was 3.97 fish per acre (2.80 – 5.83 fish per acre), based on an estimated lake trout abundance of 35,801 total fish (25,270 – 52,634 fish; Hansen et al. 2007) and a ratio of 9.5 whitefish per lake trout in gillnets in spring 2006. Density of whitefish in waters shallower than 230 ft deep was 11.93 fish per acre (8.42 – 17.53 fish per acre). During spring 2006, 136 net-days of gillnetting caught 9.5 times more whitefish (Catch = 6,305 fish; CPE = 46.36 fish/net-day) than lake trout (Catch = 662 fish; CPE = 4.87 fish per net-day).

Biomass

Biomass of whitefish vulnerable to trap netting in autumn 2005 was 219,869 pounds (95% CI = 181,014 – 288,980 pounds) and total biomass of whitefish vulnerable to gillnetting in spring 2006 was 4,107,835 pounds (95% CI = 2,553,411 – 6,478,354 pounds). Adult fish longer than 380 mm (length at 50% maturity) were 98% (215,708 lbs) of the estimated biomass in autumn 2005 and 78% (3,190,570 lbs) of the estimated biomass in spring 2006. Biomass of whitefish vulnerable to gillnetting in spring 2006 based on the ratio of whitefish to lake trout was 427,456 pounds (95% CI = 301,718 – 628,438 pounds), nearly two times higher than the average of the Schnabel and

Schumacher-Eschmeyer estimates for autumn 2005 and ~10% lower than the Chapman estimate for spring 2006.

Discussion

Size-structure of whitefish was unimodal when caught in trap nets and bimodal when caught in gill nets in Lake Pend Oreille, both of which are common in unexploited populations of whitefish (Johnson 1972, 1973, 1976; Power 1978; Mills et al. 2004). For example, unexploited whitefish populations, whether Arctic or more southerly, are characterized by dome-shaped length-frequency distributions with one or more modes (Mills et al. 2004). Length-frequency distributions for 12 unexploited Canadian whitefish populations sampled with graded-mesh gill nets were characterized by two or four modes (Mills et al. 2005). In Lake Pend Oreille, two modes of the gillnet length-frequency distribution (330 mm and 430 mm) may represent modal lengths of subadult and adult whitefish, because the second gillnet modal length of 430 mm was similar to the modal length of adult fish sampled during 2005 trap netting (450 mm). In Lake Pend Oreille, each mode was well-represented by a normal length-frequency distribution, in contrast to the leptokurtic length-frequency distributions often observed in unexploited whitefish populations from northern Canada (Johnson 1972, 1973, 1976; Power 1978; Mills et al. 2004, 2005). Such populations often show a high degree of clustering around modal values, with up to 62% of the population within a 50-mm length-class (Johnson 1976). Similarly, large numbers of individuals of uniform, large size were found in each of 12 unexploited Canadian whitefish populations (Mills et al. 2005). I found that 80% of whitefish sampled during fall trap netting were 430–480 mm in length, whereas whitefish caught during spring gill netting were much less uniform in length, thereby suggesting that large numbers of individuals of uniform, large length is not an attribute of all unexploited whitefish populations. Exploitation would truncate the population size-structure by selectively removing larger, more commercially desirable fish from the population. A compensatory increase in growth rate would increase length-at-age and thereby restore population size-structure to near pre-exploitation conditions.

The proportion of mature female whitefish sampled in trap nets during autumn in Lake Pend Oreille (0.70) was within the range of other whitefish populations (0.37 – 0.86; Jensen 1981). Temporal variation in whitefish sex composition in Lake Pend Oreille may have been caused by movement of whitefish to and from spawning grounds. The peak of spawning (greatest percentage of ripe fish) occurred from 30 November through 15 December and coincided with the highest observed proportion of females, perhaps a result of increased activity of ripening females moving to spawning grounds. The percentage of immature whitefish caught during fall trap netting was nearly equivalent, thereby suggesting that the sex-composition of the adult population was biased towards females, unless a significant increase in male mortality occured upon recruitment to the adult stock, as found in another study (Bell et al. 1977). More likely, the skewed sex-composition was caused by gender-based behavior differences during the spawning period, as in other studies (Carmichael et al. 1998; Begout Anras et al. 1999). For example, female whitefish swam at deeper mean maximum depths (6 – 8 m) than male whitefish (2 – 4 m) during the spawning period in a shallow boreal lake (Begout Anras et al. 1999). Male whitefish may have arrived on the spawning grounds sooner than females, and remained longer, thereby being less susceptible to capture in trap nets (a passive sampling gear) that were not positioned directly on the spawning grounds.

Exploitation may change the sex-composition of whitefish populations (Jensen 1981). Heavy exploitation was followed by a substantial increase in the proportion of female bloaters, *Coregonus hoyi*, in Lake Michigan (Brown 1970). However, an increase in the proportion of female whitefish in response to exploitation has never been documented, and Jensen (1981) showed through modeling that changes in the proportion of female whitefish would compensate little for exploitation.

Body condition of whitefish in Lake Pend Oreille was similar to other exploited and unexploited populations. The shape parameter of the weight-length relationship for whitefish in Lake Pend Oreille was within the range of published estimates for both exploited and unexploited populations. The shape parameter of the weight-length relationship ranged 3.1 – 3.5 for exploited whitefish populations (Healey 1975) and from 3.04 (Gabbro Lake; Bruce 1984) to 3.69 (Great Slave Lake; Kennedy 1953) for unexploited whitefish populations. The condition factor of whitefish in Lake Pend Oreille was similar to other unexploited whitefish populations, which ranged from 9.58E-10 (Lobstick Lake; Bruce 1984) to 2.04E-04 (Great Slave Lake; Kennedy 1953). Exploitation would likely reduce population density and thereby lead to increased body condition through a reduction in intraspecific competition for limited prey resources.

Growth of whitefish in Lake Pend Oreille was slower than other exploited and unexploited whitefish populations (Jensen 1981; Bruce 1984; Beauchamp et al. 2004). The instantaneous growth coefficient for whitefish in Lake Pend Oreille (K = 0.12/year; Chapter 1) was among the lowest recorded for unexploited whitefish across their range, so the population in Lake Pend Oreille should have a large capacity for growth compensation (Healey 1975). Growth coefficients ranged from 0.09/year in Great Bear

Lake (Kennedy 1949) to 0.96/year in Cliff Lake (Fenderson 1964) and averaged 0.30/year (Jensen 1981). Asymptotic lengths of whitefish from Lake Pend Oreille were shorter than for exploited populations from the Great Lakes region (572 – 685 mm; Ebener 1980; Jensen 1985; Taylor et al. 1992; Beauchamp et al. 2004) and similar to those for unexploited populations of whitefish from northern Canada (Johnson 1972, 1976; Power 1978). First year growth of whitefish in Lake Pend Oreille was within the range of values for exploited (96 – 326 mm) and unexploited (90 – 190 mm) populations (Roelofs 1958; Peterka and Smith 1970; Healey 1975; Patriarche 1977; Bidgood 1983). Annual growth increments for whitefish of age 1 and older in Lake Pend Oreille were small and declined with age, as in other unexploited whitefish populations (Healey 1975). Asymptotic maximum weight of whitefish in Lake Pend Oreille was less than in exploited Great Lakes populations (2.4 – 5.32 kg; Jensen 1981). In Lake Pend Oreille, growth differed between genders, with females reaching a larger asymptotic length, growing more slowly to their asymptotic length, and being younger at age 0 than male whitefish, as in another population (Beauchamp et al. 2004). Age-at-length was highly variable for larger whitefish in Lake Pend Oreille, thereby suggesting a weak correlation between age and length for older fish, as in other northern whitefish populations (Johnson 1972, 1976). For unexploited Canadian populations of whitefish, growth rates estimated from fin-ray ages were slower than growth rates estimated from scale ages because ages from scales were systematically underestimated (Mills et al. 2004).

My findings suggest that growth of whitefish in Lake Pend Oreille will respond strongly to exploitation through growth compensation; a powerful compensatory mechanism that helps stabilize yields when whitefish populations are exploited (Miller

1949; Healey 1975; 1980; Jensen 1981, 1985), if exploitation does not cause recruitment overfishing. For example, growth rates increased in proportion to the intensity of exploitation in three experimentally exploited Northwest Territory whitefish populations (Healey 1980). Generally, exploitation of an unexploited or an underexploited whitefish population will result in an earlier age and possibly smaller size at maturity, which would increase recruitment to the adult stock, and thereby maintain balance between recruitment and mortality (Healy 1975; 1980; Jensen 1981; 1985). Growth compensation is the most important compensatory mechanism of whitefish populations to increased fishing mortality (Healey 1980).

Mean back-calculated lengths at annulus formation for annuli 1–5 were similar among year classes, thereby suggesting that growth of whitefish was temporally stable in Lake Pend Oreille, as in another study of an unexploited whitefish population (Edsall 1960). Back-calculated lengths at annulus formation were similar among several year classes for whitefish in Munising Bay, Lake Superior (Edsall 1960). Conversely, back-calculated lengths at annulus formation varied substantially among year classes for whitefish sampled from four unexploited lakes in the Northwest Territories (Baptiste Lake, Chitty, Alexie, and Drygeese; Healey 1980). Variation in the annual exploitation rate would likely cause variation in whitefish growth rates, which alone would not likely negatively impact the population. However, exploitation rates high enough to exceed the capacity of the population to replace harvested fish with new recruits would result in recruitment overfishing and eventual stock collapse (Haddon 2001).

A small amount of positive Lee’s phenomenon in back-calculation of whitefish length at age in Lake Pend Oreille could be attributable to either size-selective mortality or size-selective sampling (Ricker 1969). If the mortality rate were positively related to length within a cohort, then I would expect to see a decline in mean back-calculated length with increasing age at capture for the first several annuli. For example, faster-growing whitefish tend to mature at a younger age than slower-growing fish (Healey 1980; Jensen 1985; Taylor et al. 1992; Beauchamp et al. 2004) and earlier age of maturity is associated with increased mortality (Jensen 1985; Beauchamp et al. 2004), which could produce positive Lee's phenomenom in an unexploited population. In addition, trap nets tend to undersample small fish in a population (Latta 1959; Laarman and Ryckman 1982; Hamley and Howley 1985) and oversample larger fish of young age classes, which would cause back-calculated lengths to be larger for young fish than for old fish. This bias decreases with increasing age at capture until the age that is fully vulnerable to sampling. I found Positive Lee's phenomenon over most age classes in the population, thereby suggesting that size-selective mortality was the causal factor. However, size-selective sampling of age classes of reduced vulnerability was also possible, because trap nets select against fish of lengths that are shorter than the length of full vulnerability to a given mesh size (Latta 1959; Laarman and Ryckman 1982; Hamley and Howley 1985).

Whitefish in Lake Pend Oreille matured at an age and length (6 years, range = 4–12 years; 383 mm, 340–440 mm) that was relatively high compared to other unexploited populations of whitefish, which usually mature at 3–10 years and 204–400 mm fork length (Healey 1975). For example, unexploited populations of whitefish from Smallwood Reservior in western Labrador reached 50% maturity at 5.2–6.6 years and 360–373 mm fork length (Bruce 1984), similar to whitefish from Lake Pend Oreille. However, age-at-first maturity was 10 for females and 7 for males, and age at full maturity was 12 for both genders in a slow-growing unexploited stock of whitefish from Munising Bay, Lake Superior (Edsall 1960). Whitefish in exploited populations generally mature at a younger age and greater length than those in unexploited populations. For example, female whitefish from 22 harvest management zones in the Great Lakes reached 50% maturity at an average age of 4.5 years and a total length of 453.4 mm, whereas males reached 50% maturity at an average age of 3.4 years and a fork length of 414.4 mm (Beauchamp et. al. 2004). In Lake Pend Oreille, male whitefish matured at a younger age and smaller size than female whitefish, as in other populations (Edsall 1960; Beauchamp et al. 2004). Immature whitefish were consistently smaller than mature whitefish of the same age and sex, particularly for females, thereby suggesting that maturity is a function of length not age, as found in other studies (Bell et al. 1977; Taylor et al. 1992).

A decrease in age at maturity resulting from a compensatory increase in growth is a powerful compensatory mechanism of whitefish populations (Jensen 1981). For example, a decrease in the age-at-maturity from age 10 to age 4–5 offset a substantial increase in fishing mortality rate (Jensen 1981). However, the relatively young age at 50% maturity for whitefish in Lake Pend Oreille (6 years) suggests that a further decline in age-at-maturity associated with growth compensation may not be likely in Lake Pend Oreille. Growth compensation alone is not an important compensatory mechanism if the age at maturity does not decline (Jensen 1981), further suggesting that growth compensation may not compensate for exploitation where the age at maturity is already low, as in Lake Pend Oreille. However, compensatory mechanisms that cannot maintain the balance between recruitment and mortality may be able to maintain the balance between biomass production and harvest mortality (Jensen 1981). Therefore, growth compensation caused by exploitation may be able to maintain high yield at high fishing mortality rates through increased production.

The instantaneous natural mortality rate for whitefish in Lake Pend Oreille (M = 0.167; Chapter 1) was among the lowest observed among unexploited populations of the species (M = 0.16 – 1.35; Healey 1975; Jensen 1981; Mills et al. 2004), so the population in Lake Pend Oreille should have a large capacity to compensate for high fishing mortality (Healey 1975). Instantaneous natural mortality (M) ranges even more widely for exploited whitefish populations (0.176 – 2.81/year; Jensen 1981; Schneeberger et al. 2004). Exploited whitefish populations may have higher apparent natural mortality rates than unexploited whitefish populations because fishing mortality is underestimated when recaptures of tagged fish are underrepresented through increased mortality of tagged fish, tag shedding, or under-reporting of tags (Ricker 1975; Hoenig et al. 1998; Denson et al. 2002; Pine et al. 2003). I found that male and female whitefish had similar mortality rates in Lake Pend Oreille, thereby suggesting that the skewed sex ratio of mature whitefish was caused by behavioral differences during the spawning period rather than increased mortality of males after recruitment to the adult stock. Populations of whitefish that suffer low mortality have large biomass in older age classes that are available for harvest and are more stable, with well-represented older age classes acting as a reproductive reserve capable of buffering against successive years of unfavorable reproduction (Healey 1975; Power 1978). Whitefish populations with youthful age structures tend to be susceptible to significant oscillations in abundance caused by reproductive failure (Miller 1949; Christie 1963; Lawler 1965; Healey 1975). Heavily exploited populations often depend on the first few mature age classes for their reproductive output, and most fish have only one opportunity to spawn (Healey 1975; Jensen 1982). Consequently, one or more years of reproductive failure can lead to stock collapse when fishing mortality is high (Healey 1975).

The instantaneous mortality rate of whitefish in Lake Pend Oreille was significantly higher when based on scale ages ($Z = 0.481$/year) than when based on sagittal otolith cross-sections ($Z = 0.167$/year), because scales underestimated ages of older fish. Similarly, mortality rates of unexploited whitefish populations in the Experimental Lakes Area of Canada were lower when based on age estimates from either fin rays or otolith cross-sections (0.16 – 0.34/year) than when based on scales (0.53 – 1.05/year) because ages from scales were systematically underestimated (Mills et al. 2004). Unexploited whitefish populations are characterized by platykurtic age-frequency distributions with positive skew and many well-represented age classes that reflect low rates of annual mortality (Power 1978). Age-frequency distributions, when biased by errors in age estimation, tend to concentrate fish in age groups where the method of age estimation begins to fail, thereby leading to age-frequency distributions that are leptokurtic or nearly normal (Power 1978). In Lake Pend Oreille, the age-frequency distribution was nearly normal when based on scale ages and positively skewed when based on otoliths. Unfortunately, most studies of unexploited populations of whitefish relied on scale ages for estimating mortality and growth, thereby likely biasing growth and mortality rates too high (Kennedy 1949, 1963; Healey 1975; Bruce 1984).

Tagged whitefish likely suffered higher mortality than untagged whitefish in Lake Pend Oreille, based on changes in the recapture rate through time. The cumulative recapture rate during autumn 2005 trap netting was 5.38%, whereas the recapture rate during spring 2006 gill netting was only 0.18%, which suggests that either mortality of tagged fish or migration of unmarked fish into the sampled population was substantial between the marking and recapture periods. Weekly Schnabel estimates increased nearly linearly during autumn 2005, which suggests that tagging mortality was relatively constant or umarked fish moved steadily into the population. Tag loss was not likely a problem in my study, because no tag loss was observed, in contrast to an 11.1% loss rate for Floy-tagged whitefish at large for one year in Lake Michigan (Ebener and Copes 1982). Movement of the immature fish into the population in spring 2006 could not alone account for the large decrease in recapture rate, because that would indicate that adult fish were just 3.7% of the total population. Nonetheless, movement of immature fish into the sampled population partially contributed to the declining recapture rate, because the gillnet length frequency included a smaller mode that was absent from the trap-net length frequency. Gill nets were also fished randomly throughout the lake to sample immature and mature fish that may not have been vulnerable to trap nets that were fished nonrandomly in a limited number of fixed locations.

Similar catch ratios of whitefish to lake trout in fall trap netting and spring gill netting suggest that whitefish were 9.1 – 9.5 times more abundant than lake trout in Lake Pend Oreille during autumn 2005 and spring 2006. Migration of unmarked whitefish into the sampled population in numbers sufficient to bias the Chapman abundance estimate would have substantially increased the catch ratio of whitefish to lake trout during spring gillnetting, relative to autumn trap netting. Any factor that causes underrepresentation of tagged fish in the sampled population will lead to an overestimate of abundance (Ricker

1975; Van Den Avyle and Hayward 1999; Pine et al. 2003). Ricker (1975) concluded that marking often (directly or indirectly) increases mortality of marked fish. For example, short-term 5-day mortality of northern pike tagged with Floy tags was 2.4% (Pierce and Tomcko 1993). Round Goby's tagged with Floy anchor tags suffered 50% mortality during a 15-week period after tagging (Wolfe and Marsden 1998). In my study, the relatively large number of tagged fish caught during trap netting suggests that short-term mortality was less important than delayed mortality. Further, tagging occurred during the spawning period when fish may have already been in a weakened condition from lack of feeding. Gillnetting began 58 – 128 days after fish were marked, thereby enabling delayed mortality to reduce the number of marked fish in the population prior to recapture sampling. My findings suggest that delayed mortality of whitefish tagged with Floy anchor tags was high in Lake Pend Oreille. Mark-recapture studies are often used to estimate exploitation and abundance of whitefish in the Great Lakes (Ebener 1980; Ebener and Copes 1982; Rowe 1984; McComb 1989), so delayed mortality of tagged whitefish should be evaluated in such studies.

Population density of adult lake whitefish in Lake Pend Oreille was low based on total surface area (1.35 fish/acre; 95% CI = 1.11–1.78 fish/acre), but average based on available whitefish habitat ≤ 230 feet deep (4.07 fish/acre; 95% CI = 3.35–5.35 fish/acre (Dryer 1964), relative to unexploited whitefish populations elsewhere. Unexploited whitefish populations often occur at high density, based on the common observation that such populations respond strongly to exploitation through increased growth, recruitment, and fecundity (Healey 1975, 1978; 1980; Jensen 1981, 1985; Mills and Chalanchuk 1988). In addition, whitefish in four unexploited lakes in the Experimental Lakes Area of northwestern Ontario (maximum depths = 39.4–105 ft; whitefish densities = 4.7–15.5 fish > age 3/acre; Mills and Chalunchuk 1988) were of much higher density than in Lake Pend Oreille. However, Lake Pend Oreille is larger and deeper than the Canadian lakes where density of most other unexploited whitefish populations has been estimated. Lake Pend Oreille lies in the Purcell Trench in the northern panhandle of Idaho and has a very low area/volume ratio and an even lower littoral area/volume ratio (Falter 2003). Very steep shorelines that surround the southern and central basins limit the amount of suitable habitat for whitefish in Lake Pend Oreille. Whitefish in the Apostle Islands region of Lake Superior, a bathymetrically similar lake, occupied depths shallower than 230 feet, with most fish of all sizes found at 60 – 174 ft (Dryer 1966). Given that the whitefish is primarily benthivorous and usually lives at depths of less than 230 feet deep, the lack of suitable habitat in Lake Pend Oreille may explain the relatively low population density. When I estimated immature and adult whitefish density over the surface area of Lake Pend Oreille covering depths ≤ 230 ft (expected whitefish habitat; Dryer 1966), whitefish density was (11.93 fish/acre; 95% CI = 8.42–17.53 fish/acre; Dryer 1964), within the range observed for unexploited populations of the species.

Under exploitation, whitefish density and biomass may decline if the exploitation rate exceeds the capacity of the population to compensate with increased recruitment and growth. A reduction in density or biomass, particularly of the older, larger fish, due to a high exploitation rate would likely increase weight at length of individual fish (i.e.body condition) due to a reduction in intraspecific competition for limited prey resources. The level of annual mortality that would cause recruitment overfishing is unknown, but likely would be high (e.g. > 70%: Clark 1984). Growth overfishing would occur if whitefish were harvested at less than the maximum yield per recruit, due to excessive harvest rates.

Management Implications

Natural mortality was low, growth was slow, and maturity was late for whitefish in Lake Pend Oreille, which indicate a high biological potential for yield to a commercial fishery (Healey 1975). Healey (1975) examined four parameters relevant to production and yield (mortality, growth, abundance, and reproduction) in exploited and unexploited populations of whitefish to optimize yield from existing fisheries and to evaluate the biological capacity of unexploited populations to support a commercial fishery. Healey (1975) concluded that unexploited populations with the greatest fishery potential would possess a low natural mortality rate, slow growth rate, and old age at reproduction, because such populations would be able to compensate for exploitation by increasing growth rate, and decreasing age-at-maturity, keeping yields stable and high and preventing recruitment overfishing. Commercial harvests from whitefish populations are constrained by four parameters (growth, mortality, reproduction, and abundance) that regulate production and yield identified by Healey (1975). In Lake Pend Oreille, abundance most likely will constrain annual yields. The bathymetry of Lake Pend Oreille does not provide ideal habitat for lake whitefish, which thrive in shallower bodies of water with dense benthic macroinvertebrate communities. However, despite this limitation, sustainable annual harvests in excess of 85,000 pounds are antipated based on knowledge of whitefish life-history and biology in Lake Pend Oreille acquired in this study, empirical and theoretical demonstration of whitefish compensation to high rates of exploitation, and the long-history of commercial exploitation of whitefish throughout Canada and the Great Lakes.

Table 1. Sample areas, locations, latitudes, and longitudes of trap-net locations used in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

Sample Area	Net Location	Lattitude	Longitude
North	1. Bottle Bay	48°15.345	116°26.932
	2. Sunnyside Bay	48°16.362	116°23.611
	3. Sunrise Bay	48°14.723	116°22.691
Mid-West	4. Warren Island	48°13.965	116°20.042
	5. Pearl Island	48°13.072	116°19.945
Mid-East	6. Thompson Point	48°11.659	116°17.619
	7. Sheepherder Point	48°11.298	116°16.886
Mid-South	8. Garfield Bay	48°10.531	116°25.984
	9. Whiskey Bay	48°03.317	116°27.473
South	10. Cape Horn	47°58.840	116°30.629
	11. Idlewilde Bay	47°57.178	116°33.913

Table 2. Length summary statistics for lake whitefish caught in trap nets from the north (N), midwest (MW), mideast (ME), midsouth (MS), and south (S) sample areas and from all sample areas combined (Lake) in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	Lake	N	MW	ME	MS	S
Number Caught	12,594	3,053	2,697	1,885	4,707	252
Mean Length	448.15	445.3	445.0	447.2	451.6	459.2
95% Confidence Limit	0.66	1.3	1.5	1.9	1.0	3.9
Standard Deviation	0.34	36.6	40.6	41.2	35.3	31.3
Kurtosis	1.74	1.34	1.86	1.56	1.74	2.07
Skewness	-0.42	-0.29	-0.38	-0.66	-0.31	-0.32
Minimum Length	254	277	263	263	254	336
Maximum Length	670	607	670	583	627	590

Table 3. Length summary statistics for lake whitefish caught in graded mesh gillnets of 2 inch, 2.5 inch, 3 inch, 4 inch, 4.5 inch, and 5.5 inch stretch measure mesh from Lake Pend Oreille, Idaho from 12 February 2006 through 6 April 2006.

	Stetch Mesh Diameter							
	2.0- 5.5"	2.0"	2.5"	3.0"	3.5"	4.0"	4.5"	5.5"
Number Caught	906	29	182	221	228	157	67	2
Mean Length	390.2	315.5	331.6	367.8	414.3	431.0	455.4	431.0
95% Confidence Limit	3.8	11.4	6.5	4.9	5.1	6.2	10.6	1385.0
Standard Deviation	58.6	30.0	44.5	36.6	38.9	39.4	43.6	154.1
Kurtosis	-0.41	1.74	1.53	1.14	12.07	2.34	9.96	-
Skewness	-0.14	1.22	1.32	0.89	-1.75	-1.14	-1.42	-
Minimum Length	127	277	234	310	127	280	238	322
Maximum Length	603	402	498	531	500	548	603	540

Note: Mesh size data was not recorded for 20 fish

Table 4. Sex-composition (proportion female) and 95% confidence interval of lake whitefish caught in trap nets from five sample areas and all areas combined over 11 weeks of sampling in Lake Pend Oreille, Idaho from 5 October 2005 through 15 December 2005. Integers in parentheses are the number of females to the left, and males to the right.

Week	North	Midwest	Mideast	Midsouth	South	Total
10/3/05	-	-	0.50 (0.10-0.90)	0.56 (0.25-0.83)	-	0.54 (0.29-0.78)
	-	-	(2,2)	(5,4)	-	(7,6)
10/10/05	-	0.62 (0.49-0.74)	0.73 (0.49-0.90)	0.83 (0.70-0.92)	0.60 (0.30-0.85)	0.71 (0.63-0.78)
	-	(29,18)	(11,4)	(34,7)	(6,4)	(80,33)
10/17/05	-	0.55 (0.39-0.70)	0.79 (0.65-0.90)	0.73 (0.63-0.81)	-	0.71 (0.64-0.77)
	-	(17,4)	(27,7)	(56,21)	-	(102,42)
10/24/05	1.00	0.50 (0.39-0.70)	0.67 (0.14-0.98)	0.33 (0.02-0.86)	0.71 (0.46-0.90)	0.61 (0.45-0.76)
	(1,0)	(5,5)	(2,1)	(1,2)	(10,4)	(19,12)
10/31/05	0.65 (0.48-0.79)	-	0.50 (0.10-0.90)	0.33 (0.02-0.86)	0.75 (0.25-0.99)	0.62 (0.48-0.74)
	(20,11)	-	(2,2)	(1,2)	(3,1)	(26,16)
11/7/05	0.50 (0.32-0.68)	0.45 (0.20-0.73)	0.52 (0.34-0.69)	-	0.44 (0.17-0.75)	0.49 (0.39-0.59)
	(12,12)	(5,6)	(13,12)	-	(4,5)	(34,35)
11/14/05	1.00	0.46 (0.29-0.64)	0.75 (0.25-0.99)	0.50 (0.03-0.97)	0.80 (0.34-0.99)	0.60 (0.47-0.73)
	(6,0)	(12,14)	(3,1)	(1,1)	(4,1)	(26,17)
11/21/05	0.27 (0.08-0.56)	-	-	-	-	0.27 (0.08-0.56)
	(3,8)	-	-	-	-	(3,8)
11/28/05	0.54 (0.36-0.71)	1.00	0.40 (0.15-0.70)	1.00	1.00	0.58 (0.44-0.71)
	(14,12)	(1,0)	(4,6)	(2,0)	(4,0)	(25,18)
12/5/05	0.79 (0.58-0.92)	0.80 (0.34-0.99)	0.86 (0.61-0.97)	1.00	-	0.83 (0.71-0.92)
	(15,4)	(4,1)	(12,2)	(4,0)	-	(35,7)
12/12/05	0.53 (0.30-0.76)	1.00	0.77 (0.51-0.93)	-	1.00	0.79 (0.68-0.88)
	(8,7)	(6,0)	(10,3)	-	(15,0)	(39,10)
Total	0.59 (0.52-0.66)	0.58 (0.50-0.65)	0.68 (0.61-0.75)	0.74 (0.67-0.79)	0.76 (0.66-0.85)	
	(79,54)	(79,58)	(86,40)	(104,37)	(48,15)	

Table 5. Weight-length equation shape parameter β, 95% confidence interval, condition factor α, coefficient of determination, and sample size used to fit the weight length equation for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	Male	Female	Total	North	Midwest	Mideast	Midsouth	South
Shape Parameter	3.44	3.38	3.36	3.46	3.35	3.28	3.30	3.19
CI (95%)	0.08	0.07	0.05	0.09	0.08	0.27	0.11	0.25
Condition Factor	6.39E-07	9.54E-07	1.05E-06	5.71E-07	1.11E-06	1.68E-06	1.64E-06	3.07E-06
Coefficient of Determination	0.97	0.96	0.97	0.97	0.98	0.97	0.96	0.91
Sample Size	209	395	665	140	158	140	164	63

Table 6. Mean otolith cross-section width (± 95% confidence intervals), relative growth rate, and sample size for annuli 1–42 for lake whitefish sampled in Lake Pend Oreille from 3 October 2005 through 15 December 2005.

Annulus	Count	Average Width	95% LL	95% UL	Growth Rate
1	621	395.1	393.6	396.6	0.345
2	621	531.3	528.8	533.9	0.164
3	613	618.6	615.3	622.0	0.113
4	573	688.4	684.2	692.7	0.085
5	524	746.7	741.6	751.8	0.071
6	457	799.8	793.8	805.8	0.062
7	424	849.0	842.0	856.0	0.053
8	382	893.9	886.1	901.6	0.047
9	364	936.1	927.6	944.7	0.043
10	347	976.6	967.3	986.0	0.042
11	324	1,017.3	1,006.9	1,027.7	0.035
12	292	1,052.5	1,040.8	1,064.2	0.028
13	272	1,082.3	1,070.4	1,094.1	0.033
14	252	1,118.4	1,105.4	1,131.4	0.030
15	235	1,151.7	1,137.7	1,165.7	0.024
16	212	1,179.7	1,164.4	1,195.0	0.022
17	189	1,205.3	1,188.8	1,221.9	0.020
18	164	1,230.0	1,212.0	1,248.1	0.020
19	149	1,254.5	1,235.1	1,274.0	0.022
20	135	1,282.4	1,261.5	1,303.3	0.025
21	124	1,313.9	1,291.3	1,336.5	0.021
22	116	1,342.0	1,317.8	1,366.2	0.021
23	106	1,370.4	1,343.6	1,397.3	0.021
24	93	1,398.7	1,368.6	1,428.8	0.020
25	87	1,427.4	1,395.4	1,459.4	0.021
26	74	1,457.1	1,420.9	1,493.3	0.025
27	63	1,494.2	1,451.8	1,536.6	0.021
28	54	1,526.3	1,477.4	1,575.2	0.004
29	42	1,532.7	1,478.0	1,587.3	0.011
30	29	1,549.5	1,470.2	1,628.8	-0.004
31	22	1,544.0	1,482.1	1,605.9	0.002
32	13	1,546.7	1,455.8	1,637.6	0.002
33	10	1,549.8	1,424.9	1,674.6	0.051
34	6	1,629.0	1,464.1	1,794.0	0.025
35	4	1,669.8	1,337.8	2,001.8	0.086
36	2	1,812.7	-252.7	3,878.1	0.101
37	1	1,995.0	-	-	0.011
38	1	2,016.8	-	-	0.009
39	1	2,035.0	-	-	0.009
40	1	2,053.8	-	-	0.012
41	1	2,078.3	-	-	0.008
42	1	2,094.8	-	-	-

Table 7. Von Bertalanffy length-at-age equation parameters for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	Male	Female	Total	North	Midwest	Mideast	Midsouth	South
Linf	494.82	532.03	537.65	562.61	521.15	523.23	546.12	529.14
K	0.153	0.125	0.125	0.109	0.144	0.147	0.113	0.127
t0	-2.441	-3.012	-2.907	-3.345	-2.133	-2.299	-3.389	-3.099

Table 8. Mean back-calculated length, upper and lower 95% confidence levels, and absolute $\left(G_a\right)$ and relative $\left(G_r\right)$ growth rates of lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

Otolith Age	Sample Size	Calc. Length	95% UL	95% LL	Ga	Gr
1	621	171.5	173.4	169.6	79.66	0.464
2	621	251.2	253.4	249.0	44.72	0.178
3	613	295.9	298.2	293.5	31.58	0.107
4	573	327.5	330.0	324.9	24.01	0.073
5	524	351.5	354.2	348.7	19.45	0.055
6	457	370.9	373.9	368.0	17.47	0.047
7	424	388.4	391.5	385.3	13.87	0.036
8	382	402.3	405.5	399.0	13.92	0.035
9	364	416.2	419.6	412.7	12.41	0.030
10	347	428.6	432.2	424.9	11.34	0.026
11	324	439.9	443.8	436.0	9.95	0.023
12	292	449.9	454.2	445.5	8.58	0.019
13	272	458.5	462.9	454.0	7.38	0.016
14	252	465.8	470.5	461.1	6.15	0.013
15	235	472.0	476.9	467.1	6.38	0.014
16	212	478.4	483.7	473.1	4.91	0.010
17	189	483.3	488.9	477.6	5.21	0.011
18	164	488.5	494.6	482.4	4.46	0.009
19	149	492.9	499.4	486.5	6.02	0.012
20	135	499.0	506.0	491.9	6.39	0.013
21	124	505.4	512.9	497.8	5.14	0.010
22	116	510.5	518.3	502.7	4.25	0.008
23	106	514.7	523.3	506.2	4.58	0.009
24	93	519.3	528.5	510.2	3.35	0.006
25	87	522.7	532.6	512.7	5.83	0.011
26	74	528.5	539.4	517.7	2.95	0.006
27	63	531.5	543.4	519.5	4.93	0.009
28	54	536.4	549.5	523.2	-2.81	-0.005
29	42	533.6	549.5	517.7	1.63	0.003
30	29	535.2	557.8	512.6	-5.23	-0.010
31	22	530.0	551.8	508.1	-1.00	-0.002
32	13	529.0	548.7	509.3	-8.52	-0.016
33	10	520.5	543.0	498.0	-9.17	-0.018
34	6	511.3	550.7	471.9	2.01	0.004
35	4	513.3	588.5	438.1	-4.94	-0.010
36	2	508.4	1186.3	-169.6	49.66	0.098
37	1	558.0	-	-	-2.44	-0.004
38	1	555.6	-	-	-4.74	-0.009
39	1	550.8	-	-	-4.31	-0.008
40	1	546.5	-	-	-0.76	-0.001
41	1	545.8	-	-	-5.77	-0.011
42	1	540.0	-	-	-	-

Table 9. Age versus 10-mm length classes for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	AGE (Years)																																		
Length Class	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	Total
260	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
270	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
280	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
290	2	2	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
300	1	11	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
310	-	11	8	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
320	-	11	7	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
330	-	3	13	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
340	-	2	8	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3
350	-	4	7	9	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
360	-	-	2	9	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
370	-	-	2	17	10	2	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5
380	-	-	1	7	7	1	1	-	2	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
390	-	-	1	5	3	14	4	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
400	-	-	-	1	1	5	5	1	1	2	1	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10
410	-	-	-	1	3	4	2	4	2	6	2	2	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	12
420	-	-	-	2	2	5	3	3	1	2	2	-	-	2	1	3	-	-	1	-	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	15
430	-	-	-	-	-	3	2	2	3	3	1	1	1	1	-	-	2	2	-	-	-	1	-	-	1	-	-	-	-	1	-	-	-	-	-	14
440	-	-	-	-	-	3	-	1	6	1	-	2	1	3	1	2	-	1	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	12
450	-	-	-	-	-	3	1	1	3	6	-	1	1	1	3	-	1	-	3	-	2	2	-	2	-	-	-	-	1	-	-	-	-	-	1	16
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470	-	-	-	-	-	-	-	1	-	5	1	1	2	3	4	2	1	1	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	13
480	-	-	-	-	-	-	-	1	-	2	1	5	-	4	2	4	-	2	2	-	1	-	1	-	2	1	1	-	-	-	-	-	1	-	-	15
490	-	-	-	-	-	-	-	-	-	1	1	2	2	2	1	1	4	1	1	1	1	-	-	1	-	-	-	1	-	-	-	-	-	-	-	14
500	-	-	-	-	-	-	-	-	2	1	2	2	1	-	4	3	1	2	-	1	2	1	3	1	1	-	-	2	-	-	-	1	-	1	-	18
510	-	-	-	-	-	-	-	-	-	-	-	1	2	1	1	2	3	-	-	-	2	1	1	1	-	2	-	-	-	-	1	-	-	-	-	12
520	-	-	-	-	-	-	-	-	-	-	1	1	1	2	2	2	-	1	1	3	-	-	-	-	-	1	1	1	-	1	-	-	-	1	-	14
530	-	-	-	-	-	-	-	-	-	-	2	-	2	1	1	1	-	1	-	-	-	2	1	1	-	1	1	2	-	-	-	1	1	-	-	14
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560	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	1	-	-	-	-	1	2	-	2	1	1	1	-	-	-	-	-	9
570	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	3	1	-	-	-	-	-	-	-	4
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670	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1

Table 10. Observed length-at-age (mm), 95% confidence intervals, minimum and maximum lengths, and length range for age 2 through age 42 lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

Age	Sample Size	Length	95% CI	Minimum	Maximum	Length Range
2	8	285.00	12.58	263	308	45
3	45	318.24	4.95	280	358	78
4	52	336.35	6.01	283	392	109
5	67	363.36	6.90	263	426	163
6	33	379.64	9.05	317	427	110
7	43	407.65	7.66	351	458	107
8	18	411.83	8.67	385	455	70
9	17	430.47	13.05	396	480	84
10	23	438.87	14.16	379	508	129
11	32	448.16	9.80	408	500	92
12	20	467.70	22.08	385	545	160
13	20	477.45	16.74	410	550	140
14	17	487.24	20.85	401	558	157
15	23	480.35	16.46	423	580	157
16	23	494.70	17.06	427	600	173
17	25	492.24	18.01	418	567	149
18	15	499.60	22.40	434	569	135
19	14	483.50	20.22	431	540	109
20	11	480.09	25.05	427	563	136
21	8	500.00	46.45	400	578	178
22	10	503.20	23.06	453	555	102
23	13	503.38	30.65	419	583	164
24	6	506.00	15.21	486	530	44
25	13	499.38	28.70	420	567	147
26	11	520.18	31.43	437	571	134
27	9	511.22	35.49	425	580	155
28	12	551.75	24.58	476	592	116
29	13	531.77	20.62	466	589	123
30	7	551.71	82.10	419	670	251
31	9	532.22	53.39	426	607	181
32	3	554.00	93.38	515	590	75
33	4	535.25	32.39	508	554	46
34	2	509.00	266.83	488	530	42
35	2	513.50	146.12	502	525	23
36	1	455.00	-	-	-	-
42	1	540.00	-	-	-	-

Table 11. Average observed weight with 95% confidence interval, absolute (grams per year) and relative growth rates, Von Bertalanffy weight-age estimates and estimated absolute (grams per year) and relative growth rates for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

Age	Number	Average Weight	95% CI	Gr	Ga	Weight Estimate	Gr Estimate	Ga Estimate
1	0	-	-	-	-	64.50	0.187	50.21
2	8	192.50	41.18	0.34	66.03	114.71	0.139	62.94
3	45	258.53	13.99	0.23	59.49	177.65	0.108	72.91
4	52	318.02	20.20	0.36	115.37	250.56	0.086	79.92
5	67	433.39	30.89	0.17	74.46	330.48	0.070	84.12
6	33	507.85	43.43	0.28	141.01	414.60	0.058	85.87
7	43	648.86	45.04	0.07	46.03	500.47	0.048	85.57
8	18	694.89	57.41	0.15	104.82	586.04	0.040	83.65
9	17	799.71	78.97	0.12	94.99	669.69	0.034	80.52
10	23	894.70	96.96	0.05	45.02	750.21	0.029	76.53
11	32	939.72	53.92	0.15	137.68	826.75	0.025	71.98
12	20	1,077.40	143.07	0.05	55.45	898.73	0.022	67.11
13	20	1,132.85	117.27	0.08	91.39	965.84	0.019	62.10
14	17	1,224.24	168.50	-0.08	-93.63	1,027.94	0.016	57.11
15	23	1,130.61	129.92	0.05	52.48	1,085.04	0.014	52.23
16	23	1,183.09	117.59	0.00	5.07	1,137.28	0.012	47.56
17	25	1,188.16	131.93	0.10	120.24	1,184.83	0.011	43.13
18	15	1,308.40	175.76	-0.18	-233.47	1,227.96	0.009	38.98
19	14	1,074.93	123.54	0.09	98.80	1,266.94	0.008	35.12
20	11	1,173.73	181.36	0.13	155.52	1,302.06	0.007	31.57
21	8	1,329.25	376.67	-0.11	-143.95	1,333.63	0.006	28.31
22	10	1,185.30	177.57	0.08	97.01	1,361.94	0.005	25.34
23	13	1,282.31	265.90	0.06	72.03	1,387.29	0.005	22.65
24	6	1,354.33	283.91	-0.03	-45.64	1,409.93	0.004	20.21
25	13	1,308.69	244.10	0.09	118.13	1,430.14	0.004	18.01
26	11	1,426.82	300.12	-0.16	-233.57	1,448.14	0.003	16.03
27	8	1,193.25	298.78	0.35	419.42	1,464.17	0.003	14.25
28	12	1,612.67	278.30	-0.08	-121.05	1,478.42	0.003	12.66
29	13	1,491.62	217.33	0.17	248.53	1,491.08	0.002	11.24
30	7	1,740.14	691.23	-0.08	-136.70	1,502.32	0.002	9.97
31	9	1,603.44	495.47	0.13	205.22	1,512.29	0.002	8.84
32	3	1,808.67	400.30	-0.10	-181.67	1,521.13	0.002	7.83
33	4	1,627.00	436.65	-0.26	-417.50	1,528.97	0.001	6.94
34	2	1,209.50	4,301.05	0.10	116.50	1,535.91	0.001	6.14
35	2	1,326.00	482.84	-0.36	-473.00	1,542.05	0.001	5.44
36	1	853.00	-	0.79	671.00	1,547.49	0.001	4.81
37	-	-	-	-	-	1,552.30	0.001	4.26
38	-	-	-	-	-	1,556.56	0.001	3.76
39	-	-	-	-	-	1,560.33	0.001	3.33
40	-	-	-	-	-	1,563.65	0.001	2.94
41	-	-	-	-	-	1,566.60	0.000	2.60
42	1	1,524.00	-	-	-	1,569.20		

Table 12. Back-calculated length-at-annulus 1-10 for estimated age-at-capture 2-42 for lake whitefish caught in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

		Annulus									
Age at capture	Sample Size	1	2	3	4	5	6	7	8	9	10
2	8	195.8	285.0	-	-	-	-	-	-	-	-
3	40	177.2	273.3	317.2	-	-	-	-	-	-	-
4	49	171.0	250.5	302.1	336.1	-	-	-	-	-	-
5	67	177.5	258.3	303.5	341.0	363.4	-	-	-	-	-
6	33	173.9	252.4	299.9	332.6	362.7	379.6	-	-	-	-
7	42	176.9	258.1	302.6	338.0	363.2	388.4	408.5	-	-	-
8	18	163.5	247.6	289.8	323.5	351.8	374.4	395.2	411.8	-	-
9	17	170.3	253.0	299.8	332.2	357.5	379.9	399.2	416.9	430.5	-
10	23	172.8	245.5	290.2	326.3	354.0	373.9	392.2	407.4	422.9	438.9
11	32	167.1	247.1	289.1	321.6	348.0	370.4	388.7	405.5	419.9	434.2
12	20	159.6	238.9	284.0	315.4	342.6	365.7	390.6	410.1	427.2	440.9
13	20	181.0	260.4	302.6	333.3	357.3	379.9	399.6	416.3	431.7	444.7
14	17	175.2	252.3	297.9	330.9	354.4	375.8	394.8	413.7	429.0	442.3
15	23	163.1	243.9	290.4	323.8	348.1	368.1	384.8	400.2	416.0	429.8
16	23	161.6	237.7	284.8	320.7	349.1	373.9	391.4	407.0	421.6	435.5
17	25	164.7	242.2	288.6	322.8	347.0	370.1	390.6	408.4	421.1	431.9
18	15	166.7	241.7	285.4	318.9	342.3	360.9	380.0	397.4	411.5	425.3
19	14	164.2	231.9	277.8	306.4	327.8	345.7	359.4	374.5	388.6	401.8
20	11	170.1	248.7	289.5	318.0	339.7	359.1	374.0	390.2	402.7	415.5
21	8	172.4	245.3	287.7	314.9	339.9	357.1	373.1	387.8	402.5	416.8
22	10	165.2	240.3	287.9	318.5	346.3	372.0	387.8	402.3	414.4	427.2
23	13	167.4	246.8	286.4	315.6	339.0	360.5	377.3	389.1	404.7	415.5
24	6	183.1	260.5	304.3	331.3	355.4	373.2	386.1	398.7	410.1	420.4
25	13	169.5	239.9	281.8	310.5	332.1	349.7	368.1	382.8	396.7	407.7
26	11	179.4	265.0	307.7	334.4	352.7	371.4	389.8	408.3	423.4	434.0
27	9	165.2	232.6	274.5	305.3	331.2	349.6	366.6	383.4	401.5	418.7
28	12	161.2	231.8	275.5	310.0	333.7	355.0	368.5	383.8	399.7	415.0
29	13	170.2	240.2	282.8	315.8	335.8	356.1	371.6	386.9	398.8	409.6
30	7	171.7	254.6	296.2	321.8	342.1	365.6	384.3	396.9	409.8	424.6
31	9	165.2	250.5	293.9	323.7	352.8	375.4	393.4	408.4	422.2	435.7
32	3	179.8	257.5	310.0	339.5	362.9	377.4	386.1	400.1	414.4	427.5
33	4	210.7	311.7	359.9	391.5	414.5	431.0	443.7	451.4	458.7	466.5
34	2	174.8	248.6	318.5	342.4	364.1	386.5	392.1	398.5	407.5	417.6
35	2	186.6	250.5	301.7	337.0	364.7	377.3	391.3	411.6	418.1	424.4
36	1	169.8	266.3	315.9	354.1	368.0	381.6	404.0	416.2	428.0	436.9
42	1	125.0	197.0	244.6	282.3	311.1	327.3	344.5	358.0	381.3	383.3

Table 13. Length- and age-at-maturity regression model parameters for full (Male, Female), reduced (Total) lake-wide, and sample area-specific models, with length- and age-at-first and full (100%) maturity for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

		Lake-Wide			Sample Areas				
		Male	Female	Total	North	Midwest	Mideast	Midsouth	South
Length	Xm	377.9	390.01	383.08	367.97	382.12	394.69	395.5	-
	r	0.186	0.0605	0.074	0.203	0.074	0.074	0.097	-
	1st Maturity	340	350	340	340	340	370	350	410
	Full Maturity	430	440	440	420	440	420	430	430
	Sample Size	200	362	562	131	126	119	132	54
Age	Xm	6.00	6.47	6.24	5.44	6.65	6.66	7.36	6.50
	r	1.84	1.12	6.24	2.38	1.62	0.90	1.05	24.69
	1st Maturity	4	5	4	5	4	5	6	5
	Full Maturity	11	12	12	12	11	9	11	10
	Sample Size	194	340	534	122	118	117	129	48

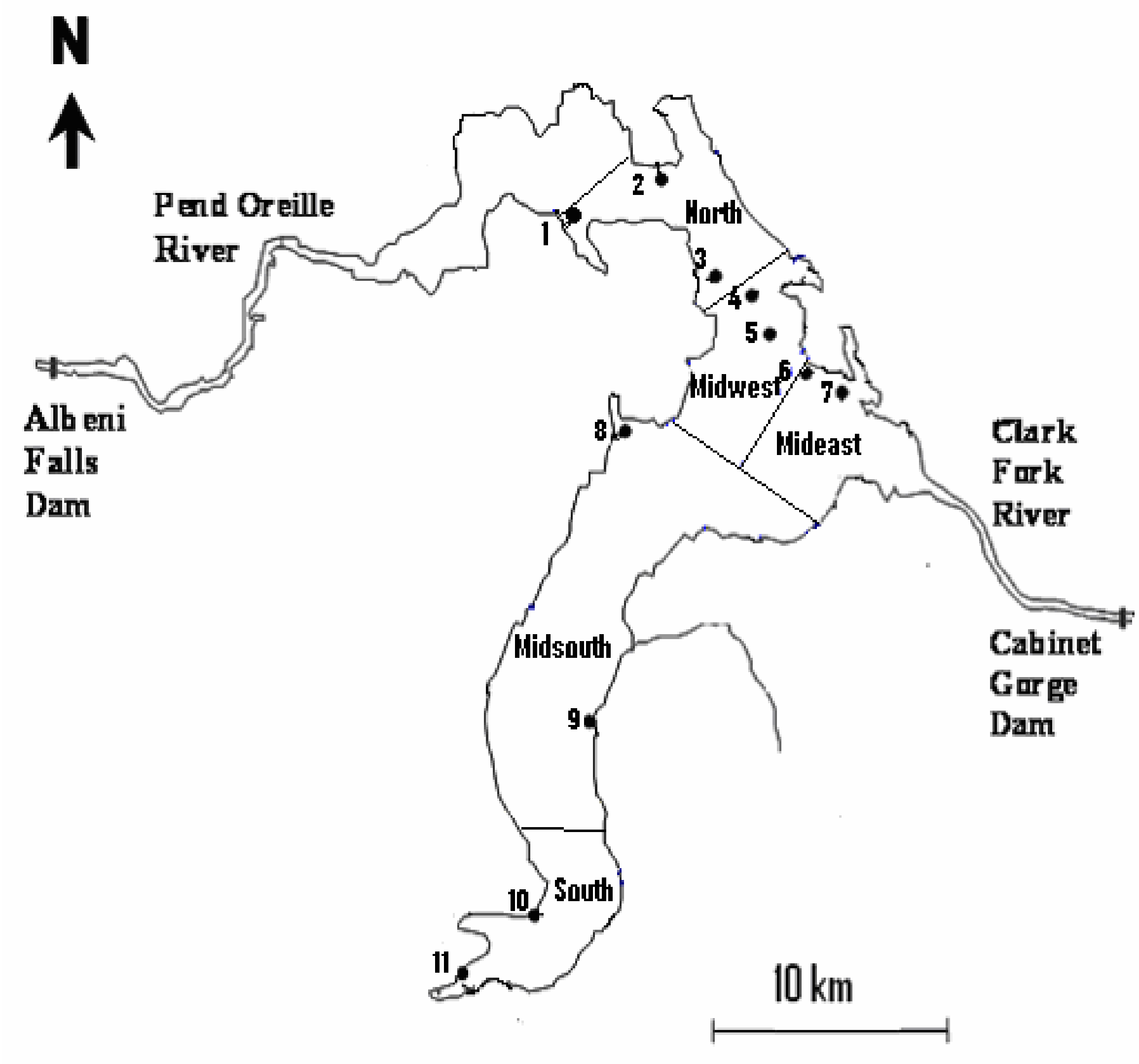

Figure 1. Trap net locations and sample regions for lake whitefish in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

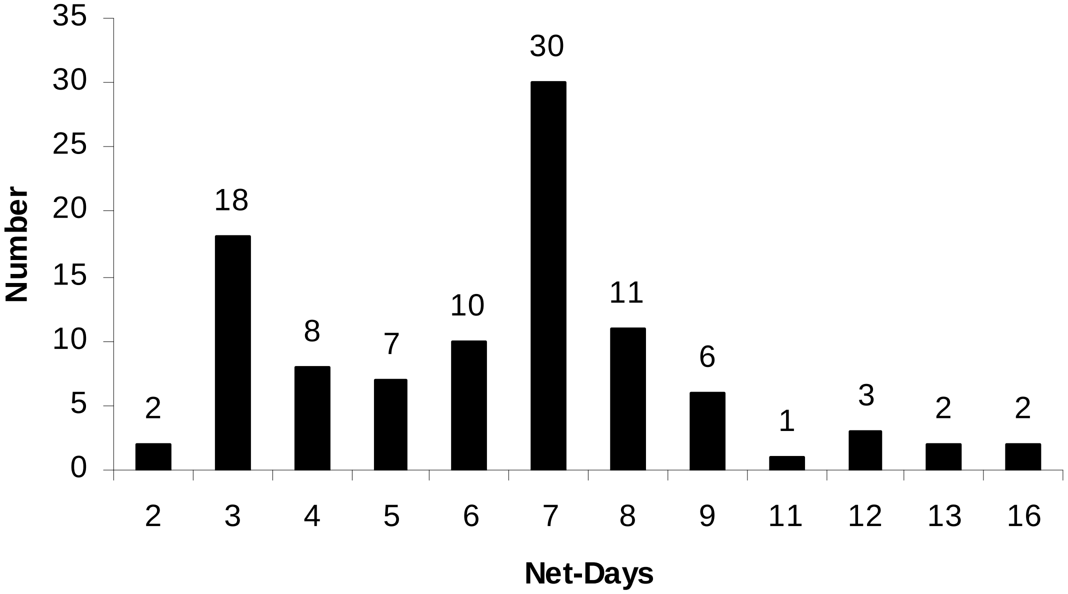

Figure 2. Number of days soaked by trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

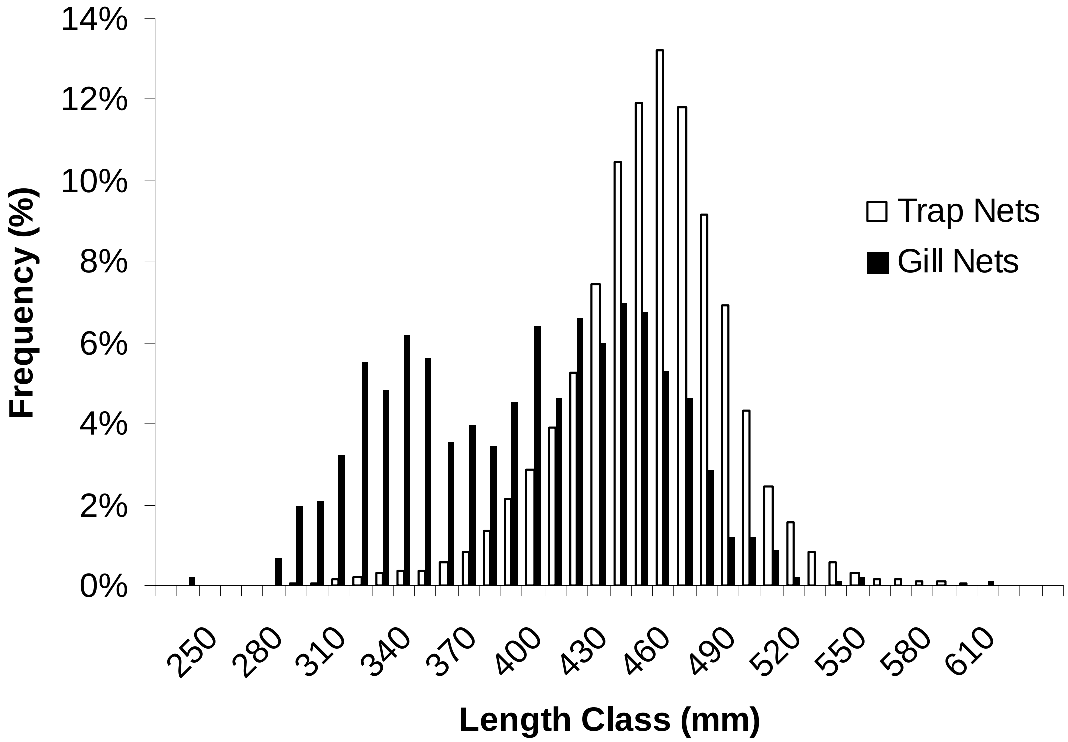

Figure 3. Length-frequency distribution of lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005 and in gill nets from 12 February 2006 through 6 April 2006.

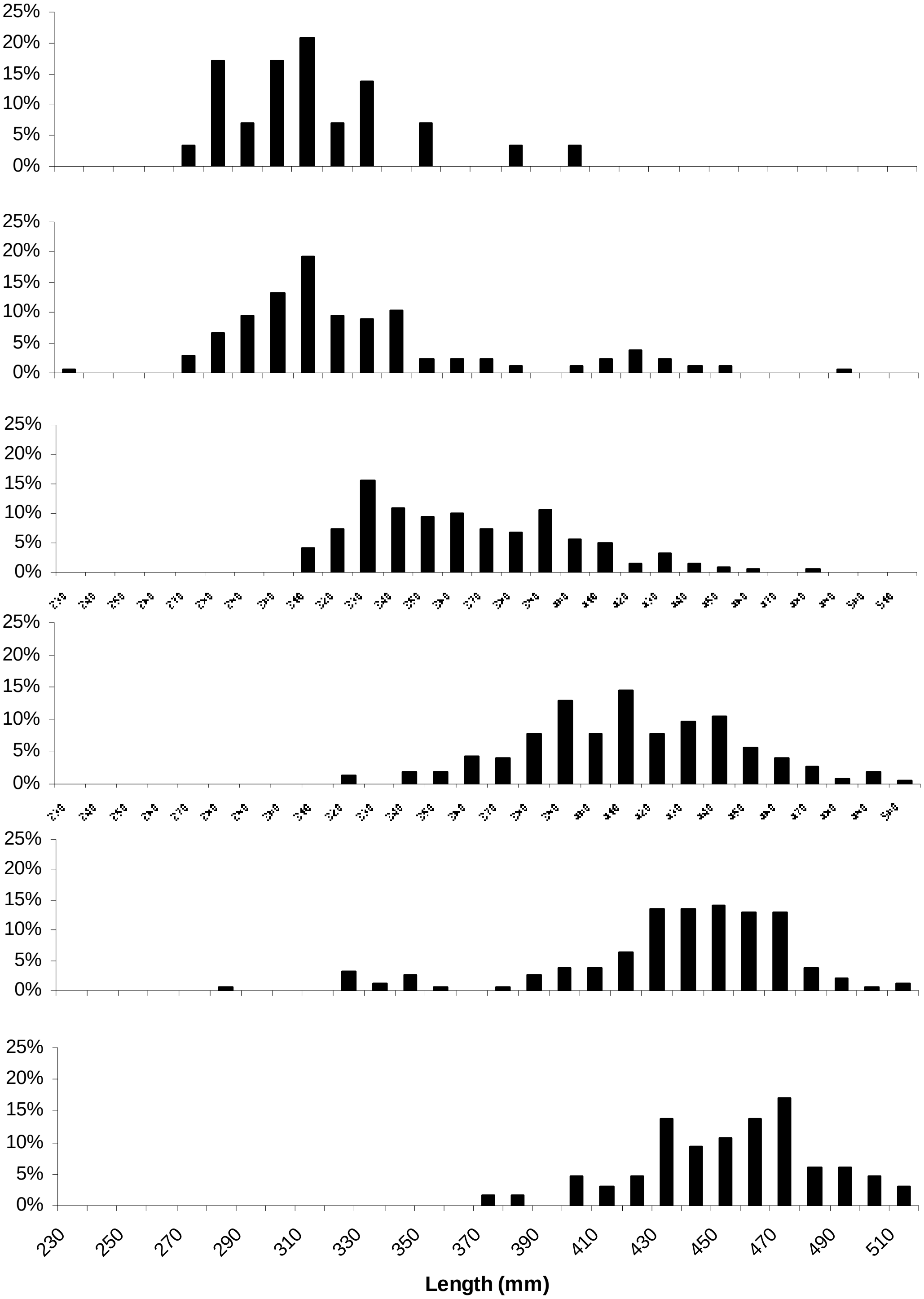

Figure 4. Length-frequency distribution of lake whitefish caught in graded mesh gill nets in Lake Pend Oreille, Idaho from 12 February 2006 through 6 April 2006 using 2-inch (top panel) through 4.5-inch (bottom panel) meshes in 0.5-inch increments.

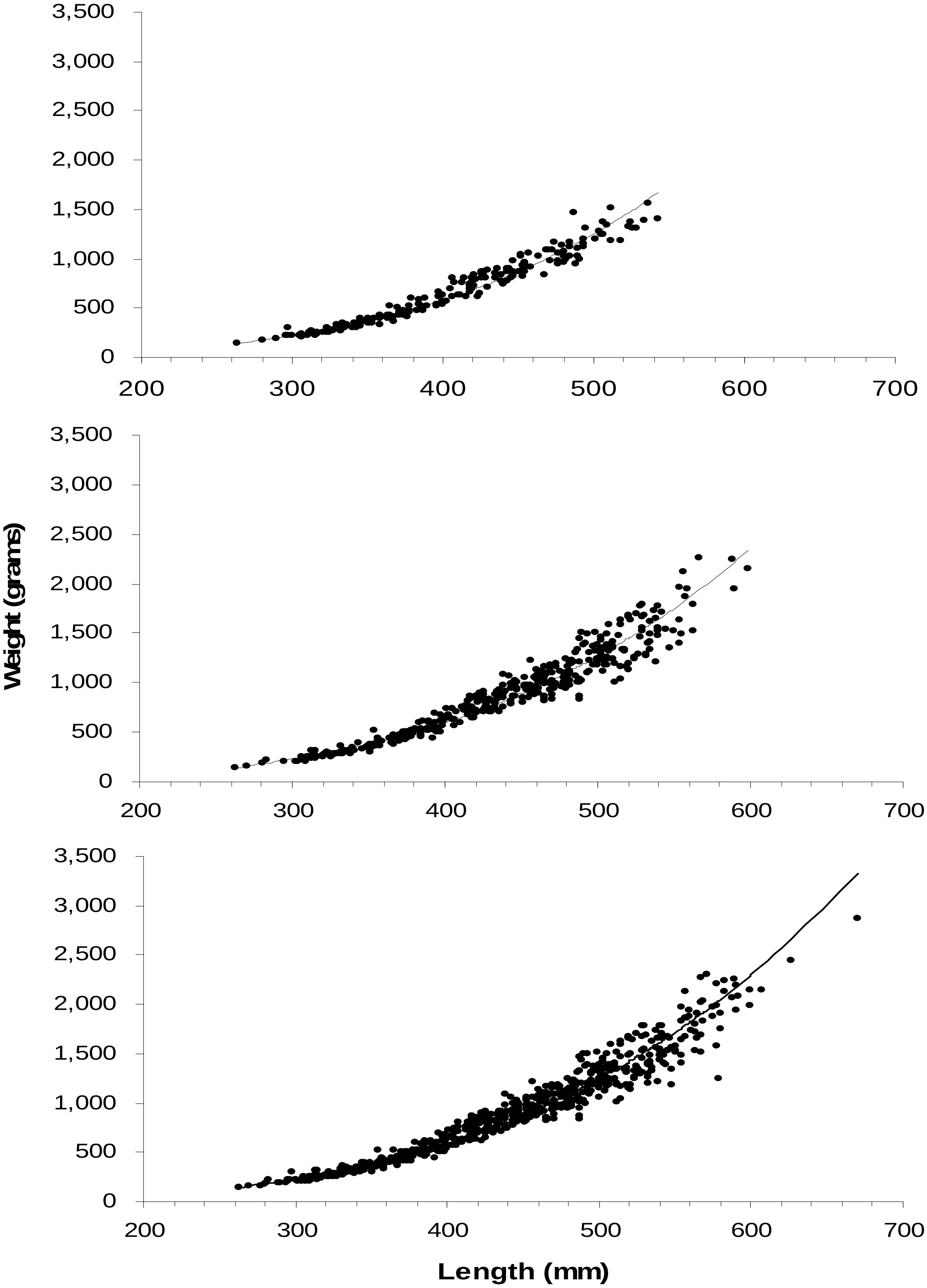

Figure 5. Weight-length relationships for male (top panel), female (middle panel), and all (bottom panel) lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

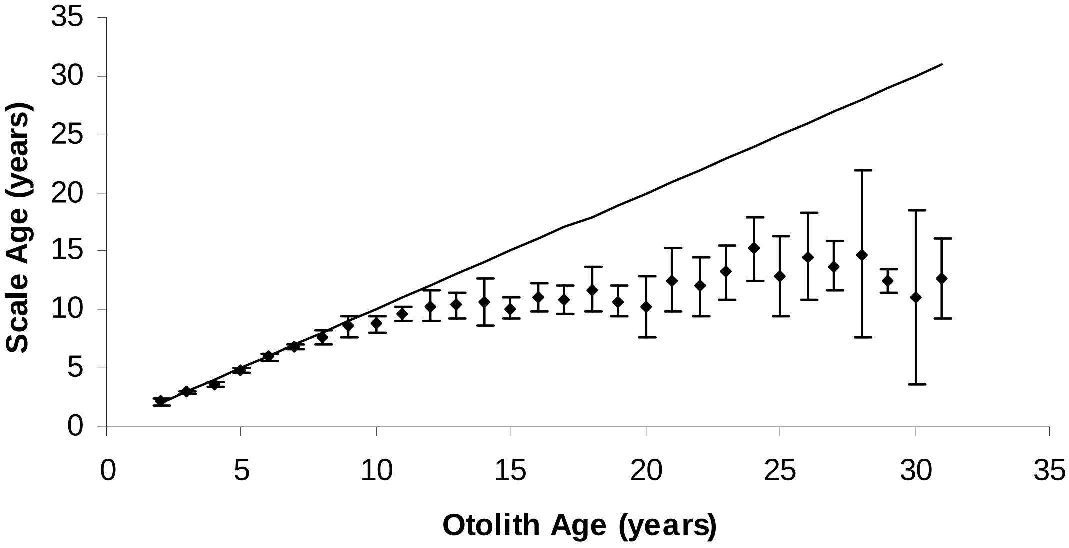

Figure 6. Age-bias plot of estimated scale age against estimated otolith age for lake whitefish caught in Lake Pend Oreille, Idaho in trap nets from 3 October 2005 through 15 December 2005.

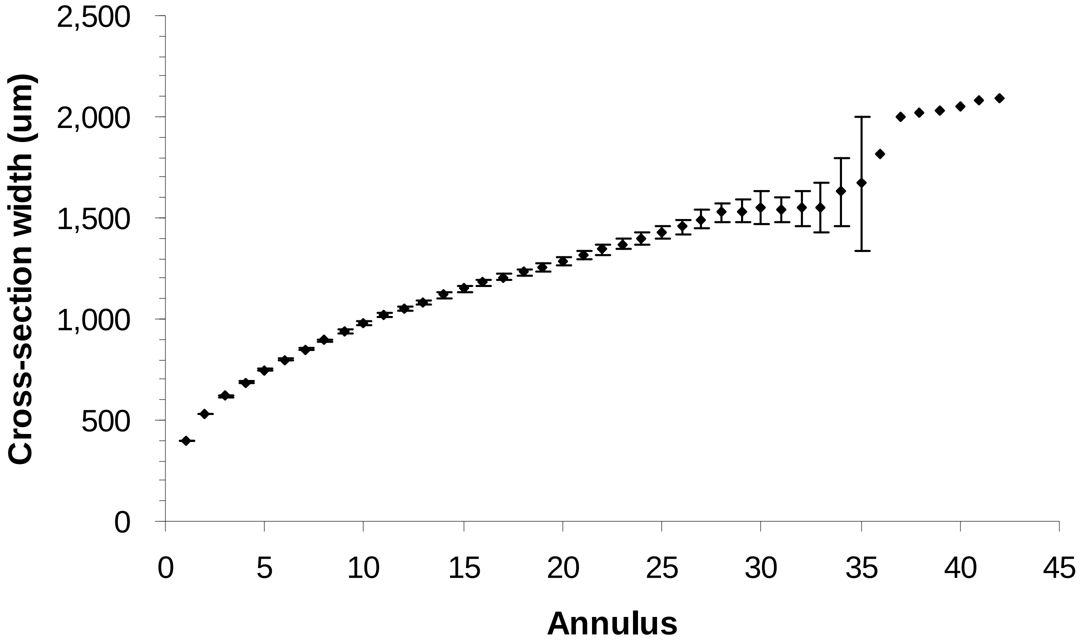

Figure 7. Otolith cross-section annulus width (± 95% confidence intervals) versus age for lake whitefish caught in Lake Pend Oreille, Idaho in trap nets from 3 October 2005 through 15 December 2005.

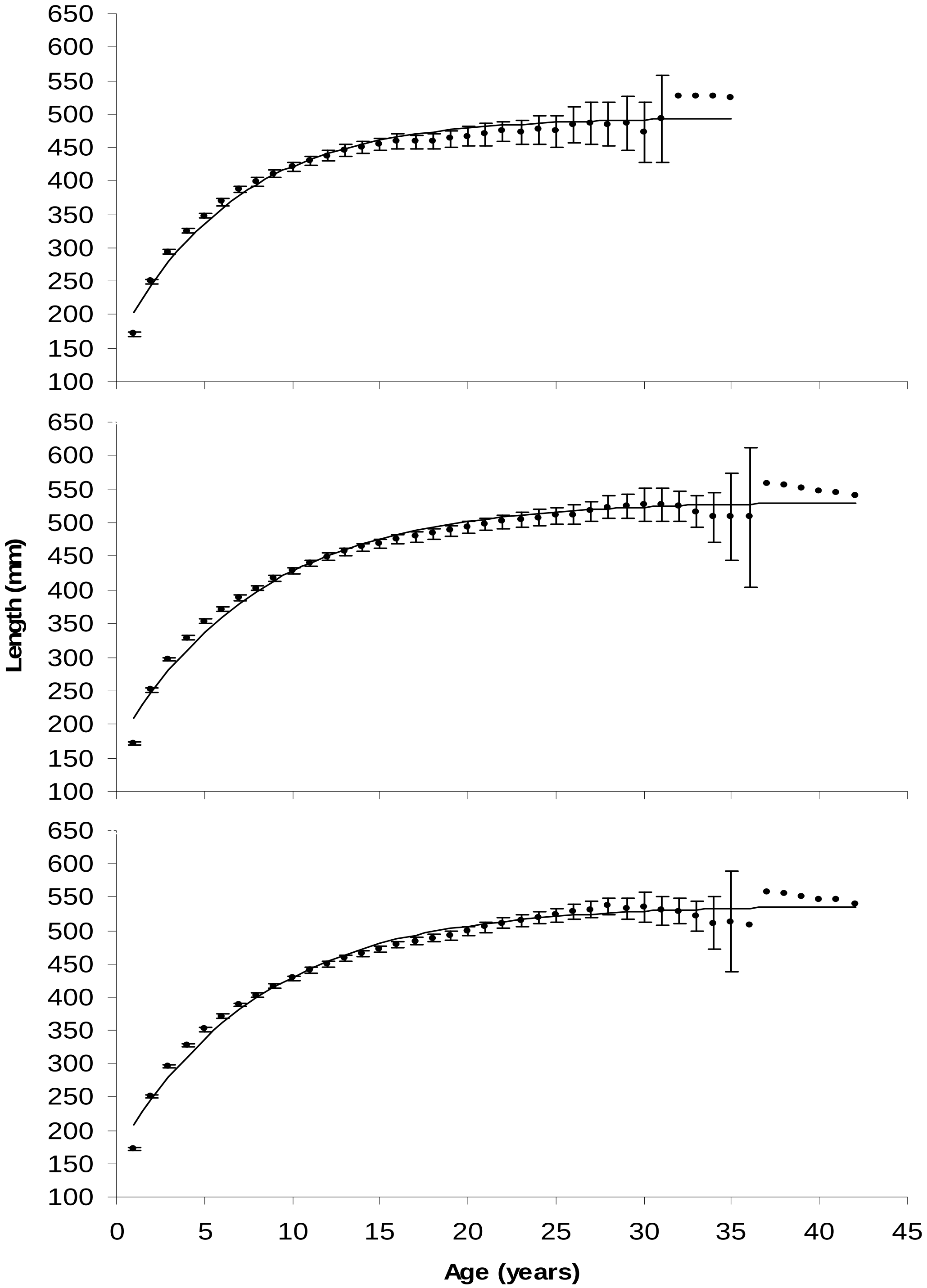

Figure 8. Back-calculated length-age (+ 95% confidence intervals) and fitted Von Bertlanaffy length-age equations for male (top panel), female (middle panel), and combined gender (bottom panel) lake whitefish caught in Lake Pend Oreille, Idaho in trap nets from 3 October 2005 through 15 December 2005.

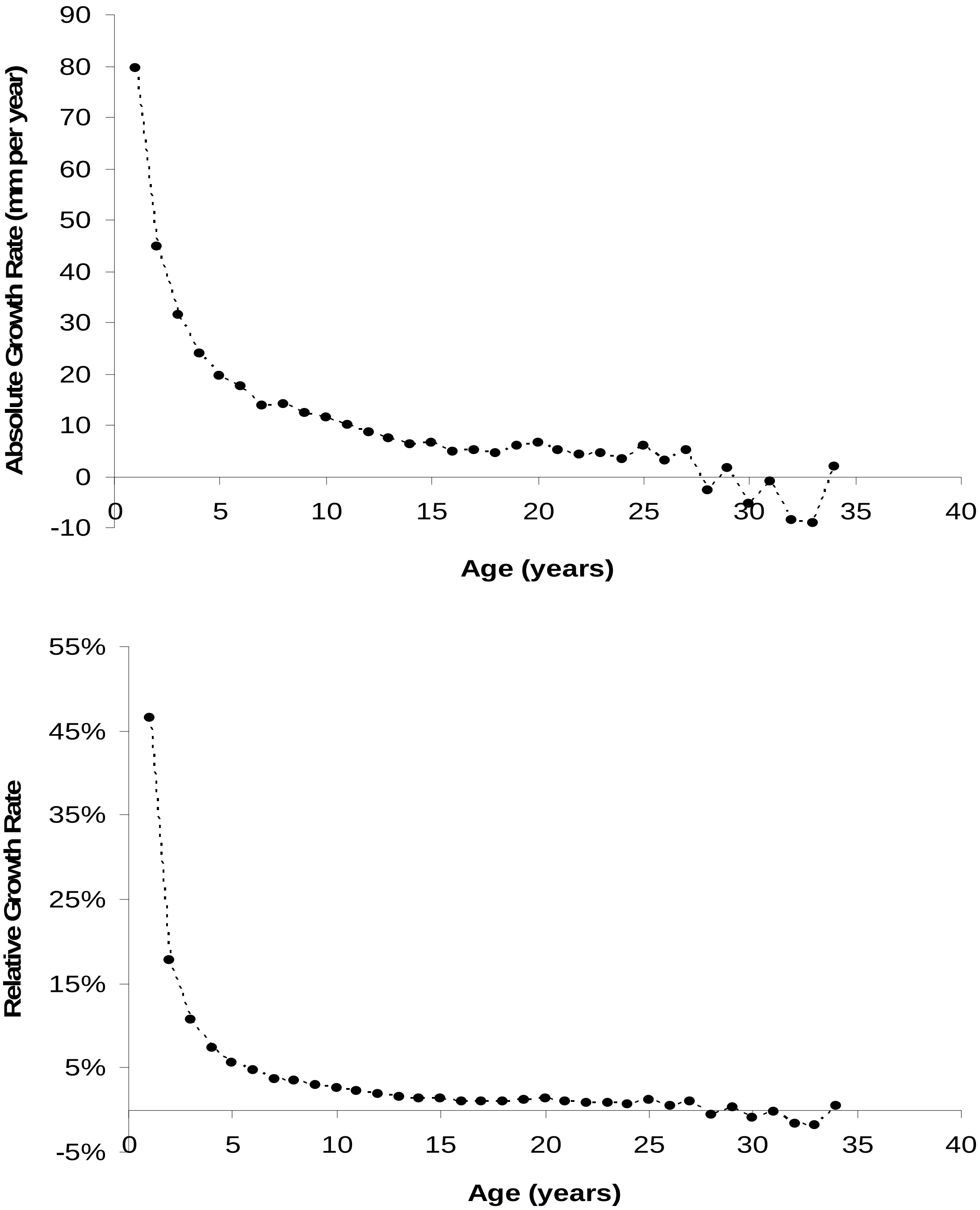

Figure 9. Absolute (top panel) and relative (bottom panel) growth rates estimated from mean back-calculated length-age data summarized as mean length at age of lake whitefish caught in Lake Pend Oreille, ID in trap nets from 3 October 2005 through 15 December 2005.

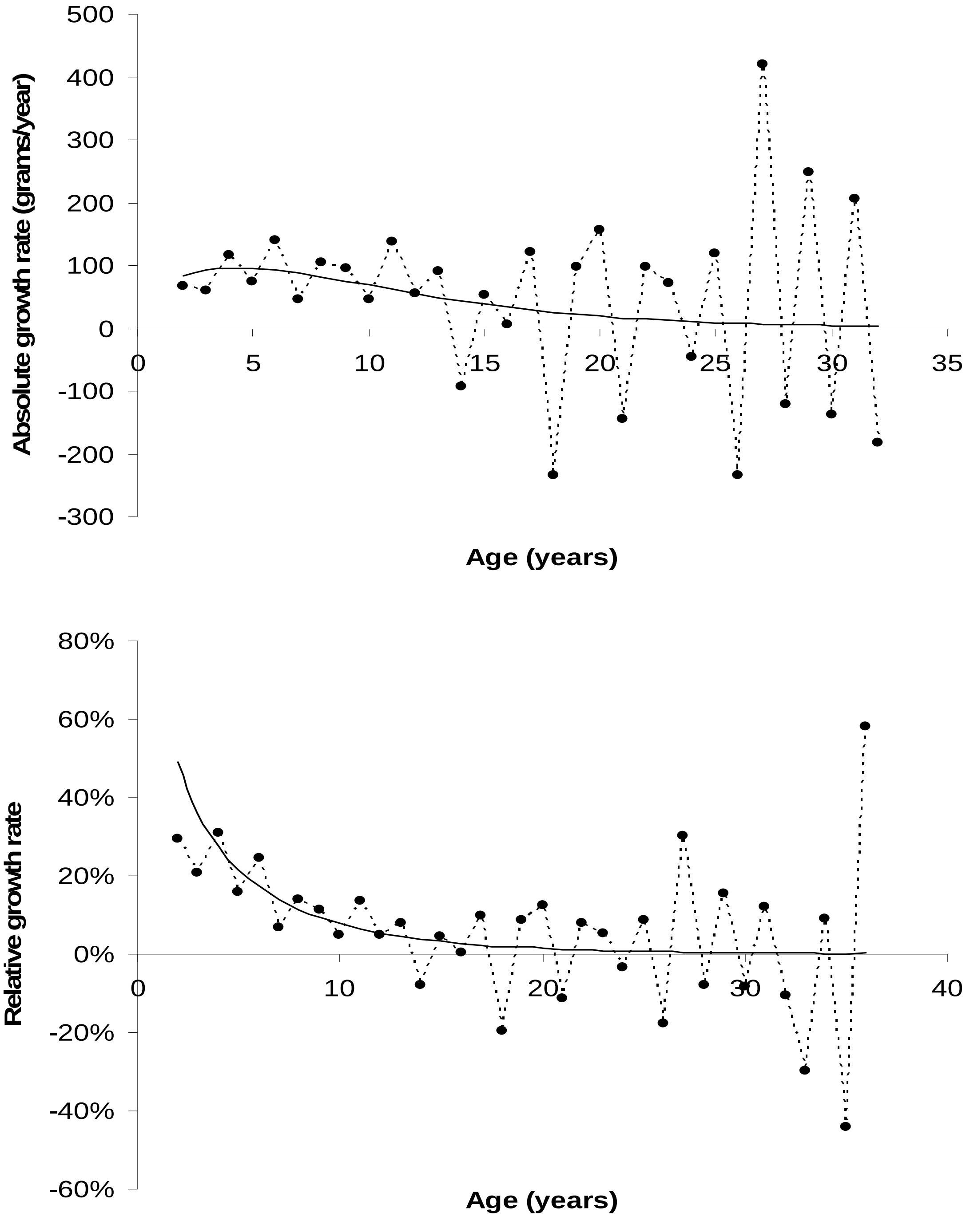

Figure 10. Absolute (top panel) and relative (bottom panel) growth rates estimated from mean weight-at-age data and the fitted Von Bertalanffy weight-age equation (smooth line) of lake whitefish caught in Lake Pend Oreille, Idaho in trap nets from 3 October 2005 through 15 December 2005.

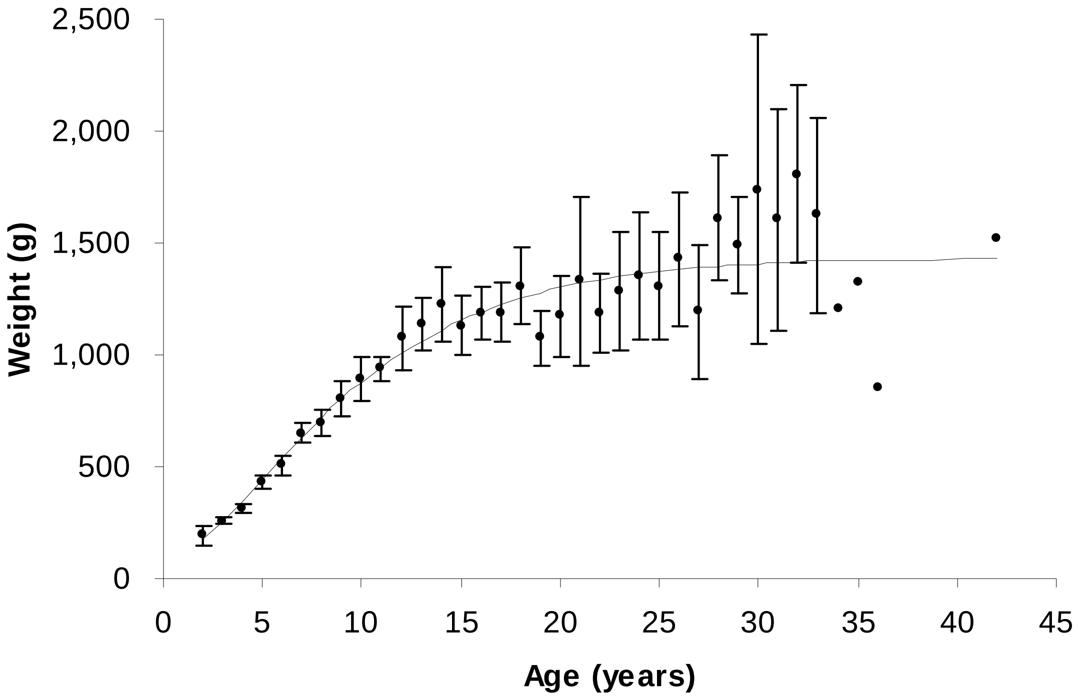

Figure 11. Mean weight-at-age data (± 95% confidence intervals) and fitted Von Bertlanaffy weight-age equation for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

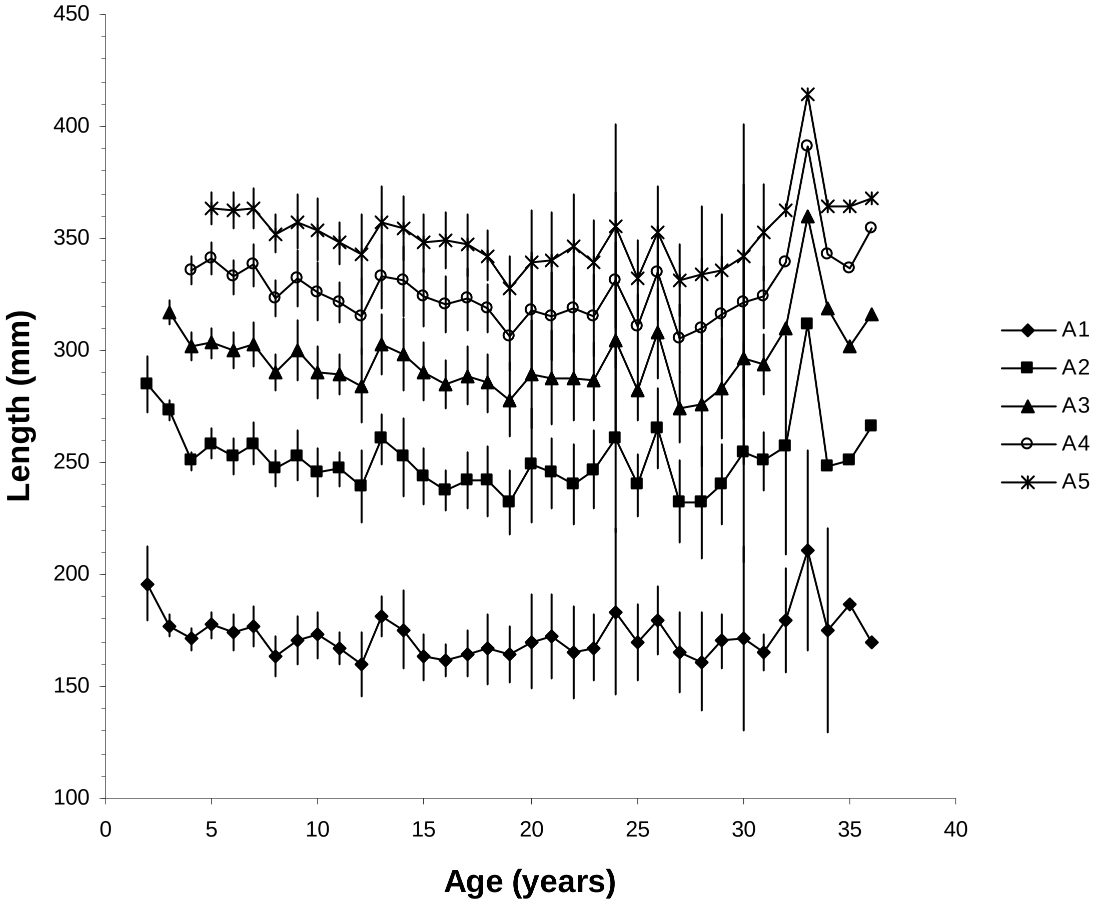

Figure 12. Back-calculated mean length at annuli 1-5 for otolith ages 2–36 for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

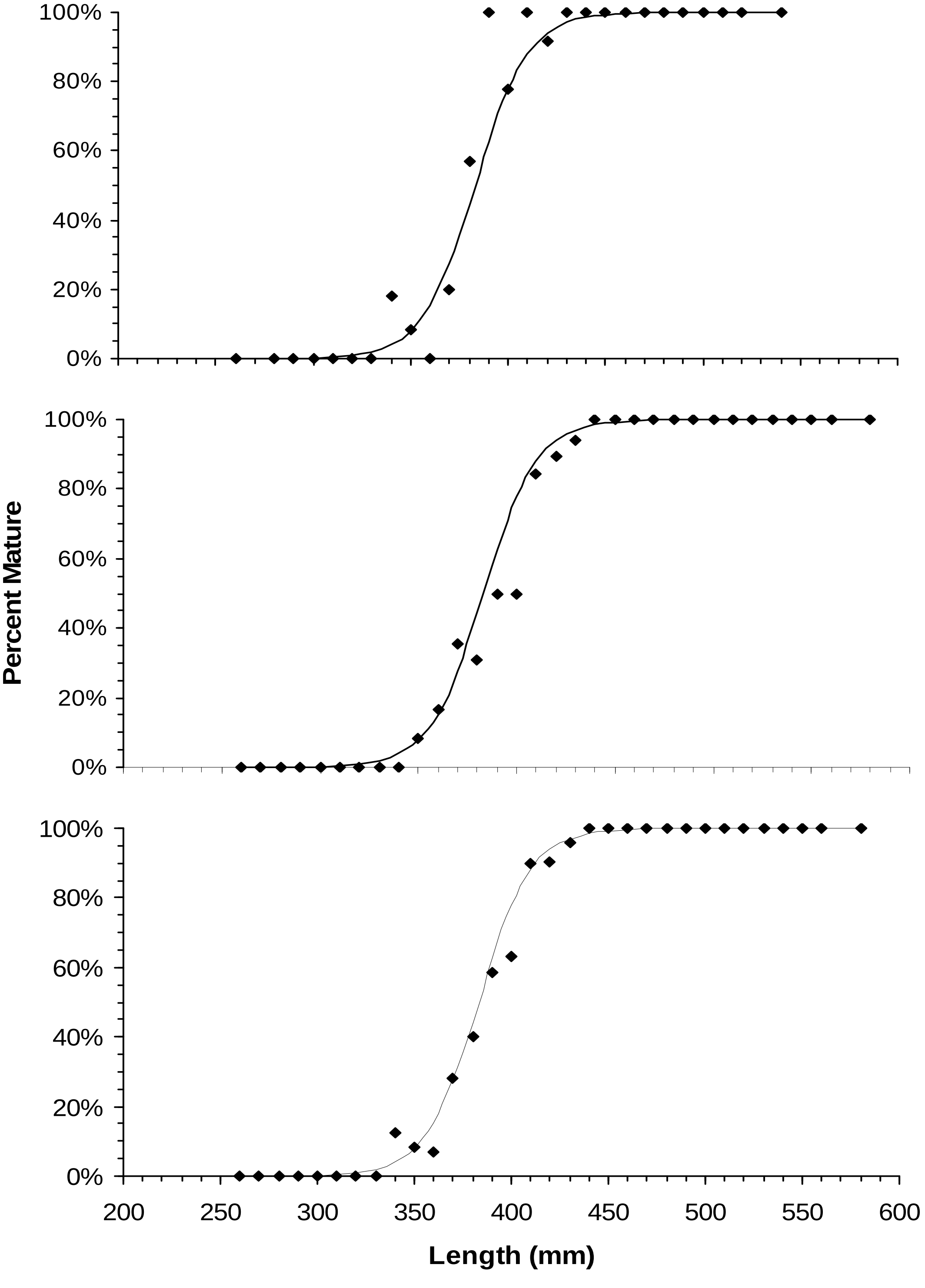

Figure 13. Percent mature in each 10-mm length class and fitted logistic regression model for male (top panel), female (middle panel), and all (bottom panel) lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

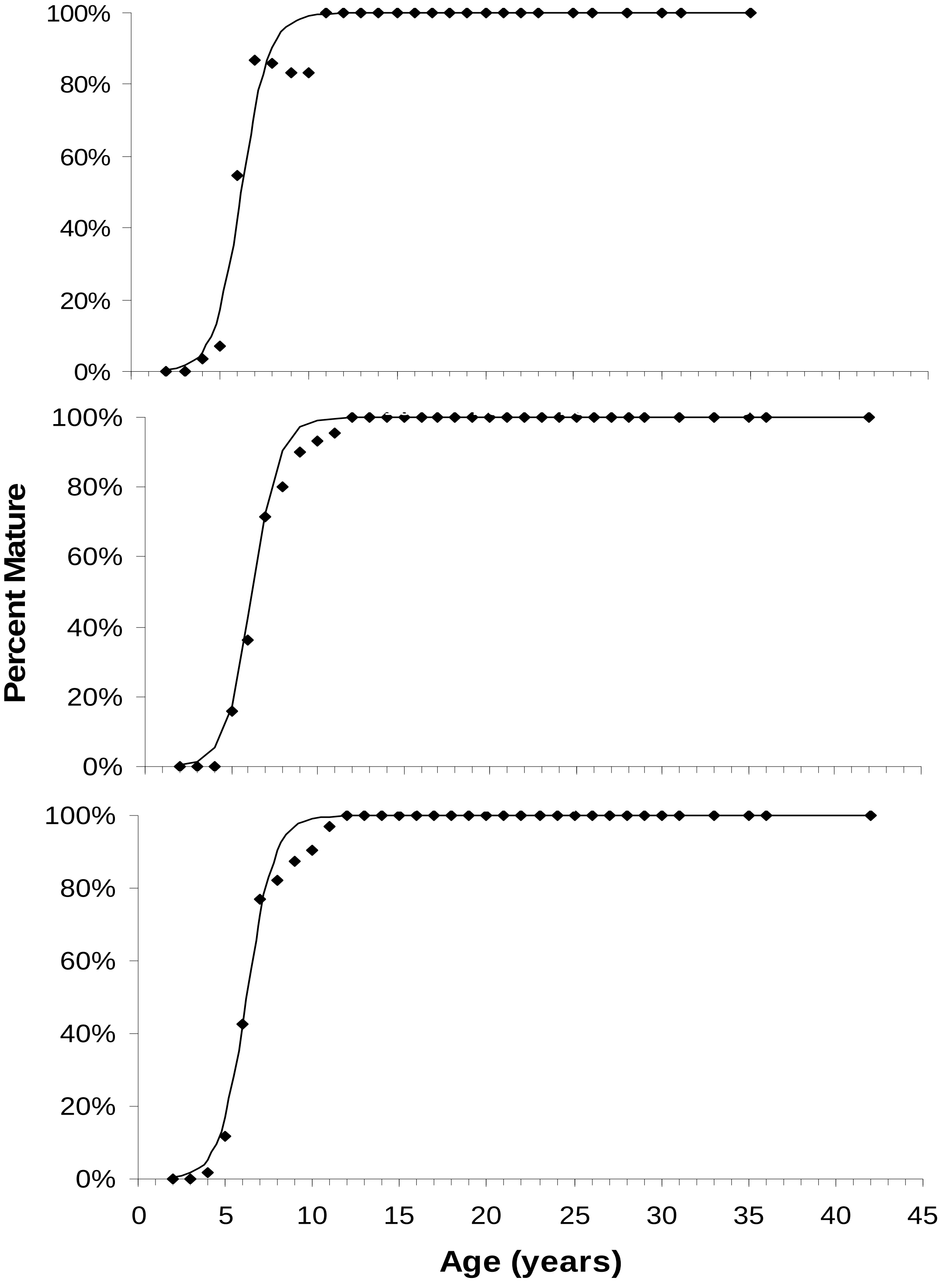

Figure 14. Percent mature at each age and fitted logistic maturity regression curve for male (top panel), female (middle panel) and all (bottom panel) lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

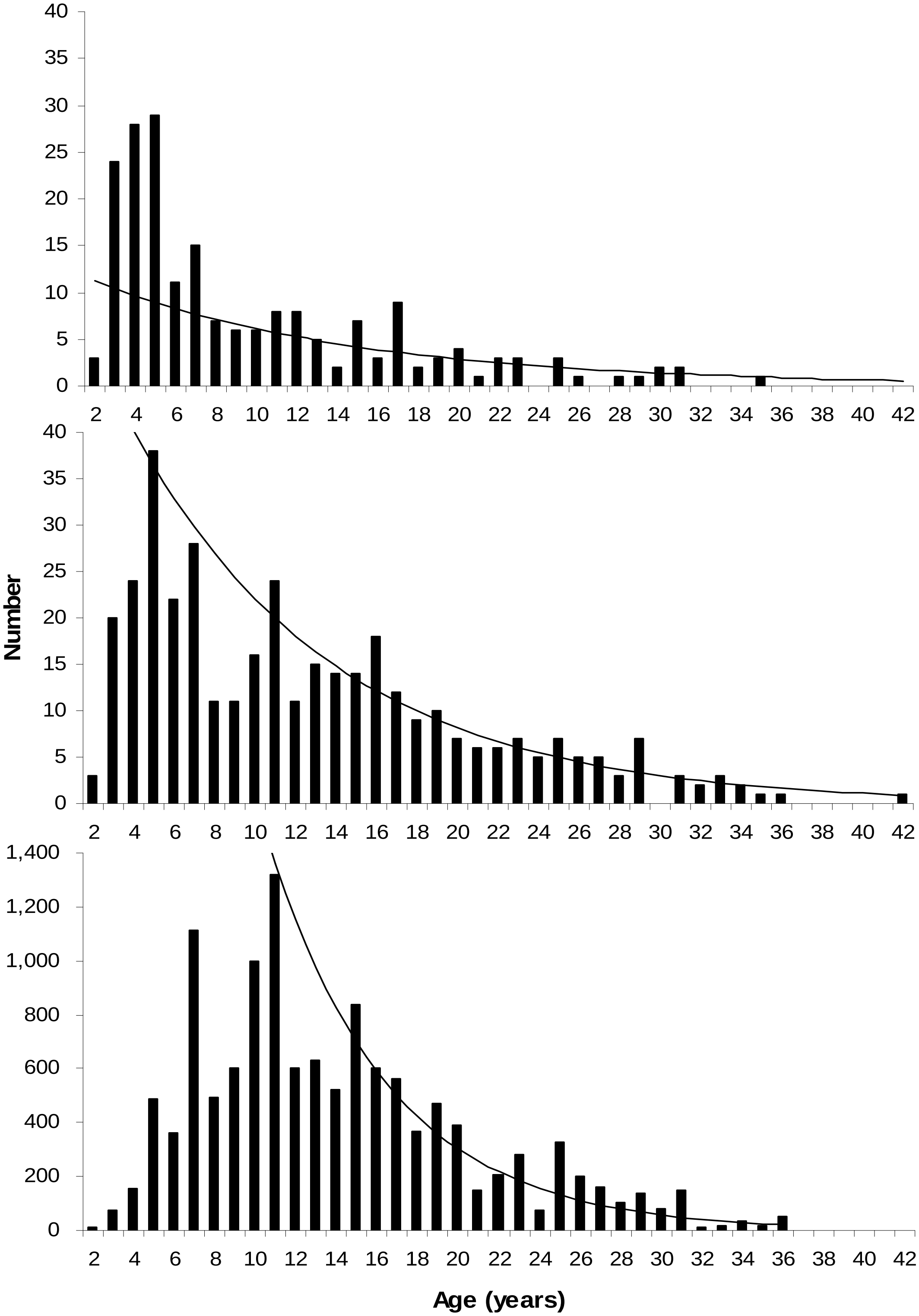

Figure 15. Age frequency and catch-curve for male (top panel), female (middle panel), and combined gender (bottom panel) lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

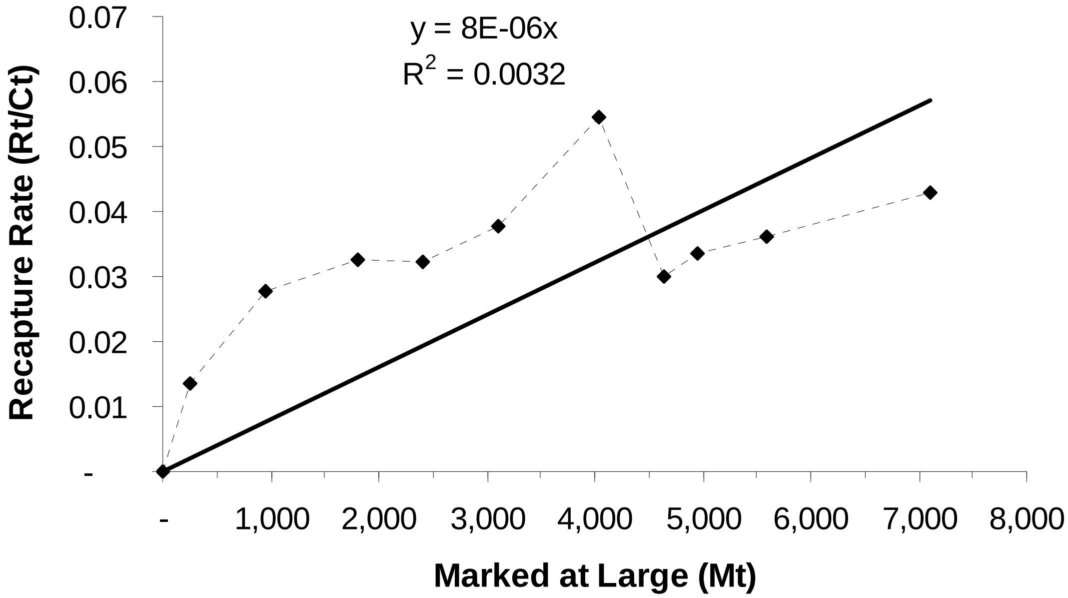

Figure 16. Schumacher-Eschmeyer multiple-census mark-recapture model of the recapture rate of previously marked lake whitefish (Rt/Ct) versus the number of marked lake whitefish at large (Mt) over 10 weekly sampling periods in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

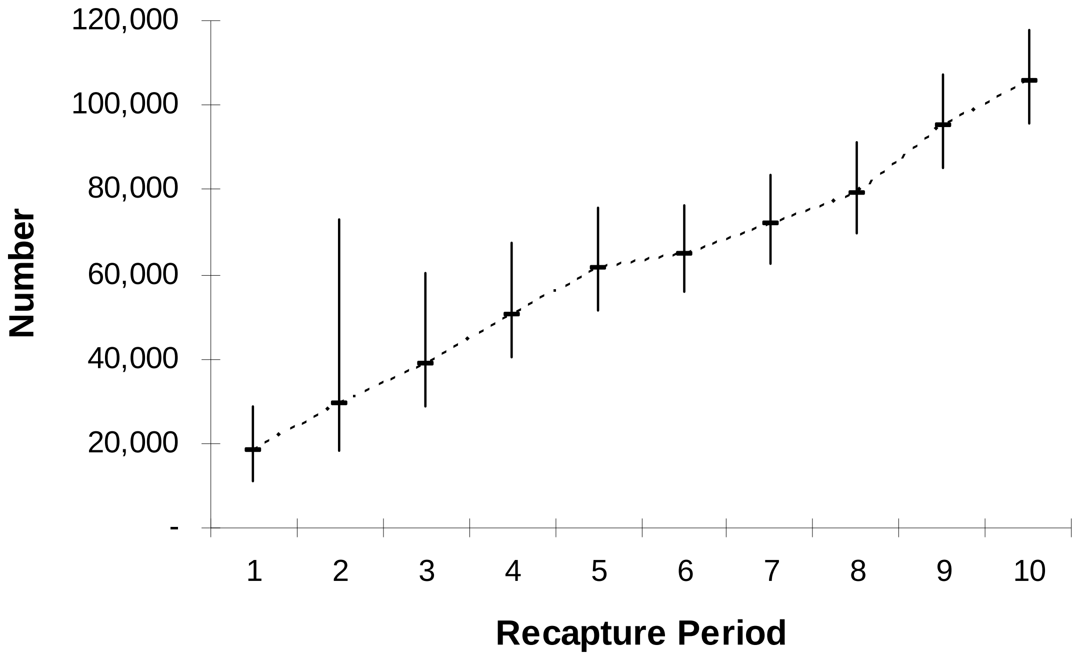

Figure 17. Schnabel multiple-census mark-recapture model of lake whitefish abundance over 10 weekly recapture periods in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

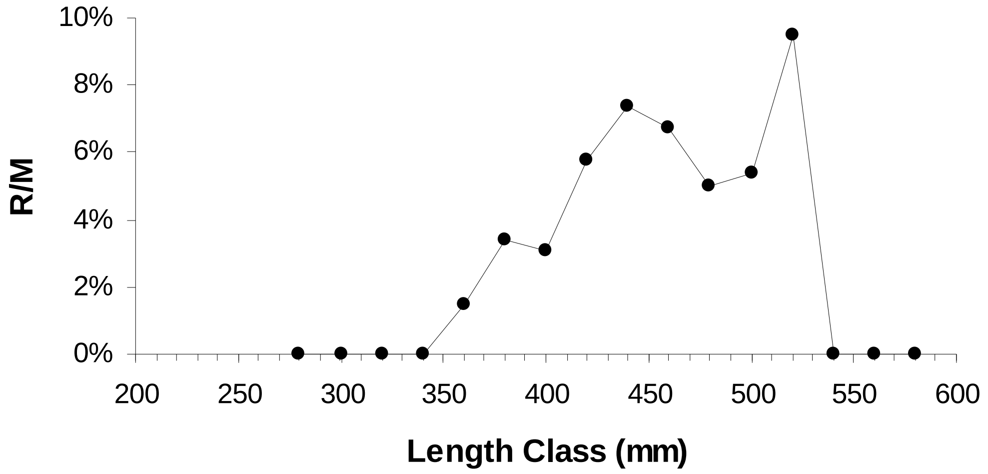

Figure 18. Recapture rate as a function of length class (20 mm) of lake whitefish marked and recaptured in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

Chapter 2:

Evidence for Subpopulations of Lake Whitefish in Lake Pend Oreille, Idaho

Abstract – To determine if subpopulations of whitefish were present in Lake Pend Oreille, Idaho, I compared population attributes and movement among putative subpopulations. To enable comparison, the population was divided into five putative subpopulations based on bathymetry and geographical separation. Mean length increased from north (445.3 mm) to south (459.2 mm) and size-structure differed significantly among putative subpopulations. Female proportion increased from north (0.59) to south (0.76). Body condition differed significantly among putative subpopulations and was highest in the south and lowest in the north. Length-at-age differed significantly among putative subpopulations, though the average maximum difference in length-at-age among putative subpopulations ranged from only 13 mm (SD = 5.2 mm) for the first 20 age classes to 19 mm (SD = 7.7 mm) for all age classes combined. Length- and age-at-50% maturity differed significantly among putative subpopulations, and increased from north (367.97 mm; 5.44 yr) to south (395.5 mm; 7.36 yr). Mortality rates did not differ significantly among putative subpopulations. Whitefish tended to be recaptured in the sampling area where they were tagged and overall fidelity was 81%. Recaptured fish tagged in the north, midwest, and mideast areas were predominantly recaptured (96.4%) within these three areas, and recaptures tagged in the mid-south were predominantly recaptured (85.1%) in the mid-south area, which suggests the presence of two discrete spawning subpopulations. Population attributes generally differed most from north to south, but were relativeily similar among north, midwest, and mideast areas, further suggesting the presence of at least two spawning subpopulations.

Introduction

Lake whitefish *Coregonus clupeaformis* (hereafter, termed whitefish) tend to form subpopulations in large bodies of water (Van Oosten and Deason 1939; Casselman et al. 1981; Ihssen et al. 1981; Ebener and Copes 1985; Koziol 1982; Walker 1993; Peck 1994). Subpopulations of whitefish have often been found to be genetically distinct from other subpopulations (Kirkpatrick and Selander 1979; Casselman et al. 1981). For example, using electrophoresis to study biochemical variation among allopatric and sympatric whitefish populations has proven especially useful in identifying distinct genotypes (Lindsey et al. 1970; Frazin and Clayton 1977; Kirkpatrick and Selander 1979; Kristofferson 1978; Imhoff et al. 1980; Ihssen et al. 1981; Bernatchez and Dodson 1990). Campana and Casselman (1993) concluded that in principle, stock discrimination based on genotype should be used for inferences regarding distinct stocks. However, sampling or analysis constraints may render this method unfeasible (Watkinson 2001). According to Casselman et al. (1981) and Ebener and Copes (1985), a stock or subpopulation may be defined as a group of fish subject to similar rates of recruitment, growth, and mortality and which return to the same spawning ground each year.

Stock discrimination is the process of distinguishing stocks based on quantifiable differences (Waldman et. al. 1997), which must be evaluated from fish sampled when stocks are discrete, as often occurs during spawning (Waldman and Fabrizio 1994; Begg and Waldman 1999). Stock discrimination methods such as Fourier analysis of scale and otolith outlines, and morphometric or meristic techniques can accurately classify fish of unknown stock origin in a mixed stock fishery to known spawning stocks (Jarvis 1978; Casselman et al. 1981; Campana and Casselman 1993; Watkinson and Gillis 2003).

However, these methods first require identification of the number of spawning stocks and their spawning grounds so that each stock can be quantified separately to determine the features that can accurately discriminate stocks (Waldman et al. 1988, 1994, 1997). Discriminating features can then be incorporated into algorhithms to classify individual fish sampled from a mixed stock to a stock of known origin and to determine relative contributions of each stock to the mixed stock fishery (Waldman and Fabrizio 1994).

Population parameters, biological attributes, and tagging data have been used to identify spawning stocks of whitefish (Van Oosten and Deason 1939; Dryer 1962; Casselman et al. 1981; Ihssen et al. 1981; Koziol 1982; Ebener and Copes 1985; Scheerer and Taylor 1985; Walker 1993; Peck 1994). Population parameters are typically the attributes used to recognize sympatric stocks first, because such attributes reflect the environment occupied by the stock due to their sensitivity to environmental variables (Ihssen et al. 1981; Begg et al. 1999). Recapture data is later used to assess whether putative stocks are reproductively discrete (Begg et al. 1999). The identification of discrete spawning stocks and their spawning grounds enables the application of stock discrimination methods that are used to determine relative stock contributions to mixed stock fisheries, which is inherently more sustainable than managing for a single lake-wide population when multiple subpopulations exist that overlap in home range (Waldman et. at. 1994, 1997). Furthermore, stock discrimination enables the conservation of genetic diversity within metapopulations, which is currently a consideration in the precautionary approach to fisheries management (Begg and Waldman 1999). Commonly, tagging data, mortality rates, growth rates, weight-length relationships, size and age structures, and maturity are compared among putative spawning subpopulations to identify discrete subpopulations. For example, based on mark-recapture data, differences in year-class abundance and mortality provided evidence that whitefish from North and Moonlight Bays (NMB) and Big Bay de Noc (BBN) were discrete stocks within Lake Michigan (Ebener and Copes 1985). Similarly, two discrete whitefish stocks were found to occur in south and north areas of Upper Entry in Michigan waters of Lake Superior, based on differences in age composition and back-calculated length-at-age (Peck 1994).

My objective was to determine if discrete spawning subpopulations of whitefish were present in Lake Pend Oreille, Idaho. If multiple subpopulations of whitefish are found to exist, management can then proceed on a stock by stock basis, which improves fishery sustainability and optimizes yield (Larkin, 1977; Walker et al. 1993). Whitefish were introduced into Lake Pend Oreille, Idaho in 1889, so sufficient evolutionary time may not have elapsed for genetic differentiation to occur. Nonetheless, environmental subpopulations may form sympatrically because of physiochemical, geological, and distance barriers that limit dispersal (Casselman et al. 1981; Scheerer and Taylor 1985; Walker et al. 1993). If whitefish dispersal is limited in Lake Pend Oreille, and environmental conditions differ sufficiently in different regions of the lake to create differences in population attibutes of whitefish, then I expect to find evidence for the existence of whitefish subpopulations in Lake Pend Oreille. The methodological approach relied on movement data and location-specific biological statistics of whitefish sampled throughout the lake by trap netting in autumn 2005 to test for the presence of discrete spawning subpopulations. This approach to stock identification has been used to identify discrete stocks of whitefish in the Great Lakes and elsewhere (Van Oosten and

Deason 1939; Casselman et al. 1981; Ihssen et al. 1981; Koziol 1982; Ebner and Copes 1985; Jacobson and Taylor 1985; Scheerer and Taylor 1985; Walker et al. 1993; Peck 1994; Begg et al. 1999).

Methods

Study Area

Lake Pend Oreille, a temperate, oligotrophic lake located in the northern panhandle of Idaho, is the state's largest natural lake with 85,960 surface acres and a shoreline length of 111 miles. The lake basin is deep and steep-sided with a maximum depth of 351 m and a mean depth of 164 m, and is located in the Pend Oreille drainage basin. The Clark Fork River is the largest tributary to the lake and the outflow from the lake forms the Pend Oreille River, which flows into the Upper Columbia River. Thermal stratification occurs from late June to September, and the thermocline typically lies between 10 and 24 m. Summer water temperature (May – October) averages about 9 C in the upper 45 m of water (Rieman 1977; Bowles et al. 1987, 1988, 1989). Surface temperatures are as high as 24 C in hot summers. Littoral areas are limited and mostly characterized by having a very steep bottom, although some littoral areas are characterized by gradual or moderately sloping bottoms (found mostly in the northern end of lake and in bays). Most fish habitat occurs in the pelagic area of the lake.

Field Sampling and Laboratory Analysis

Lake Pend Oreille was apportioned into five sample areas (Figure 1) for purposes of defining the number of sub-samples to be taken during fall 2005 trap netting. These five sample areas served as an initial estimate of the number and approximate regions of putative spawning stocks of whitefish in Lake Pend Oreille. Net location was recorded for all sample and subsample data, so patterns could be used to define new sample areas (putative subpopulation regions) that more accurately represent putative subpopulation regions, if evidence supported the existence of discrete spawning subpopulations. Up to nine trap nets were fished simulataneously among the five sample areas (Figure 1). In 2005, most trap nets were soaked between lifts for three or seven nights, with some nets soaked for up to 16 nights (Figure 2).

A sub-sample was defined to include all whitefish from a sample area that were collected for biological data. A stratified sub-sampling approach for estimating age composition of each putative spawning stock was used (Ketchen 1949). The practice of sampling a population of individual fish, grouping the fish into length-groups, and then selecting a random sample from each group is formally termed double sampling for stratification (Bettoli and Miranda 2001). Fixed-age sub-sampling, one form of double sampling for stratification, ensures over-sampling of the largest length-groups, each of which will likely contain several age classes, and therefore ensures that older, rarer fish are represented in the sub-sample (Bettoli and Miranda 2001). Fixed-age sub-sampling is logistically simple to conduct in the field, so was used in this study.

All fish captured from each sample area were measured in total length and the first five fish captured in each 10-mm length class were sub-sampled for measurement of weight, collection of age-estimation tissues (scales and sagittal otoliths), and estimation of gender, maturity status, and stage of maturity. For length classes with five or fewer fish, all biological attributes were measured, collected, or determined, whereas for length classes with more than five fish, all biological attributes were recorded only for the first five randomly-selected fish in each 10-mm length class. Total length was measured to the nearest mm, wet-weight was measured to the nearest gram, and 10–20 scales were removed from each fish from below the anterior region of the dorsal fin above the lateral line, and then placed in an envelope labeled with a unique identification number, capture date, and net location. Gender was determined by direct inspection of the gonads. If gender could not be determined, the fish was classified as unknown gender.

Fish maturity status was classified as mature, immature, or resting. Mature male whitefish had testes that contained at least some milt upon dissection, or appeared as if milt was about to form by being developed in thickness and length and mostly white in coloration. Mature female whitefish had ovaries filled with eggs that were medium to large in size, opaque or clear orange, and extended from one-half to two-thirds of the distance from the anterior portion of the body cavity to the vent. Female whitefish that were not obviously mature or immature were subjectively classified based on whether a given female whitefish was capable of maturing between the time of capture and the end of the spawning season. Female whitefish in a resting state had ovaries that were fully developed in a continuous strand of tissue exceeding half of the body cavity length, but occupied only half of the body cavity volume because eggs were small and not fully developed. Male whitefish in a resting state were nearly impossible to discern from mature, spent males. Mature fish were classified as green if their gonads were mature but sexual products did not expel from the vent under gentle abdominal pressure, ripe if their gonads were mature and sexual products expelled from the vent under gentle abdominal pressure, or spent if their gonads were mature but sexual products did not expel from the vent under gentle abdominal pressure because sexual products were expended.

Age was estimated for all sub-sampled fish from scales and otoliths. Otoliths are the preferred structure for estimating age of older fish because otoliths continue to grow and record cyclic seasonal growth and age through periods of reduced or negligible somatic growth, whereas scales of older fish fail to grow or record annuli and may resorb or erode (Casselman 1990; Campana and Thorrold 2001; Moritta and Matsuisihi 2001). Otoliths were glued to glass microscope slides using Crystalbond 509 adhesive. After drying for 2 hr, a ~500-µm section was cut from the region containing the nucleus with a low-speed saw and diamond-coated blade. Each slide was heated to the flow temperature of the adhesive and the loosened section was removed and adhered back onto the slide and allowed to dry for 2 hr. The sections were ground and polished using 500–600-grit wet-dry sandpaper to a thickness of ~300 µm, viewed under a dissecting scope with immersion oil, and photographed for back-calculation of growth history. Image Pro Plus software was used to measure annular radii. Scales were cleaned of dried slime and examined under a microfiche projector. Annuli were characterized by a distinct change in the spacing and continuity of circuli in the posterior and lateral portions of the scale that extends throughout the anterior and lateral fields, and by cutting over of circuli in lateral fields. For each fish, 4–6 clean dry scales were placed between two microscope slides, taped together, and age estimated.

To determine the age and length of fish at which scales failed to accrue additional discernable annuli, an age-bias plot was constructed with otolith age on the X-axis and scale age on the Y-axis (Campana et al. 1995). For age-bias plots, I assumed that otoliths provided unbiased estimates of true age (hence, their use on the X-axis), because Mills and Chalanchuk (2004) validated otoliths as estimators of true age for whitefish from unexploited arctic populations. If scales failed to reveal additional discernable annuli above a particular age relative to otoliths, age of fish younger than the cutoff age may be estimated from scales, whereas age of fish older than the cutoff age must be estimated from otoliths. The cutoff age could be converted to a cutoff length with the Von Bertalanffy length-age model to ensure that an optimal combination of efficiency and accuracy for age estimation is used for future research of this population. Scale age was substituted for otolith age when otolith age was unavailable for a given fish of length equal to or less than the cutoff length.

All fish in good condition (active, submerged, and uninjured) and not killed for sub-sampling were double-marked by insertion of a uniquely numbered Floy T-bar anchor tag as the primary mark and adipose fin removal as the secondary mark. Double marking was used to estimate tag loss. The adipose fin was chosen for removal because it is the least harmful fin to remove on a fish (Murphy and Willis 1996). Tags were inserted into the muscle tissue that lies below the anterior-central region of the dorsal fin, and then rotated 90 degrees while withdrawing the tagging gun to secure the tag between the fin rays. Tagged fish were released at the site of capture. Substantial numbers of whitefish were not in suitable condition for tagging (primarily distended gas bladders). For these fish, lengths were recorded and then either sub-sampled or submerged and released into the lake. Tag numbers and lengths of previously-tagged or fin-clipped fish caught during the marking period were recorded, along with the date and location of capture. Substantial numbers of whitefish that had been tagged prior to 2005 were captured, and for these fish, tag numbers and total lengths were recorded, and each fish was then considered a newly tagged fish. Recaptured fish therefore consisted of fish tagged during the 2005 marking period and the 2003–2004 marking periods. Tagged fish caught during the study period were released at the location of recapture if they were submerged, active, and uninjured. Recaptured fish that were dead, floating, or injured were kept for additional biological data and their tag numbers were recorded.

Data Analysis

Size-structure was compared among putative spawning stocks (sample areas) using chi-square contingency table analyses. First, putative spawning subpopulations were compared in an overall chi-square test. The null hypothesis was that length frequencies of all putative stocks did not differ significantly from one another, and the alternative hypothesis was that at least one stock differed significantly in its length-frequency distribution from other stocks. If the alternative hypothesis was supported, putative stocks were compared pairwise to determine which stocks differed from one another. To construct the contingency table, I used 2.0-cm length bins, which provided approximately 21 bins. Length bins ≤320 mm and ≥540 mm were used to ensure that expected cell frequencies exceeded 6.0, to eliminate statistical bias (Zar 1999).

The sex-composition (proportion female) was estimated for each putative spawning stock and for each week of sampling during fall trap netting. Whitefish whose gender could not be determined were excluded from the analysis. I calculated 95% confidence intervals for the proportion of females using exact 95% confidence limits for a binomial proportion (Zar 1999).

Body condition was estimated separately for each putative spawning stock using a power function for describing the rate at which weight increases with length:

$$W_i = \alpha L_i^{\beta} e^{\varepsilon_i} .$$

In the weight-length model, W_i = weight of the ith fish, α = condition factor, L_i = length of the ith fish, β = the shape parameter, and ε_i = multiplicative process error. The weight-length relationship was fit from weight-length data for individual fish, so model parameters were estimated for the multiplicative-error model using linear regression on the $\log_{10}$-transformed model:

$$\log_{10}(W_i) = \log_{10}(\alpha) + \beta \log_{10}(L_i) + \varepsilon_i .$$

The multiplicative error model assumes that logarithms of the residuals are equally distributed at all lengths, and that variability in weight is an increasing function of length. This model is appropriate for data on weight and length of individual fish. I examined residual plots to determine if residuals were equally distributed at all lengths.

Body condition was compared among putative spawning stocks with a general linear model (GLM):

$$\log_{10}(W_i) = \log_{10}(\alpha) + \beta \log_{10}(L_i) + b_1 X + b_2 (X * \log_{10}(L_i)) + \varepsilon_i .$$

In the GLM, X = putative spawning stocks (the main effect), and other terms are as defined for the weight-length model. I first tested for homogeneity of shape parameters (β) among sampling areas using the interaction between the main effect and the covariate. If the interaction term (b_2) was significant ($P \leq 0.05$), I estimated separate weight-length models for each putative stock. If the interaction term was not significant ($P > 0.05$), then I dropped the interaction term and tested for homogeneity of mean condition among sample areas (X = putative spawning stocks).

Growth of each putative spawning stock of whitefish was modeled with Von Bertalanffy growth curves fitted to mean back-calculated length-at-age:

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) + \varepsilon_i\,;$$

where L_∞ = average asymptotic length, K = the instantaneous rate at which an average fish grows from L_t to L_∞, t_0 = the hypothetical age at which length is zero, and ε_i = additive process error (Ricker 1975). Parameters were estimated with nonlinear least squares methods. To ensure that residuals were equally distributed at all values of age, residuals were plotted against age.

Fish lengths at annulus formation were back calculated for each sub-sampled fish from otolith cross sections to increase the total amount of length-age data for growth analyses and to provide length-age data for lengths of fish that were too small to be sampled (Campana 1990; Francis 1990, 1995; Moritata and Matsuishi 2001). To address the potential bias in back-calculated lengths at age and associated absolute growth rates resulting from a lack of proportionality between fish and otolith growth rates, I applied the back-calculation model of Morita and Matsuishi (2001). The Morita-Matsuishi back-calculation model incorporates fish age into the otolith-fish length regression:

$$O = \alpha + \beta L + \gamma t + \varepsilon_i\,.$$

In the otolith-fish length regression, O = otolith length, L = fish body length, t = fish age, α, β, and γ = parameters estimated using multiple-linear regression, and ε_i = additive process error. If multiple regression analysis indicated that the age effect, λ, was significant ($P \leq 0.05$), I used the full back-calculation model:

$$L_t = -\frac{\alpha}{\beta} + \left(L_T + \frac{\alpha}{\beta} + \frac{\gamma}{\beta} T \right) \frac{O_t}{O_T} - \frac{\gamma}{\beta} t + \varepsilon_i \, .$$

In the back-calculation model, L_t = back-calculated fish body length at age *t*, L_T = fish body length at time of capture *T*, O_t = otolith length at annulus (age) *t*, O_T = otolith length at time of capture *T*, α, β, and γ are parameters estimated for the otolith-fish length regression model, and ε_i = additive process error.

The Morita-Matsuishi model is a scale-proportional model modified to account for age effects in which the otolith increases in size continuously, even though somatic growth is zero (Secor and Dean 1992; Holmgren 1996; and Morita and Matsuishi 2001). The basis for this model is the hypothesis that many back-calculation models overestimate fish somatic growth rates for slow-growing fish because the otolith increases in size, despite little somatic growth, coupled with the fact that traditional back-calculation models assume that fish growth is proportional to otolith growth.

Growth was compared among putative spawning stocks with likelihood ratio tests of Von Bertalanaffy growth curves for all areas sampled (full model) versus a Von Bertalanffy growth curve for all areas combined (reduced model). I used the likelihood ratio test to compare the hypothesis that all growth curves were similar (each was a sample from the same population) to the hypothesis that all growth curves were from different populations. Likelihood ratio tests can be used to compare any non-linear equations fitted to data if the residuals are additive and normally distributed (Haddon 2001). Parameters were estimated separately for each putative spawning stock (full model) and for a single model across all putative spawning stocks (reduced model). Residual sums-of-squares were then compared for full and reduced models. I accepted the full model (individual growth curves) if the residual sum-of-squares was significantly lower for the full model than for the reduced model. I accepted the reduced model (homogenous growth curves) if the residual sum-of-squares was not significantly lower for the full model than for the reduced model. If the reduced model was rejected, I compared growth curves for each pair of putative spawning stocks (likelihood ratio tests) to determine which growth curves differed.

Length and age at maturity were compared among putative spawning stocks using likelihood-ratio tests that were based on the logistic regression model that related the proportion of mature fish of each putative spawning stock to each 10- mm length class and to each age class:

$$M_x = \frac{1}{1+e^{-r(X-X_m)}}\varepsilon_i .$$

In the maturity model, M_x = the proportion of mature fish at length or age X, r = the instantaneous rate at which the proportion mature approaches 1.0, X_m = the length or age at which 50% of the fish are mature, and ε_i = multiplicative process error (Quinn and Deriso 1999). Likelihood-ratio tests were constructed in the same manner as growth curves. Significant differences in length or age at 50% maturity among sampling areas would support the alternative hypothesis that sampling areas supported discrete spawning stocks. If the reduced model was rejected, I compared maturity curves for each pair of putative spawning stocks using likelihood ratio tests to determine which maturity curves differed.

Catch-curves were estimated for each putative spawning stock by using separate age-length keys for each sample area and then extrapolating each key to sample data for each area. A catch-curve is a graph of log-number against age, thereby enabling estimation of survival and mortality rates from a sample of a single population. Catch-curve analysis is based on the concept that a decline in the number of individuals present from one age group to the next reflects the combined effect of mortality and difference in initial year-class strength (mean recruitment) for the age groups represented in the catch curve (Robson and Chapman 1961). If the population experiences mortality and recruitment that do not trend upwards or downwards through time for fully recruited ages, then the number present in each fully recruited age class would decline exponentially with age (Haddon 2001):

$$N_t = N_0 e^{-Zt} e^{\varepsilon}.$$

In the catch-curve model, N_t = number present at age t, N_0 = average annual recruitment, Z = instantaneous total mortality, t = age for fully recruited ages, and ε_i = multiplicative process error. The first fully recruited age of whitefish caught during fall in trap nets was estimated by examining the dome and descending limb of catch-curves, because Ricker (1975) showed that the modal age in the catch often lies close to the first year in which recruitment is complete. The multiplicative-error model was $\log_e$-transformed to estimate Z using linear regression of $\log_e(N_t)$ against age t (for fully recruited ages):

$$\log_e\left(N_t\right) = \log_e\left(N_0\right) - Zt + \varepsilon.$$

The slope of the model is the instantaneous total mortality rate (Z) and its 95% confidence interval. The intercept, $\log_e(N_0)$, when back-transformed, provides an estimate of average recruitment to the fishery for fully-recruited ages. The coefficient of determination (r^2) describes relative variation in recruitment, for which positive residuals reflect relatively strong recruitment and negative residuals reflect relatively weak recruitment.

Total instantaneous mortality rates (Z) and mean recruitment [$\log_e(N_0)$] were compared among sample areas using a general linear model (GLM):

$$\log_e(N_t) = \log_e(N_0) - Zt + b_1X + b_2(X * t) + \varepsilon \, .$$

In the GLM, X = sample area (main effect), t = age (covariate), and other terms are as defined for the catch-curve model. The GLM is a likelihood-ratio test for a full model (separate means for each area) versus a reduced model (all areas combined). First, I tested for homogeneity of slopes among areas using the interaction (b_2) between the main effect X and the covariate t. If the interaction was significant ($P \leq 0.05$), then slopes differed significantly among areas, so separate catch curves were used for each area. If the interaction term was not significant ($P > 0.05$), then slopes did not differ significantly among areas, so the interaction term was dropped and the resulting model tested for homogeneity of mean recruitment among sample areas (main effect).

Assumptions of catch-curve analysis include: (1) recruitment does not trend upward or downward through time; (2) fishing and natural mortality do not trend upward or downward through time; and (3) vulnerability to fishing gear is constant for all fully recruited ages (Hilborn and Walters 2001). Younger fish are less vulnerable to capture, but become increasingly vulnerable to capture, as they grow older, until they are fully recruited to the fishery at a certain age. For fish older than the age of full recruitment, catch-at-age is assumed proportional to the abundance of an age class (fish do not become less vulnerable with age). When vulnerability increases with age up to the age of full vulnerability, the catch curve is dome-shaped with ages of increasing vulnerability to capture (ascending limb and dome), followed by ages of full vulnerability that experience an exponential decline in numbers with age (descending limb).

Movement of recaptured whitefish from their location of tagging to their location of recapture in Lake Pend Oreille during trap netting in 2005 was quantified using data on locations and dates of capture. For each recaptured whitefish, the net location and sampling area of tagging in trap nets was cross tabulated with the net location and sampling area of recapture in trap nets to quantify rates of movement from locations of tagging to recapture during the autumn spawning period. Movement was quantified as the proportion of all recaptures at a tagging location or sampling area that originated in a different tagging location or sampling area. Tagging site fidelity was quantified as the proportion of recaptured fish tagged at a particular net location or sampling area that had been recaptured at their location of tagging. A high degree of fidelity would suggest limited dispersal from the net location or sampling area of tagging. Limited dispersal would indicate that putative spawning subpopulations (whose detection is contingent on evidence gathered from the prior analyses) were discrete.

Results

Mean length increased from north to south (Figure 19). Length-frequency histograms for each sample area were normally distributed and umimodal (Figure 20), but differed significantly among sampling areas ($\chi^2 = 216.08$; df = 52; $P < 0.001$). Putative subpopulations all differed from one another (Pairwise comparisons; $P \leq 0.05$), except between the mid-west and mid-east areas ($\chi^2 = 19.63$; df = 15; $P = 0.186$; Table

14). Mean length was highest for the south sample area and lowest for the mid-west sample area (Table 2).

The proportion of female whitefish increased from north to south (Figure 21) and fluctuated among weeks within sample areas (Table 4). The average overall proportion of females was 0.66 (95% CI = 0.63-0.70) and ranged from 0.76 in the south sample area to 0.59 in the north sample area. The proportion of females was similar between the north (0.59) and mid-west areas (0.58), and between the mid-south (0.74) and south areas (0.76). The proportion of females in the mid-east area (0.68) was intermediate between the north and south areas. The proportion of females declined from the week of 17 October 2005 (0.71) through the week of 7 November 2005 (0.49), then increased through the week of 14 November 2005 (0.60), declined to a low the week of 21 November 2005 (0.27), and then increased quickly to a peak during the week of 5 December 2005 (0.83).

Shape parameters β of weight-length relationships did not differ significantly among sample areas ($F_{4,\,655} = 2.29$; $P = 0.059$), so the interaction term was dropped from the general linear model. Mean condition α differed significantly among sampling areas ($F_{4,\,659} = 9.31$; $P < 0.001$), so separate weight-length equations were estimated for each sample area (Table 5). Residuals of the general linear model were distributed evenly across the range of lengths. The shape parameter (β) decreased from north to south (Figure 22**)**, whereas the condition parameter (α) increased from north to south (Figure 23). Confidence limits for β overlapped among sampling areas (Table 5). The largest difference in shape parameter was between north ($\beta = 3.46$) and south ($\beta = 3.19$) sample areas. Shape parameters were similar between mid-east ($\beta = 3.28$) and mid-south ($\beta =$

3.30) areas. Differences in condition among areas were relatively larger than differences in shape parameters. The largest difference in condition was between south ($\alpha = 3.067 \times 10^{-6}$) and north ($\alpha = 5.708 \times 10^{-7}$) sample areas, where the south sample area condition parameter was approximately 81% larger.

Length-age growth curves differed significantly among sample areas ($F_{12,\,164} = 3.66$; $P < 0.001$), so separate growth curves were estimated for each area (Table 7). Differences in fitted growth curves were generally small (Figure 24). For the first 20 age classes, the greatest absolute difference among growth curves was at age 1 between south and mid-west areas (25.8 mm difference) and the smallest absolute difference was at age 13 between mid-east and mid-south areas (7.24 mm difference; Figure 24). Differences in length-at-age among areas increased steadily beyond age 20 (Figure 24) up to a maximum of 34.1 mm at age 33 between north and mid-west areas. Growth curves differed significantly between north and mid-west, north and mid-east, north and south, mid-west and mid-south, and mid-east and mid-south areas, but not between north and mid-south, mid-west and mid-east, mid-west and south, mid-east and south, or mid-south and south sample areas (Table 15). Mean back-calculated lengths-at-age were similar among areas for each age class and 95% confidence intervals overlapped substantially for most age classes (Table 16). Fish from the mid-west sample area were the smallest for the first 13 years of life, afterwhich fish from the south area were the smallest until age-26 (Table 16). Sample size was generally small for fish age-20 and older (Table 16).

Length at maturity differed significantly among areas ($F_{6,\,107} = 24.49$; $P < 0.001$), so separate length-at-maturity models were estimated for each area (Table 13). Length at maturity differed significantly ($P \leq 0.05$) between all pairwise comparisons of areas except between mid-east and mid-south areas (Table 17). Length at first maturity ranged from 340 mm in the north and mid-west sample areas to 410 mm in the south sample area (Table 13). Length at 100% maturity ranged from 420 mm in the north and mid-east sample areas to 440 mm in the mid-west sample areas (Table 13). The length at maturity model for the south sample area did not converge, so the likelihood ratio test excluded south sample area data. The maximum difference in length at 50% maturity was 27.5 mm (mid-south – north), the maximum difference in maturation rate was 0.129 (north – mid-west and mid-east), the maximum difference in length at first maturity was 70 mm (south – mid-west), and the maximum difference in length at 100% maturity was 20 mm (mid-west – north and mid-east).

Age at maturity differed significantly among areas ($F_{8,\,118} = 19.64$; $P < 0.001$), so separate age-at-maturity models were estimated for each sample area (Table 17). Age at maturity differed significantly ($P \leq 0.05$) among all pairwise sample area comparisons, so separate logistic models were used for each sample area (Table 13). Age at first maturity ranged from age 4 in the mid-west sample area to age 6 in the mid-south sample area (Table 13). Age at 100% maturity ranged from age 9 in the mid-east sample area to age 12 in the north sample area (Table 13). The maximum difference in age at 50% maturity was 1.9 years (mid-south – north), the maximum difference in age at first maturity was 2 years (mid-south – mid-west), and the maximum difference in age at 100% maturity was 3 years (north – mid-east).

Ripe fish were caught primarily in the north sample area. Of the 31 ripe fish that were sampled, 20 were caught in the north sample area, including 13 at Bottle Bay and 7 at Sunrise Bay. Of the remaining 11 ripe fish that were sampled, five were caught in the midsouth area (four at Garfield Bay), two in the mid-west area, and two in the mid-east area. Only nine of 31 ripe fish sampled were males, including eight from the north sample area, and one from the south sample area.

Mortality did not differ significantly among areas, but mean recruitment differed significantly among areas for whitefish in Lake Pend Oreille. Instantaneous total mortality did not differ significantly among sample areas because the interaction term between age and sample areas was not significant ($F_{4, 93} = 0.99$; $P = 0.417$). In contrast, mean annual recruitment differed significantly among sample areas because the main effect of sample areas was significant ($F_{4, 97} = 16.15$; $P < 0.001$).

Whitefish did not disperse randomly from tagging locations because recaptures within sample areas significantly exceeded expected recaptures ($\chi^2 = 1002.1$; df = 4; $P < 0.001$), calculated by dividing the number of fish tagged within a sample area by the total number of tagged fish, and then multiplying against the total number of recaptures from a sample area. Whitefish tended to be recaptured in the sampling area (Table 18) and net location (Table 19) where they were tagged. Whitefish tagged in the north (94.3%) and mid-south (85.1%) sample areas had the highest site fidelity (fish recaptured in the sampling area where they were tagged), while whitefish tagged in the south sample area had the lowest site fidelity. The overall site fidelity was 81% (sum of the total number of recaptures in the same area where they were tagged divided by the total number of recaptures), indicating that 19% of recaptured fish were recaptured away from the location where they were tagged. Of all recaptures tagged in the mid-south sample area, 14.9% were recaptured elsewhere (Table 18). Of all recaptures tagged in the north sample area, 5.7% were recaptured elsewhere. Of all recaptures tagged in the mid-west sample area, 37% were recaptured elsewhere. Of all recaptured fish tagged within the mid-east sample area, 39.4% were recaptured elsewhere. Only five of 142 fish tagged in the south sample area were recaptured, one in the north, three in the mid-south, and one in the south. The longest movement was a fish that traversed the entire length of the lake from Idlewilde on 18 October 2005 to Sunnyside on 31 October 2005. Fish that moved away from their location of tagging strongly tended to move north (Table 19).

Discussion

Length-frequency distributions for whitefish differed significantly among sample areas and mean length increased from north to south, which suggests that discrete subpopulations of whitefish live in Lake Pend Oreille. However, the greatest difference in mean length was only 14.2 mm (between the mid-west and south sample areas) and the next largest difference in mean length was only 6.6 mm (between the mid-west and mid-south sample areas). Similarly, mean length of the 1977 year-class of whitefish from the Leland area of northeastern Lake Michigan was 10–35 mm larger than mean length of whitefish from the North Shore (Scheerer and Taylor 1985). In contrast, mean lengths of four whitefish stocks in Lake Superior (415.3, 490.2, 457.2, and 431.9 mm) differed by as much as 74.9 mm and as little as 25.3 mm (Dryer 1962). The north to south increase in proportions of females in Lake Pend Oreille may have contributed to the north to south increase in mean length, because females (438.7 mm) were larger than males (398.6 mm), as in other populations (Van Oosten and Hile 1949; Beauchamp et al. 2004).

Mean body condition differed significantly among sample areas and increased from north to south, which also suggests that discrete subpopulations of whitefish live in Lake Pend Oreille. Shape parameters and condition factors can vary widely among sympatric stocks of whitefish, and within stocks between both seasons and years (Patriarche 1977; Gunderson 1978; Ebener 1980; Scheerer and Taylor 1985; McComb 1989). For example, shape parameters ranged from 3.178 – 3.455 and condition factors ranged from 5.71E-07 – 3.09E-06 for three whitefish stocks from northern Lake Michigan (Patriarch 1977). For example, the shape parameter of whitefish from the North-Moonlight Bays stock (3.364) was greater than from the Big Bay de Noc stock (2.952) in Lake Michigan (Ebener 1980). Similarly, shape parameters differed among four putative stocks of Lake Michigan whitefish (3.075 – 3.6047; Gunderson 1978), five stocks of whitefish from northern Lake Michigan (3.25 – 3.528; McComb 1989), and three stocks in Lake Michigan (Scheerer and Taylor 1985). In Lake Pend Oreille, shape parameters ranged from 3.46 in the north to 3.19 in the south, and the range was within the range of whitefish stocks elsewhere (Patriarche 1977; Ebener 1980). The north to south increase in proportions of females in Lake Pend Oreille may have contributed to the greater body condition of whitefish from the south, because females (α = 9.54E-07) had significantly greater body condition than males (α = 6.39E-07).

Growth of whitefish differed significantly among sample areas in Lake Pend Oreille, though differences in growth among areas were small. For example, the average maximum difference among sample areas in Lake Pend Oreille was only 13 mm (SD = 5.2 mm) for the first 20 age classes and 19 mm (SD = 7.7 mm) for all age classes combined. Previously, differences in back calculated lengths at age have been used to differentiate stocks of whitefish in the Great Lakes (Koizol 1982; Ebener and Copes 1985; Walker et al. 1993; Peck 1994). For example, length-at-age differed by 50 mm between northern and southern populations of exploited whitefish at Isle Royale, Lake

Superior (Koizol 1982). Similarly, whitefish from the western arm of Grand Traverse Bay, Lake Michigan had a pre-recruit growth advantage of 22 mm over those from the eastern arm that began in the first year and increased 9 mm in the second year (Walker et al. 1993). Growth of Lake Superior whitefish varied substantially among ports of capture (putative stocks) and length at the end of the first year of life ranged 129.5–167.6 mm (Dryer 1962). Whitefish from the Leland area of Lake Michigan grew significantly faster than whitefish from either the North Shore or Beaver Island (Scheerer and Taylor 1978). Conversely, weighted mean back-calculated lengths were similar and did not differ significantly among six stocks of whitefish from northern Lake Michigan (Hastreiter 1984). Similarly, growth rates and mean back-calculated lengths did not differ significantly among four stocks of whitefish from Lake Michigan (Gunderson 1978).

Length and age at maturity differed significantly among all areas sampled, which suggest that discrete subpopulations of whitefish live in Lake Pend Oreille. The north to south increase in the proportion of females in Lake Pend Oreille may have contributed to the north to south increase in length and age at maturity, because female whitefish were 12 mm longer and 0.5 years older at 50% maturity than male whitefish. In Lake Superior, whitefish in Munising Bay first matured at 292 mm and age 7 and were 100% mature at 381 mm and age 11, whereas whitefish at Bayfield first matured at 368.3–378.5 mm and age 5 and reached 100% maturity at 431.8–441.96 mm and age 7 (Dryer 1962). Length at 90% maturity ranged 450 – 525 mm (SD = 28.1 mm) among four sympatric whitefish stocks from northeastern Lake Michigan (Taylor et al. 1992). Unfortunately, estimates of length and age at maturity for sympatric stocks of whitefish are uncommon in the literature, and are largely unavailable for comparison with my findings for Lake Pend Oreille.

Mortality rates did not differ significantly among areas, while mean recruitment differed significantly among areas in Lake Pend Oreille, which suggests that average abundance but not mortality differed among subpopulations. Differences in mortality rates have been used to differentiate discrete spawning subpopulations of whitefish (Ebener and Copes 1985; McComb 1989). At Isle Royale, Lake Michigan, mortality rates of whitefish did not differ significantly between northern and southern stocks that differed in growth rates (Koizol 1982). Similarly, at Upper Entry, Lake Michigan, mortality rates of whitefish did not differ significantly between northern and southern stocks that differed in growth rates (Peck 1994). Differences in recruitment among sample areas in Lake Pend Oreille may have been caused by differences in habitat quantity or quality, or differences in sampling effort among areas.

Site fidelity of whitefish in Lake Pend Oreille was generally high during trap netting in autumn 2005, which suggests that whitefish mixed little among sample areas during the spawning period. Whitefish movement rates have typically been estimated from tagging studies in which fish are tagged during the spawning period and later recaptured in a fishery, thereby enabling estimation of home range, spawning site fidelity, and differentiation of discrete spawning subpopulations (Smith and Van Oosten 1940; Roelofs 1958; Dryer 1964; Ebener and Copes 1985; Walker et al. 1993). Tag-return studies provide the most direct information on spatial and temporal distributions and discreteness of putative stocks of fish (Casselman et al. 1981). For example, home ranges of spawning stocks of whitefish overlapped significantly in the West, Outer, and

East bays of Grand Traverse Bay, Lake Michigan, where fish were tagged at the onset of spawning in November and recaptured during the ensuing angling season (Walker et al. 1993). Whitefish that were tagged at the onset of the spawning season and recaptured during the following spawning season were all recaptured at their tagging location, which suggests that spawning stocks were reproductively isolated (Walker et al. 1993). Results of other tag-return studies were generally similar (Ebener 1980; Ebener and Copes 1985; Ihssen et al 1981; Scheerer and Taylor 1985). In contrast, whitefish from five putative stocks in Lake Huron mix little during spawning or nonspawning periods, despite the absence of physical barriers to dispersal, and whitefish from two putative stocks that were separated by only 2 km did not mix at all (Casselman et al. 1981).

Despite an overall high rate of spawning site fidelity in Lake Pend Oreille, 18.9% of all whitefish were recaptured away from their tagging area (range = 3.8 – 80%), which suggests that putative spawning stocks were not reproductively isolated. Fish from the north, mid-east, and mid-west areas in Lake Pend Oreille primarily moved within these three areas, which suggests that a single stock of whitefish may inhabit the north-central region of the lake. In contrast, fish from the mid-south area largely remained in the same area, which suggests that a separate spawning stock of whitefish may inhabit that area. Too few recaptured fish were tagged from the south area to permit evaluation of the south sample area as a discrete stock.

Management Implications

I found evidence to support my hypothesis that the whitefish population in Lake Pend Oreille is a metapopulation consisting of multiple discrete spawning populations, though I was unable to determine the number and geographic locations of the subpopulations. Mark-recapture data suggested that site fidelity was high but that stocks were not reproductively isolated. However, the mark-recapture study began prior to the onset of spawning, so dispersal of tagged fish may have occurred as fish migrated to their spawning grounds. Fish sampled prior to the onset of spawning were potentially of multiple spawning stocks that may not have fully separated until the onset of spawning, as in another study (Walker et al. 1993). Tag-return studies could be used in the future to estimate home ranges and spawning-site fidelity of fish captured during spawning in one year and recaptured during spawning in subsequent years, as in other studies (Smith and Van Oosten 1940; Roelofs 1958; Dryer 1964; Ebener and Copes 1985; Walker et al. 1993). Such tag-return studies require knowledge of the number and location of spawning areas in the lake, and are logistically difficult and financially expensive if not conducted in cooperation with a commercial fishery.

My findings suggest that whitefish spawn primarily in the northern area near Bottle Bay and Sunrise Bay and in the mid-south area near Garfield Bay. A single whitefish spawning ground in the northern region of the lake would indicate the existence of a single lakewide spawning stock, whereas multiple dispersed spawning grounds would increase the likelihood of multiple discrete spawning stocks if whitefish home to natal spawning grounds, as elsewhere (Walker et al. 1993). Whitefish spawn in littoral areas where they broadcast their eggs in depths of 2–4.5 m over sand, gravel, flat stone, cobble, and boulder (Dumont and Fortin 1978; Fudge and Bodaly 1984; Nester and Poe 1984; Anras et al. 1999). Therefore, areas meeting these criteria could be investigated for spawning activity during the peak of the spawning season that extends from late November through mid-December.

Differences in biological parameters among putative spawning stocks were consistently greatest between the north area and the mid-south and south areas, which suggest the presence of at least two discrete stocks in Lake Pend Oreille. Differences in biological parameters, though significant, were generally small between the mid-west and mid-east, which suggests that a single stock occupies these two areas. Differences in biological parameters were generally larger between the north and both the mid-west and mid-east, which suggests that one discrete stock occupies the north. Ihssen et al. (1981) concluded that exploitation enhances the utility of population parameters for stock identification by increasing contrast between stocks that might otherwise be similar due to environmental similarity. Therefore, I expected that differences in biological parameters would likely be small unless environment conditions like food quality or quantity, predator density, or habitat availability varied substantially throughout the lake. Variation in whitefish habitat in Lake Pend Oreille is most likely related to bathymetry.

Stock identification is most important in mixed-stock fisheries when stocks differ in population attributes, because reliance on data from a relatively abundant stock having unique population parameters may lead to overfishing of less abundant stocks that overlap in home ranges (Larkin 1977; Walker et al. 1993). If whitefish stocks are mixed during the nonspawning period in Lake Pend Oreille, then stocks may collapse if fished beyond their capacity to compensate for increased exploitation. This could occur if a mixed stock fishery is managed with biological parameters and model estimates of yield estimated from a numerically predominant stock whose stock parameters support a harvest rate that would induce recruitment overfishing in numerically less abundant stocks whose compensatory scope is smaller (Jensen 1981). If whitefish stocks do not overlap during the nonspawning period and all stocks are fished heavily at the same harvest rate, depletion or collapse of stocks that possess a smaller compensatory scope may occur (Jensen 1981). Reliance on data from numerically dominant stocks may lead to mismanagement of numerically less abundant stocks. Therefore, to prevent stock collapse and local extirpation, the number and location of discrete stocks of whitefish must be determined in Lake Pend Oreille. Initial harvest should be conservative to lessen the likelihood of depleting or collapsing stocks that possess less compensatory scope, until the number, location, and parameters of all discrete stocks are determined.

Table 14. Test-statistics (Chi-square), degrees freedom, and p-values for pairwise comparisons of lake whitefish size structure caught in trap nets from five sample areas in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	North	MidWest	MidEast	MidSouth	South
North	-	-	-	-	-
MidWest	Chi (15)=30.22;P=0.011	-	-	-	-
MidEast	Chi (14)=53.20;P=1.75E-6	Chi (15)=19.63;P=0.186	-	-	-
MidSouth	Chi (13)=80.48;P=8.97E-12	Chi (15)=99.77;P=1.4E-14	Chi (16)=78.72;P=2.82E-10	-	-
South	Chi (11)=1.99;P=1.99E-6	Chi (12)=46.44;P=5.83E-6	Chi (13)=33.32;P=0.0015	Chi (10)=19.02;P=0.040	-

Table 15. Test-statistics (F-test), degrees of freedom, and p-values for pairwise likelihood ratio tests of Von Bertalanffy length-age models of lake whitefish caught in trap nets from five sample areas in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	North	Mid-West	Mid-East	Mid-South	South
North	-	-	-	-	-
Mid-West	F (3,63)=7.00;P=0.000	-	-	-	-
Mid-East	F (3,60)=7.78;P=0.000	F (3,63)=0.89;P=0.448	-	-	-
Mid-South	F (3,69)=2.65;P=0.056	F (3,72)=4.32;P=0.007	F (3,69)=4.98;P=0.003	-	-
South	F (3,62)=5.36;P=0.002	F (3,65)=0.83;P=0.481	F (3,62)=0.69;P=0.561	F (3,71)=2.09;P=0.109	-

Table 16. Mean back-calculated length-at-age, 95% confidence interval (CI), and sample size (#) for lake whitefish caught in trap nets from five sample areas (N = north, MW = mid-west, ME = mid-east, MS = mid-south, S = south) of Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005. Confidence intervals were estimated for all age classes with > 1 fish.

Age	N	CI	MW	CI	ME	CI	MS	CI	S	CI	# N	# MW	# ME	# MS	# S
1	173.9	3.9	165.3	4.0	172.5	4.2	172.8	3.7	176.1	7.6	131	146	132	156	56
2	253.8	4.3	244.5	4.7	254.1	4.6	251.3	4.6	255.2	8.7	127	146	132	156	56
3	297.8	4.7	289.0	4.7	298.3	5.1	296.5	4.7	302.2	9.1	120	145	129	156	56
4	329.3	5.1	319.4	5.2	329.4	5.4	329.0	5.1	334.4	9.4	111	130	116	152	55
5	353.2	5.6	341.8	6.1	354.3	5.9	352.5	5.2	359.9	10.1	100	112	104	144	53
6	375.3	6.3	362.8	6.8	373.1	6.1	370.3	5.6	376.5	10.4	91	98	84	128	47
7	392.4	6.9	382.1	6.8	390.6	6.7	387.2	5.9	392.4	10.4	75	91	78	119	45
8	405.8	7.9	395.5	7.0	406.7	7.4	401.4	6.1	404.6	10.1	70	85	69	111	42
9	420.0	8.5	408.9	7.4	421.4	7.8	415.1	6.3	418.2	10.8	69	79	65	109	41
10	432.4	8.7	422.4	8.0	434.7	8.4	427.3	6.6	427.5	11.5	67	75	61	107	35
11	443.7	9.2	433.0	8.0	448.0	9.7	438.3	7.2	438.1	12.1	60	68	55	100	34
12	455.2	10.2	443.5	8.4	458.4	11.4	448.2	8.0	444.7	13.3	53	63	46	94	29
13	464.5	10.8	450.8	8.2	463.3	11.2	459.1	8.4	453.3	13.9	50	57	43	91	28
14	471.9	11.7	459.8	8.1	470.7	11.7	466.6	9.2	457.5	13.9	46	57	37	83	25
15	474.9	11.8	467.7	8.5	478.6	13.2	473.3	9.6	462.1	15.1	43	56	33	78	22
16	480.6	12.8	475.6	9.2	481.9	14.3	480.3	10.2	468.5	18.3	38	53	25	73	18
17	483.5	14.6	482.2	10.2	488.3	15.8	484.5	10.6	475.1	18.7	31	49	22	62	18
18	493.0	17.2	489.3	11.4	489.6	17.3	488.3	10.6	477.2	20.4	27	43	19	55	16
19	491.4	17.9	496.2	11.9	490.6	16.6	494.4	11.5	482.4	28.6	23	42	18	50	12
20	498.1	20.2	502.1	12.8	497.6	18.2	498.9	12.4	491.6	34.2	18	38	16	48	10
21	507.7	22.7	507.8	13.8	502.2	17.5	504.5	13.5	501.1	39.4	16	36	16	45	9
22	511.2	25.5	515.0	14.8	507.2	17.9	508.6	13.6	506.0	44.1	14	35	16	41	8
23	521.9	28.1	521.4	15.7	504.0	19.1	511.7	14.5	506.6	66.9	12	33	14	39	6
24	535.0	26.3	527.1	17.1	511.7	18.8	512.8	15.6	503.1	85.2	12	28	12	36	5
25	538.5	25.7	530.8	18.4	515.4	21.4	514.5	17.6	508.4	118.6	9	27	11	33	4
26	555.0	16.7	533.7	20.9	515.5	25.5	519.3	19.0	530.5	176.5	8	25	9	28	3
27	557.4	18.0	535.2	24.1	512.7	24.2	525.2	21.6	531.4	171.0	8	22	8	22	3
28	559.1	20.4	542.6	25.4	506.0	55.8	528.6	23.1	529.1	163.7	4	19	4	20	3
29	569.5	48.2	537.3	32.8	520.1	69.2	525.9	25.5	528.1	163.7	2	14	3	18	3
30	576.7	407.3	545.9	49.2	519.3	-	519.8	32.8	555.7	487.8	2	10	1	14	2
31	573.1	430.5	523.5	58.2	526.2	-	521.5	30.4	554.0	478.4	1	7	1	10	2
32	535.9	-	508.1	68.0	538.4	-	533.1	22.8	552.2	480.2	1	4	1	5	2
33	532.0	-	505.8	69.9	547.0	-	530.6	55.8	510.5	-	1	4	1	3	1
34	-	-	489.5	88.3	-	-	546.7	212.3	505.9	-	-	3	-	2	1
35	-	-	490.7	435.9	-	-	569.8	-	502.0	-	-	2	-	1	1
36	-	-	455.0	-	-	-	561.7	-	-	-	-	1	-	1	-
37	-	-	-	-	-	-	558.0	-	-	-	-	-	-	1	-
38	-	-	-	-	-	-	555.6	-	-	-	-	-	-	1	-
39	-	-	-	-	-	-	550.8	-	-	-	-	-	-	1	-
40	-	-	-	-	-	-	546.5	-	-	-	-	-	-	1	-
41	-	-	-	-	-	-	545.8	-	-	-	-	-	-	1	-
42	-	-	-	-	-	-	540.0	-	-	-	-	-	-	1	-

Table 17. Test statistic (F), degrees of freedom, and p-values of pairwise likelihood ratio tests of length- and age-at-maturity models of lake whitefish caught in trap nets from five sample areas in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

		North	Midwest	Mideast	Midsouth	South
Age	North	-	-	-	-	-
	Midwest	F (2,51)=67.37;P=4.8E-15	-	-	-	-
	Mideast	F (2,46)=30.34;P=3.96E-9	F (2,47)=4.25;P=0.020		-	-
	Midsouth	F (2,52)=114.09;P=9.61E-20	F (2,53)=14.35;P=1.04E-5	F (2,48)=5.04;P=0.010		-
	South	F (2,44)=32.74;P=1.95E-9	F (2,45)=13.41; P=2.69E-5	F (2,40)=10.95;P=0.000	F (2,46)=28.92;P=7.36E-9	
Length	North	-	-	-	-	-
	Midwest	F (2,55)=22.35;P=7.86E-8	-	-	-	-
	Mideast	F (2,56)=89.52;P=3.61E-18	F (2,55)=6.07;P=0.004	-	-	-
	Midsouth	F (2,52)=114.09;P=9.61E-20	F (2,52)=11.07;P=9.8E-5	F (2,53)=1.04;P=0.359	-	-
	South	-	-	-	-	-

Table 18. Recaptures of previously tagged lake whitefish in five sample areas in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	Tagging Area					
Recapture Area	North	Mid-West	Mid-East	Mid-South	South	Total
North	51	15	1	29	1	97
Mid-West	-	34	10	4	-	48
Mid-East	2	2	20	10	-	34
Mid-South	-	3	2	246	3	254
South	-	-	-	-	1	1
Total Recaptures	53	54	33	289	5	434
Total Tagged	2,025	1,772	1,192	3,182	142	8,313
Percent Recovery	2.6%	3.0%	2.8%	9.1%	3.5%	5.2%
Percent Fidelity	96.2%	63.0%	60.6%	85.1%	20.0%	81.1%

Table 19. Recaptures of previously tagged lake whitefish in 11 trap net locations in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005. Names of tagging locations are abbreviated as defined in parenthesis for recapture locations.

	Tagging Location											
Recapture Location	BB	SYB	SB	WI	PI	TP	SP	GB	WB	CH	IB	Total
Bottle Bay (BB)	12	7	3	3	1	-	-	3	-	-	-	29
Sunnyside Bay (SYB)	1	17	1	8	-	-	-	6	2	-	1	36
Sunrise Bay (SB)	1	2	6	2	1	-	1	16	3	-	-	32
Warren Island (WI)	-	-	-	23	2	3	7	3	1	-	-	39
Pearl Island (PI)	-	-	-	1	8	-	-	-	-	-	-	9
Thompson Point (TP)	-	2	-	-	-	4	3	2	-	-	-	11
Sheepherder Point (SP)	-	-	-	2	-	1	12	2	6	-	-	23
Garfield Bay (GB)	-	-	-	-	-	-	-	68	6	-	1	75
Whiskey Bay (WI)	-	-	-	3	-	1	1	3	167	2	-	177
Cape Horn (CH)	-	-	-	-	-	-	-	-	-	-	-	0
Idlewilde Bay (IB)	-	-	-	-	-	-	-	-	-	-	1	1
Total Recaptures	14	28	10	42	12	9	24	103	185	2	3	432
Total Tagged	624	901	500	1,574	198	457	735	1,493	1,689	100	42	8,313
Percent Recovery	2.2%	3.1%	2.0%	2.7%	6.1%	2.0%	3.3%	6.9%	11.0%	2.0%	7.1%	5.2%
Percent Fidelity	85.7%	60.7%	60.0%	54.8%	66.7%	44.4%	50.0%	66.0%	90.3%	0.0%	33.3%	73.6%

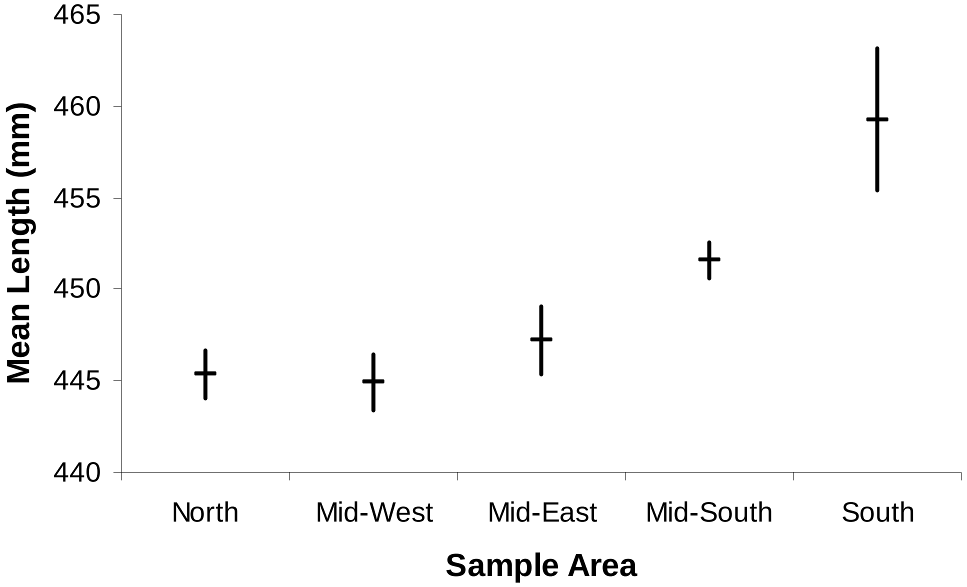

Figure 19. Mean length (± 95% confidence intervals) for lake whitefish from five sample areas caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

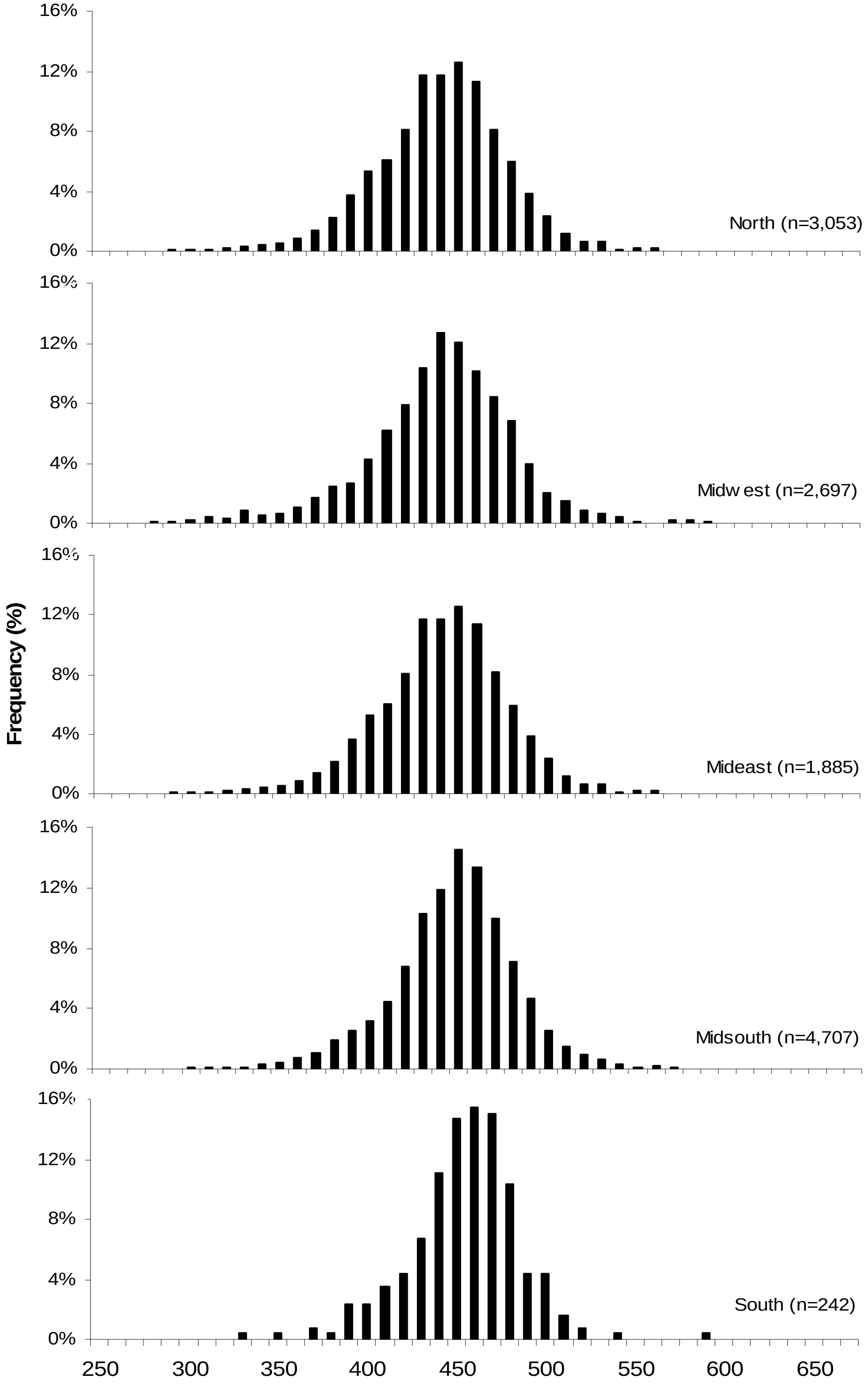

Figure 20. Length-frequency distributions of lake whitefish from five sample areas caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

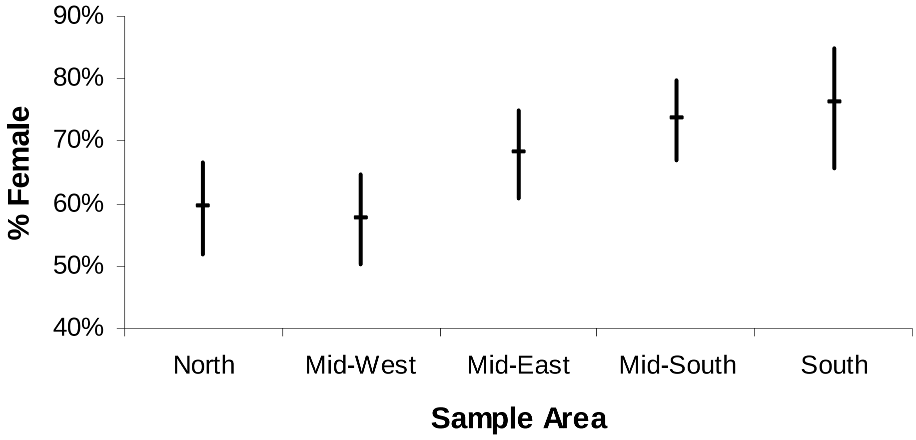

Figure 21. Percentage female lake whitefish caught in trap nets from five sample areas in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

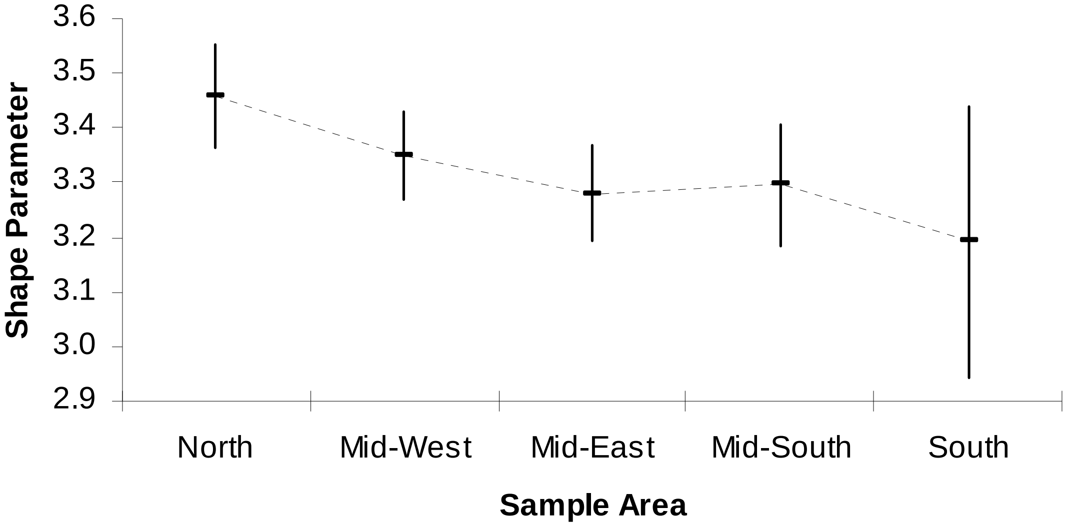

Figure 22. Shape parameter (*β*) of weight-length equations for lake whitefish from five sample areas caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

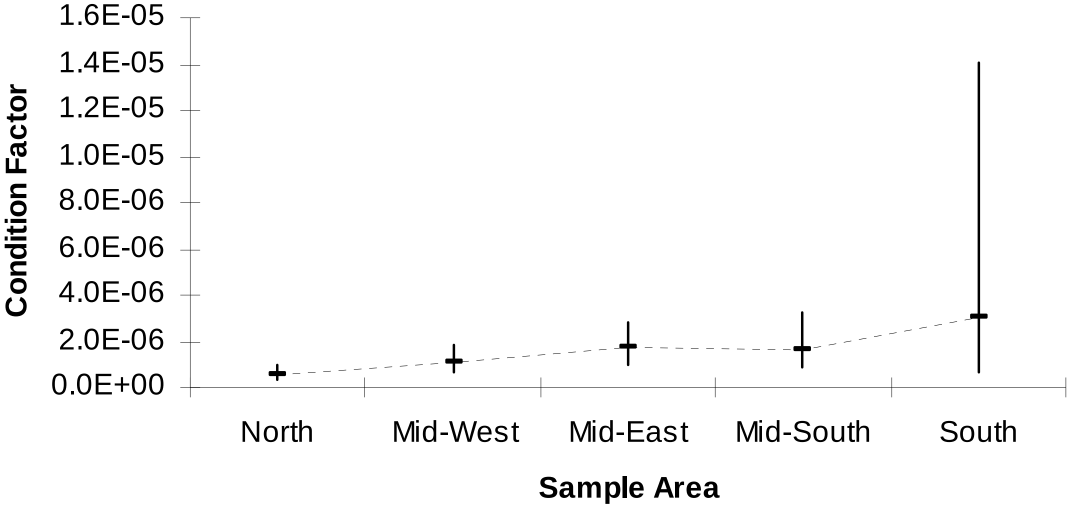

Figure 23. Condition factor (α) of weight-length equations for lake whitefish from five sample areas caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

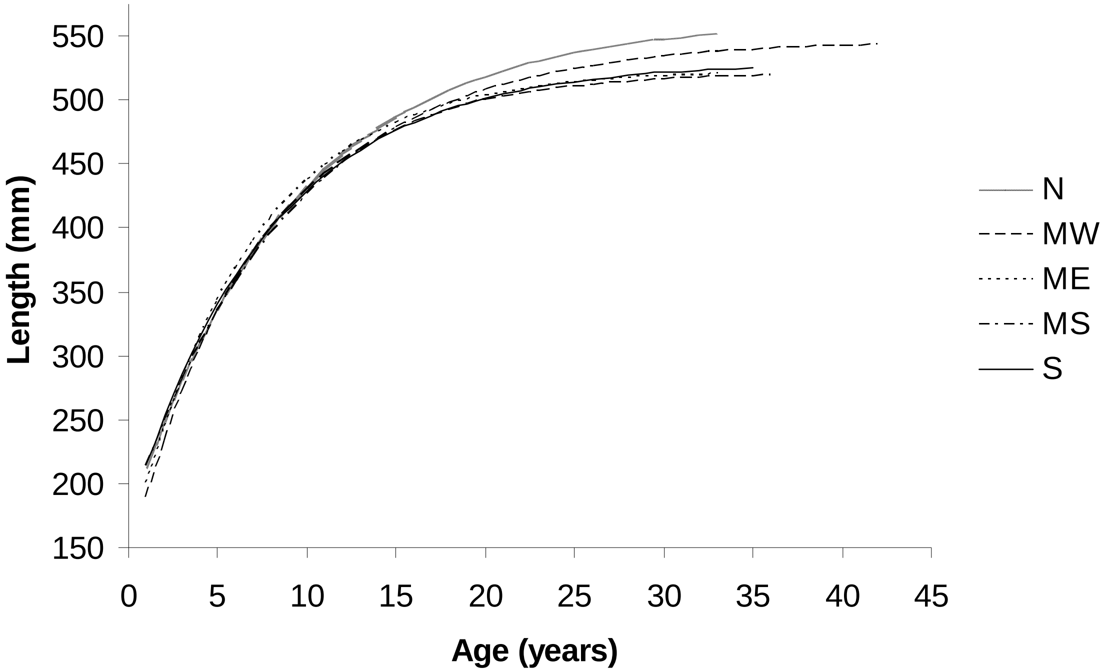

Figure 24. Length-age growth curves fitted to back-calculated mean length-at-age data for lake whitefish caught in trap nets in five sample areas (N=north, MW=midwest, ME=mideast, MS=midsouth, and S=south)in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

Chapter 3:

Harvest Recommendations for Lake Whitefish in Lake Pend Oreille, Idaho

Abstract – To provide harvest recommendations for optimizing yield of lake whitefish in Lake Pend Oreille, Idaho, I used a Beverton-Holt yield/recruit model to estimate yield for each fully recruited whitefish, calculated catch rates of whitefish in trap nets spatially and temporally, and estimated annual yield based on yield/recruit results and an estimate of adult age-structured abundance. Maximum yield/recruit (YPR_{MAX}) was 111.37 g at an instantaneous fishing mortality rate of $F_{MAX} = 3.59$ (annual fishing mortality rate = 63.2%) and t_r = age 6. For $t_r \geq$ age 6, yield/recruit could not be maximized for reasonable values of fishing mortality. Increases in yield/recruit above age 4 were small and yield/recruit was similar for t_r = ages 4–8. Whitefish reached 50% sexual maturity between the ages of 6 and 8 years, and 95% of YPR_{MAX} was at $F = 0.50$ (105.4 g) for t_r = age 6, $F = 0.70$ for t_r = age 7 (105.1 g), and $F = 0.80$ for t_r = age 8 (101.1 g). Catch rate was highest at Sunnyside Bay (CPE = 69.7) in the north (CPE = 34.0) and lowest at Idlewilde Bay (CPE = 0.9) in the south (CPE = 1.8). Catch rate peaked during the weeks of 3 and 17 October, 14 November, and 12 December 2005. Harvesting fish older than age 7 at a fishing mortality rate of $F = 0.5$ would result in a 48.6% total annual mortality rate and an estimated annual yield of 86,512 lbs, similar to the annual commercial lake whitefish harvest from Red Lakes Minnesota (93,136 lbs). I conclude that the whitefish population in Lake Pend Oreille can sustain a commercial fishery if harvest is maintained within sustainable limits.

Introduction

According to Healey (1975), biological attributes such as growth rate, mortality rate, population density, age structure, and age-at-maturity can be used to judge the long-term sustainability of fisheries for lake whitefish *Coregonus clupeaformis* (hereafter, termed whitefish) populations. For example, whitefish stocks with the greatest fishery potential would be of large population size, low natural mortality rate, and slow growth rate, because the compensatory reserve of such populations to exploitation would be near the biological maximum for the species. Such populations would be able to sustain high fishing mortality rates and would compensate through increased growth and recruitment. In contrast, stocks with the lowest fishery potential would be of small population size, high mortality rate, and high growth rate, because such stocks possess little scope for compensation and significant competition between fishing and natural mortality. Populations of whitefish with youthful age structures often appear susceptible to large oscillations and stock collapses associated with recruitment failure, whereas populations of whitefish with older age structure are typically more stable and have more exploitable age classes for a fishery (Healey 1975). Whitefish populations that mature at an older age are able to respond to exploitation by maturing at a younger age through increased growth (Healey 1975). Populations of whitefish from large water bodies with high density and biomass are more likely to support commercial fisheries than populations of low biomass from smaller water bodies.

Single-species fishery management problems can generally be divided into two groups: (1) amount-of-harvest problems related to how many fish should be caught; and (2) method-of-harvest problems related to sizes of fish to be caught. Amount-of-harvest problems deal with controlling fishing effort (F) to achieve management objectives, such as maximizing yield-per-recruit ($F = F_{\max}$). Method-of-harvest problems deal with regulating the age or size to be harvested. A method of harvest can be defined to be a set of age-specific or size-specific gear selectivity coefficients (Norris 1991). Beverton and Holt (1957) first developed yield-per-recruit analysis to provide scientific advice on solving both of these problems. Their method assumes that management has only two control variables: total fishing mortality (F), which is regulated by controls on fishing effort; and age of recruitment to the fishery (t_R), which is regulated by controls on legal size of fish that can be harvested (Norris 1991).

Fish yield can be modeled as a trade-off between fishing mortality and age of entry to the fishery, given a fixed level of recruitment. Recruitment is held constant by standardizing to an arbitrary level, which eliminates the need to estimate recruitment. Yield is therefore estimated per arbitrary unit of recruitment (yield-per-recruit). Growth is included in the model to account for changes in biomass at each vulnerable age and mortality is included in the model to account for loss of individuals and biomass. Yield-per-recruit is estimated for combinations of fishing mortality and age of recruitment to the fishery. Yield-per-recruit analysis is used to set management guidance for a combination of fishing mortality (by regulating fishing effort) and age of recruitment to the fishery (by regulating size of fish harvested).

Catch-per-effort, otherwise known as relative abundance, in theory, removes the effect of variable effort in the measurement of population size (Kohler and Huber 1999). Catch-per-effort may be used to compare relative abundance among stocks that occupy different areas and changes in relative abundance of a single stock through time, under the assumption that catchability of the species to a specific capture method is the same for each stock in different areas occupied or for the same stock at different points in time.

My objective was to provide harvest recommendations that would optimize the commercial yield of whitefish in Lake Pend Oreille. To evaluate relative yield, I used growth and mortality rates estimated in Chapter 1 in a Beverton-Holt yield/recruit model to estimate the fishery yield for each fully recruited whitefish in Lake Pend Oreille. Results of my yield/recruit model will be useful to identify mortality rates and ages-at-harvest that would maximize yield of whitefish in Lake Pend Oreille, if a commercial fishery is implemented.

Methods

Study Area

Lake Pend Oreille, a temperate, oligotrophic lake located in the northern panhandle of Idaho, is the state's largest natural lake with 85,960 surface acres and a shoreline length of 111 miles. The lake basin is deep and steep-sided with a maximum depth of 351 m and a mean depth of 164 m. The lake is in the Pend Oreille drainage basin situated in the glacially formed Purcell Trench (Falter 2003). The Clark Fork River is the largest tributary to the lake and the outflow from the lake forms the Pend Oreille River, which flows into the Upper Columbia River. Thermal stratification occurs from late June to September, and the thermocline typically lies between 10 and 24 m. Summer water temperature (May–October) averages about 9 C in the upper 45 m of water (Rieman 1977; Bowles et al. 1987, 1988, 1989). Surface temperatures are as high as 24 C in hot summers. Littoral areas are limited and mostly characterized by having a very steep bottom, although some littoral areas are characterized by gradual or moderately sloping bottoms (found mostly in the northern end of lake and in bays). Most fish habitat occurs in the pelagic area of the lake.

A virtually unexploited population of whitefish, introduced in 1889 by the US Fish Commission (IDFG-Fishery Management Plan), now resides in Lake Pend Oreille. Presently, no commercial fishery exists for whitefish on Lake Pend Oreille and the sustainability of such a fishery is unknown. Recent studies by the Idaho Department of Fish and Game have concluded that the future of recreational fisheries for trophy rainbow trout, lake trout, bull trout, and kokanee are in jeopardy in Lake Pend Oreille. In 1999, studies of predator-prey relationships led to the conclusion that predators and prey were unbalanced due to a rapid decline in the kokanee population because of low survival of older-aged fish (Maiolie et al. 2002). Since 2000, the greatest threat to the kokanee population has been too many predators, including native bull trout, trophy rainbow trout, and a rapidly-expanding lake trout population that collectively constitute a major source of predation on kokanee that threaten to collapse the kokanee population (Vidergar 2000). Trophy rainbow trout and bull trout fisheries would collapse if kokanee are lost, and lake trout would dominate the fishery without sustained high exploitation, as in Priest Lake, Idaho, and Flathead Lake, Montana (IDFG-Fishery Management Plan). During 2006, an aggressive removal program based on angler incentives and netting reduced the lake trout population by nearly 60% (Hansen et al. 2007), but the kokanee population has yet to recover. Because the public would not likely support a meaningful reduction in the rainbow trout population and the bull trout is protected under the Endangered Species Act (ESA), suppression of lake trout was pursued through angling and netting removals. A commercial fishery for whitefish, which have sustained commercial fisheries in North

America for over a century, may be sustainable and may harvest, as bycatch, sufficient numbers of lake trout to prevent the collapse of the kokanee salmon population.

Model Derivation

For the period prior to recruitment $r = t_R - t_0$, the initial number N_0 of fish decreases exponentially only by natural mortality M, so that the number remaining at time of recruitment R is:

$$R = N_0 e^{-Mr} .$$

Where t_R = age of recruitment and t_0 = hypothetical age at zero length

After recruitment, catch in numbers C is equal to the rate of fishing F times the average number in the population:

$$C = F \int_{t=t_R}^{t=t_\lambda} \mathrm{Re}^{-Z(t-t_R)dt} .$$

Where Z = total mortality, t = age, and t_λ = maximum age.

Yield in weight is therefore:

$$Y = F \int_{t=t_R}^{t=t_\lambda} R w_t e^{-Z(t-t_R)dt} .$$

Omitting F, this integral constitutes the sum of the yearly average biomass of all fish in a year-class for all years that contribute to the fishery. If recruitment is constant among years, then biomass is the weight of the present stock (Ricker 1975). The fishing rate is assumed to be constant after a specific age of recruitment to the fishery (termed knife-edge selectivity), which is problematic if gear size-selectivity changes with age or size. Knife-edge selectivity is a simplifying assumption that is often reasonable and will be used in this analysis.

Growth in weight is described by the Von Bertalanaffy growth model:

$$w_t = W_\infty \left(1 - e^{-K(t-t_0)}\right)^3 .$$

Where w_t = weight at age t, W_∞ = asymptotic weight, K = Brody growth coefficient, and t_0 = hypothetical age at zero length. Isometric growth is assumed (which is generally close to the truth) and weight is an exponentially increasing function of age. Algebraic expansion of the weight-at-age model yields:

$$\overline{w_t} = W_\infty \left(1 - 3e^{-K(t-t_0)} + 3e^{-2K(t-t_0)} - e^{-3K(t-t_0)}\right).$$

Substituting the expanded weight-at-age model for w_t of the yield in weight integral and integrating gives:

$$Y = RFW_\infty \left(\frac{1-e^{-Z\lambda}}{Z} - \frac{3e^{-Kr}\left(1-e^{-(Z+K)\lambda}\right)}{Z+K} + \frac{3e^{-2Kr}\left(1-e^{-(Z+dK)\lambda}\right)}{Z+2K} - \frac{e^{-3Kr}\left(1-e^{-(Z+3K)\lambda}\right)}{Z+3K} \right).$$

Where the maximum post-recruitment life span $\lambda = t_\lambda - t_R$.

When examining different recruitments, Ricker (1975) recommended combining the recruitment model with the yield model:

$$Y = FN_0 e^{-Mr} W_\infty \left(\frac{1-e^{-Z\lambda}}{Z} - \frac{3e^{-Kr}\left(1-e^{-(Z+K)\lambda}\right)}{Z+K} + \frac{3e^{-2Kr}\left(1-e^{-(Z+dK)\lambda}\right)}{Z+2K} - \frac{e^{-3Kr}\left(1-e^{-(Z+3K)\lambda}\right)}{Z+3K} \right)$$

Terms containing $\lambda = t_\lambda - t_R$ are all close to unity for old maximum age (t_λ), so by making $t_\lambda = \infty$, the terms containing λ equate to unity and are omitted from the equation:

$$Y = FN_0 e^{-Mr} W_\infty \left(\frac{1}{Z} - \frac{3e^{-Kr}}{Z+K} + \frac{3e^{-2Kr}}{Z+2K} - \frac{e^{-3Kr}}{Z+3K} \right)$$

Dividing both sides by N_0 and then setting $N_0 = 1$ gives the Beverton-Hold model:

$$Y = Fe^{-Mr} W_\infty \left(\frac{1}{Z} - \frac{3e^{-Kr}}{Z+K} + \frac{3e^{-2Kr}}{Z+2K} - \frac{e^{-3Kr}}{Z+3K} \right).$$

Model Assumptions

The Beverton-Holt yield-per-recruit model assumes that all members of a cohort reach fishable size at the common age t_R, at which they are fully vulnerable to the fishery. This assumption is known as *knife-edge selectivity*, and implies that yield is constant for all individuals of fully recruited ages (each fish above age t_R is subjected to the same F). Constant F across all fully recruited ages is seldom realistic because all capture methods are size selective (Quinn and Deriso, 1999). For example, trap net selectivity most often results in unrepresentative samples of fish too small to be efficiently retained by the gear and of fish that are not present in the sampling area (e.g. young fish spatially separated from the parental stock; Laarman et al. 1982; Hamley et al.1985). However, trap net selectivity is relatively constant for fish older than the age of full recruitment, so the assumption of knife-edge selectivity is reasonable.

The natural mortality rate M is assumed constant for all ages prior to the age of recruitment to the fishery. Natural mortality likely varies for pre-recruited ages of most animals, and increases with age in unexploited whitefish populations (Ricker 1949). However, such increases are typically restricted to the oldest-aged individuals in the population that often contain relatively few fish, so most age classes of fish typically suffer similar rates of natural mortality.

Growth in weight is described by the Von Bertalanffy growth model and is assumed to be isometric ($\beta = 3$). This assumption is generally close to the truth, but errors in yield increase if growth is not isometric. For example, yield/recruit is underestimated if the exponent is less than three and overestimated if the exponent is greater than three (Ricker 1975). However, the absolute level of yield from a Beverton-Holt model is not usually of primary interest, but rather, provides an estimate of the yield obtained from a given number of fish of some conventional age. Typically, interest lies in the difference in yield that would result by varying F or t_R. The relative error in such differences, when using an incorrect exponent, is generally small (Ricker 1975).

Because recruitment is not modeled explicitly and is assumed invariable, the Beverton–Holt yield/recruit model does not address the issue of whether the fishing mortality rate is sustainable (Haddon 2001). Empirical evidence suggests that $F_{\max}$ tends to be too high and may lead to recruitment over-fishing and stock collapse (Hilborn and Walters 2001). Simple yield/recruit models avoid considering reproductive constraints by assuming that recruitment is constant and independent of stock size. For example, when fishing effort is age specific and unlimited ($F_{\max}$), the optimal harvesting strategy from a yield/recruit model is to take all of the harvest at the critical age when the cohort reaches its maximum biomass (Ricker 1975; Norris 1991). A potential consequence of this harvest policy is that the fishery will be unsustainable if the critical age is younger than the age of sexual maturity. An *ad hoc* method of controlling for recruitment over-fishing is to utilize a $F_{0.1}$ harvest policy that is determined numerically by finding the fishing mortality rate at which the slope of the yield-per-recruit curve is 10% of the slope at the origin. An $F_{0.1}$ harvest policy lacks theoretical justification, but has been found to be more conservative (risk averse) and therefore more sustainable than an $F_{\max}$ harvest policy (Haddon 2001). Whitefish populations exhibit a large scope for compensation to exploitation (Jensen 1981; Mills et al. 2004), so utilizing an $F_{\max}$ harvest policy will maximize yield with little risk of recruitment over-fishing.

The Beverton-Holt yield per recruit model assumes that the population has attained equilibrium with respect to mortality, thereby resulting in a fixed age structure. This assumption implies that recruitment and mortality are constant with time and age and the fate of one cohort as it ages represents the fate of all cohorts, so any cohort represents a cross-section of the entire population at any time (Haddon 2001). The model essentially assumes that total yield in any year from all age classes (pseudocohorts) is the same as that from a single cohort over its entire life span (King 1990). Whitefish populations often exhibit substantial annual fluctuations in recruitment that are mostly attributable to biotic and abiotic factors such as spawning biomass, winter severity (ice-cover), spring temperature, and food supply (Taylor et al. 1987; Freeberg et al. 1990). However, if the age structure of the population is at or near equilibrium, the yield/recruit model will be accurate.

Data Analysis

A single yield per recruit model was developed for the lake-wide population, because mortality rates did not differ significantly and growth parameters were similar among putative subpopulations (Chapter 2). Parameters for the yield/recruit model were previously estimated for whitefish sampled in Lake Pend Oreille during autumn 2005 (Chapter 1). Growth parameters for the yield/recruit model were estimated from the Von Bertalanffy length-age model fit to mean back-calculated length-at-age ($L_{\infty} = 537.65$ mm;

$K = 0.12$/year, $t_0 = –2.91$ years). Natural mortality was estimated from the trap-netting age-frequency using catch-curve analysis ($M = 0.167$). Asymptotic weight was estimated from the weight-length relationship ($\alpha = 1.045E\text{-}06$, $\beta = 3.363$) and asymptotic length L_∞ ($W_\infty = 1{,}591$ grams).

Recruitment was eliminated from the yield/recruit model by setting $N_0 = 1$ and dividing both sides by N_0. For each average age of recruitment to the fishery (t_R), maximum yield occurs at some F. Yield per recruit was modeled for $F = 0.0 – 2.0$ and $t_r = 1 – 12$ to ensure that the full behavior of the yield per recruit model was evaluated.

Catch-per-effort.―Catch-per-unit-effort (CPE = whitefish caught per net-day) was calculated for each net location and sampling area for all whitefish caught during trap netting in autumn 2005. Estimates of CPE provided information on relative abundance of whitefish at each net location and sampling area.

Results

Maximum yield per recruit (Y_{MAX}) was 111.37 g at an instantaneous fishing mortality rate of $F_{MAX} = 3.59$ (annual fishing mortality rate = 63.2%) and t_r = age 6 for whitefish in Lake Pend Oreille (Table 20). For $t_r \geq$ age 6, yield/recruit could not be maximized for reasonable values of fishing mortality (Table 20). For $t_r = 1 – 12$, yield per recruit increased sharply to near maximal levels (90% F_{MAX}) at $F = 1.0$ (annual fishing mortality rate = 63.2%; Figure 25**)**. Whitefish reached 50% maturity between the ages of 6 and 8 (Chapter 1), and 95% of maximum yield per recruit for $t_r = 6$ was obtained at $F = 0.50$, $F = 0.70$ for t_r = age 7, and $F = 0.80$ for t_r = age 8. Increases in yield per recruit above $F = 0.5$ were small (Figure 25). Increases in yield per recruit above t_r = age 4 were small and yield per recruit peaked at t_r = age 6 and declined thereafter (Figure 26). Yield per recruit was similar for t_r = age 4 – age 8 (Figure 26). Differences in maximum yield per recruit were small among putative stocks, and the greatest differences occurred between the mideast (YPRMAX > 122.1 grams) and north (YPRMAX > 103.1 grams) putative stocks.

Catch rate varied substantially among sample areas, net locations, and dates. Catch rate was highest in the north (CPE = 34.0) and lowest in the south (CPE = 1.8; Table 23). Catch rate was highest at Sunnyside Bay (CPE = 69.7) and lowest at Idlewilde Bay (CPE = 0.9; Table 24). Catch rate was highest when sampling began (CPE = 54.6) and lowest during the week of 28 November (CPE = 11.5; Table 23). Fluctuations in catch rate with time were synchronous among sample areas (Figure 27), and to a lesser extent, among net locations (Figure 28). Catch rates peaked during the weeks of 3 and 17 October, 14 November, and 12 December.

Discussion

Maximum yield per recruit of whitefish from Lake Pend Oreille (YPR_{MAX} = 0.245 lbs/recruit) was low relative to other whitefish stocks for which yield per recruit has been estimated (Jensen 1979; Woldt et al. 2004). For example, yield per recruit averaged 1.29 lbs/recruit for five stocks of whitefish in Lake Superior, 0.547 lbs/recruit for four stocks of whitefish in Lake Huron, and 0.56 lbs/recruit for seven stocks of whitefish in Lake Michigan (Woldt et al. 2004). Yield per recruit of whitefish in Lake Pend Oreille was low because the instantaneous growth rate K (0.12/year) and asymptotic weight W_∞ (1,591 g) were both low. In contrast, average yield per recruit of whitefish along the north shore of Lake Michigan was 0.926 lbs/recruit because W_∞ = 5,420 g and K = 0.22/year (Jensen 1979). Under exploitation, yield per recruit may increase if the growth rate and asymptotic length increase as a compensatory response to reduced population density (Jensen 1981). In Lake Pend Oreille, harvesting whitefish at age 6 (the age at 50% maturity) and an instantaneous fishing mortality rate $F = 0.45$ (46% annual mortality) would produce a yield per recruit of 100.5 grams. Harvesting whitefish at age 7 (one additional spawning season) and $F = 0.45$ would also produce a yield of 100 grams. Allowing whitefish to spawn at least twice would guard against large oscillations in recruitment due to reproductive failure (Healey 1975; Jensen 1982). A low rate of natural mortality enables yield per recruit to be maximized at low levels of fishing mortality (King 1995), as in Lake Pend Oreille.

The catch rate of whitefish in trap nets was temporally and spatially variable during autumn 2005 in Lake Pend Oreille. The catch rate was highest in the mid-south and north sample areas, which suggests that these areas are important feeding areas or spawning grounds for whitefish. The observed temporal synchrony in catch rates among sampling areas may reflect seasonal changes in catchability of whitefish (Hamley and Howley 1985). Periods of increased activity would likely cause catchability to increase, and thereby cause the catch rate in trap nets to increase.

Management Implications

The whitefish population in Lake Pend Oreille can sustain a commercial fishery if the harvest is maintained within sustainable limits. Given that whitefish populations have historically been capable of sustaining annual mortality rates approaching 70% per year without serious risk of stock collapse (Clark 1984), an instantaneous fishing mortality rate of $F = 0.79$ would subject the population to a 70% annual mortality rate (fishing + natural mortality) and would yield an annual harvest of 120,092 lbs. If harvest is managed at a more conservative fishing mortality rate (annual mortality rate = 50%), the annual harvest would be 76,119 lbs. For comparison, average annual commercial harvest of whitefish from Red Lakes, Minnesota during 1950–1963 was 93,136 pounds (Peterka and Smith 1970), similar to the predicted annual yield from Lake Pend Oreille at $F = 0.425$. Compensatory responses of the whitefish population in Lake Pend Oreille to exploitation are not incorporated in yield per recruit or equilibrium yield models, but would maintain yield. To maximize yield per recruit and ensure that whitefish spawn at least once before being harvested, exploitation could target fish of ≥ age-7 and F = 0.5, which is equivalent to harvesting fish 381 mm and longer at an annual exploitation rate of 39.3%. Total annual mortality would be 48.6% and estimated harvest would be 86,512 lbs per year.

Sustained exploitation would truncate the population age structure by reducing the biomass of older age classes (Ricker 1962; 1975), which would precipitate compensatory responses that would sustain yield (Healey 1975, 1978, 1980; Jensen 1981). In theory, a small amount of annual harvest mortality (33%) could reduce stock biomass to only 16% of the original biomass and substantially truncate the age-structure, if the stock did not compensate for the exploitation by increasing recruitment or growth rates (Ricker 1962). Some researchers have suggested that adult whitefish from unexploited populations may suppress recruitment of juveniles into the adult stock (Johnson 1972, 1973, 1983; Healey 1980) and that strong recruitment depends on the loss of adult fish (Healey 1980). If so, exploitation should cause increased recruitment. For example, experimental exploitation of whitefish in three lakes in the Canadian Northwest Territories resulted in increased growth and recruitment that were proportional to the degree and duration of exploitation

(Healey 1980). Growth should increase with exploitation because prey availability will increase as population density declines (Healey 1975; 1980; Jensen 1981, 1985), and fish will reach mature size at a younger age (Jensen 1981; Beauchamp et al. 2004), thereby maintaining both stock biomass and recruitment over a range of annual mortality rates set by the populations' capacity to compensate for exploitation.

Concerned citizens of the Lake Pend Oreille angling community have suggested that commercial exploition of lake whitefish, an abundant benthivore in Lake Pend Oreille, may significantly affect the trophic ecology of the lake, with possible negative effects on the fish community in general and kokanee in particular. Whitefish may indirectly interact with kokanee, through opossum shrimp *Mysis relicta*, which were first collected in Lake Pend Oreille in 1972 and reached an annual average density of 1,980 per m^2 in 1978, greater than in any other lake (Rieman and Bowler 1980). *Mysis relicta* were suspected to be responsible for the kokanee collapse in Lake Pend Oreille, which began during the period of *Mysis relicta* establishment (Rieman and Bowler 1980; Paragamian and Bowles 1995; Clarke and Bennet 2002, 2004; Clarke et al. 2004). However, research results suggest a complex and ambiguous mechanism of *Mysis* impact on kokanee early life stages, mediated by complex interactions between *Mysis* depletion, alteration of autumn zooplankton communities, and changes in kokanee feeding behavior in response to a rapidly increasing lake trout population, which itself may be a consequence of enhanced recruitment caused by juvenile lake trout consumption of abundant, energy-rich *Mysis* (Beattie et al. 1990; Clarke et al. 2004). Autumn zooplankton communities were depleted and community composition shifted towards copepod dominance as a consequence of intense *Mysis* zooplanktivory (Clarke et al.

2004). Kokanee salmon sampled in November 1952 (pre-mysis) had a 5-fold higher prey biomass than those captured in November 2001 (Clarke et al. 2004), likely because of reduced zooplankton density caused by *Mysis* predation. Poor autumn feeding conditions for kokanee may render individuals more vulnerable to increased size-dependent predation by a rapidly expanding lake trout population (Clarke and Bennett 2002; Hansen et al. 2007), in addition to higher overwinter mortality (Clarke et al. 2004).

Results of the mysid-kokanee research conducted on Lake Pend Oreille and elsewhere imply that if whitefish indirectly impact kokanee salmon in Lake Pend Oreille, the ecological mechanism would likely involve *Mysis*. For example, harvest of whitefish may reduce whitefish density, thereby causing *Mysis* density to increase to the potential detriment of the collapsed kokanee population, assuming whitefish comsume *Mysis* and that consumption of *Mysis* is heavy enough to constrain *Mysis* density. Whitefish diet data is lacking for Lake Pend Oreille, so the extent to which whitefish consume *Mysis* in Lake Pend Oreille is unknown. However, whitefish diet information from lakes where *Mysis* are present suggests that whitefish typically do not prey heavily on *Mysis* (Tohtz 1993; Pothoven et al. 2001; Carl and McGuiness 2006; Pothoven et al. 2006). For example, *Mysis* only comprised 0–8% of total ingested prey numbers for whitefish shorter than 499 mm, and 22% of ingested prey for whitefish 500 mm and longer in Flathead Lake, Montana (Tohtz 1993). Similarly, *Mysis* comprised 4–31% of ingested biomass of whitefish collected from Lake Michigan (Pothoven et al. 2001), and only 6% or less of ingested biomass of whitefish from Lake Huron during 2002–2004 (Pothoven et al. 2006). *Mysis* were not found in the diet of whitefish from three south-central Ontario lakes, which fed predominantly on cladocerans and dipterans, so *Mysis* did not influence whitefish growth or density (Carl and McGuiness 2006). Further, lake-wide whitefish density in Lake Pend Oreille is relatively low (chapter 1), and whitefish may be restricted to waters less than 230 meters deep (chapter 1), which suggests that effects of whitefish predation on *Mysis* would be limited to a small fraction (≤ 33%) of the lake-wide *Mysis* population. In conclusion, the predatory impact of whitefish on the *Mysis* population in Lake Pend Oreille is likely minimal, so harvest of whitefish would not likely contribute to increased *Mysis* density, the only apparent mechanism by which whitefish harvest could negatively affect the kokanee population.

Table 20. Maximum yield (grams) per age 1 through age 12 recruit and instantaneous fishing mortality rate needed to harvest maximum yield per age at recruitment for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

Age at recruitment	Ymax	Fmax
1	84.91	0.23
2	93.14	0.31
3	100.24	0.43
4	105.78	0.65
5	109.51	1.17
6	111.37	3.59
7	111.16	>4.00
8	108.13	>4.00
9	102.92	>4.00
10	96.24	>4.00
11	88.69	>4.00
12	80.75	>4.00

Table 21. Yield (grams) per age 1 through age 12 recruit for instantaneous fishing mortality rates of 0 through 2.0 for lake whitefish caught in from trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	Age at full recruitment											
F	1	2	3	4	5	6	7	8	9	10	11	12
0	0	0	0	0	0	0	0	0	0	0	0	0
0.05	52.9	52.6	51.4	49.3	46.5	43.3	39.8	36.2	32.6	29.1	25.9	22.8
0.1	73.7	75.4	75.2	73.4	70.3	66.2	61.4	56.3	51.0	45.9	40.9	36.2
0.15	81.9	85.8	87.3	86.4	83.7	79.6	74.4	68.6	62.6	56.5	50.5	44.9
0.2	84.6	90.6	93.6	93.9	91.9	88.0	82.8	76.8	70.3	63.7	57.2	50.9
0.25	84.8	92.6	97.1	98.5	97.2	93.7	88.6	82.5	75.8	68.9	62.0	55.3
0.3	83.9	93.1	98.9	101.3	100.7	97.6	92.8	86.7	79.9	72.8	65.6	58.6
0.35	82.4	92.9	99.8	103.1	103.1	100.5	95.8	89.8	83.0	75.7	68.4	61.3
0.4	80.8	92.4	100.2	104.2	104.8	102.6	98.2	92.3	85.4	78.1	70.7	63.3
0.45	79.1	91.6	100.2	104.9	106.0	104.2	100.0	94.2	87.4	80.0	72.5	65.0
0.5	77.5	90.7	100.1	105.4	106.9	105.4	101.4	95.8	89.0	81.6	74.0	66.5
0.55	75.9	89.8	99.8	105.6	107.6	106.4	102.6	97.1	90.3	82.9	75.3	67.7
0.6	74.5	88.9	99.5	105.7	108.1	107.1	103.6	98.1	91.4	84.0	76.4	68.7
0.65	73.1	88.1	99.1	105.8	108.5	107.8	104.4	99.0	92.4	85.0	77.3	69.6
0.7	71.9	87.3	98.7	105.8	108.8	108.3	105.1	99.8	93.2	85.8	78.1	70.4
0.75	70.7	86.5	98.3	105.7	109.0	108.7	105.6	100.5	93.9	86.6	78.8	71.0
0.8	69.7	85.8	97.9	105.6	109.1	109.1	106.1	101.1	94.6	87.2	79.4	71.6
0.85	68.7	85.1	97.5	105.5	109.3	109.4	106.5	101.6	95.1	87.8	80.0	72.2
0.9	67.8	84.4	97.1	105.4	109.4	109.6	106.9	102.0	95.6	88.3	80.5	72.6
0.95	66.9	83.8	96.8	105.3	109.4	109.8	107.2	102.4	96.0	88.7	80.9	73.1
1	66.1	83.3	96.4	105.1	109.5	110.0	107.5	102.8	96.4	89.1	81.3	73.5
1.05	65.4	82.7	96.1	105.0	109.5	110.2	107.8	103.1	96.8	89.5	81.7	73.8
1.1	64.7	82.2	95.8	104.8	109.5	110.3	108.0	103.4	97.1	89.8	82.0	74.2
1.15	64.1	81.7	95.5	104.7	109.5	110.4	108.2	103.6	97.4	90.1	82.4	74.5
1.2	63.5	81.3	95.2	104.6	109.5	110.5	108.4	103.8	97.6	90.4	82.6	74.7
1.25	63.0	80.9	94.9	104.5	109.5	110.6	108.5	104.1	97.9	90.7	82.9	75.0
1.3	62.5	80.5	94.7	104.3	109.5	110.7	108.7	104.3	98.1	90.9	83.1	75.2
1.35	62.0	80.1	94.4	104.2	109.5	110.8	108.8	104.4	98.3	91.1	83.4	75.4
1.4	61.5	79.8	94.2	104.1	109.5	110.8	109.0	104.6	98.5	91.3	83.6	75.6
1.45	61.1	79.4	94.0	104.0	109.4	110.9	109.1	104.8	98.7	91.5	83.8	75.8
1.5	60.7	79.1	93.8	103.9	109.4	110.9	109.2	104.9	98.9	91.7	83.9	76.0
1.55	60.3	78.8	93.6	103.7	109.4	111.0	109.3	105.0	99.0	91.9	84.1	76.2
1.6	59.9	78.5	93.4	103.6	109.4	111.0	109.4	105.2	99.2	92.0	84.3	76.3
1.65	59.6	78.3	93.2	103.5	109.3	111.1	109.4	105.3	99.3	92.2	84.4	76.5
1.7	59.3	78.0	93.0	103.4	109.3	111.1	109.5	105.4	99.4	92.3	84.6	76.6
1.75	59.0	77.8	92.8	103.3	109.3	111.1	109.6	105.5	99.5	92.4	84.7	76.8
1.8	58.7	77.5	92.7	103.3	109.3	111.1	109.7	105.6	99.7	92.6	84.8	76.9
1.85	58.4	77.3	92.5	103.2	109.2	111.2	109.7	105.7	99.8	92.7	84.9	77.0
1.9	58.1	77.1	92.4	103.1	109.2	111.2	109.8	105.7	99.9	92.8	85.1	77.1
1.95	57.9	76.9	92.2	103.0	109.2	111.2	109.8	105.8	100.0	92.9	85.2	77.2
2	57.6	76.7	92.1	102.9	109.2	111.2	109.9	105.9	100.0	93.0	85.3	77.3

Table 22. Absolute yield (pounds) per age 1 through age 12 recruit for instantaneous fishing mortality rates of 0 through 2.0 for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

	Age at full recruitment							
F	5	6	7	8	9	10	11	12
0	0	0	0	0	0	0	0	0
0.05	7,935	8,019	8,074	7,807	7,702	7,490	7,003	6,237
0.1	11,410	11,775	12,057	11,817	11,787	11,567	10,897	9,766
0.15	13,037	13,700	14,229	14,104	14,197	14,034	13,301	11,980
0.2	13,809	14,740	15,496	15,507	15,727	15,642	14,899	13,474
0.25	14,155	15,317	16,271	16,414	16,754	16,749	16,020	14,537
0.3	14,279	15,637	16,761	17,027	17,474	17,545	16,840	15,325
0.35	14,283	15,808	17,078	17,453	17,996	18,136	17,460	15,928
0.4	14,224	15,889	17,286	17,758	18,385	18,589	17,942	16,402
0.45	14,130	15,917	17,422	17,981	18,683	18,943	18,325	16,783
0.5	14,020	15,911	17,510	18,146	18,914	19,225	18,635	17,095
0.55	13,903	15,884	17,566	18,271	19,098	19,455	18,891	17,354
0.6	13,785	15,845	17,600	18,366	19,245	19,643	19,104	17,573
0.65	13,669	15,799	17,618	18,439	19,365	19,801	19,285	17,759
0.7	13,558	15,748	17,625	18,495	19,464	19,934	19,439	17,920
0.75	13,452	15,696	17,624	18,539	19,547	20,048	19,572	18,059
0.8	13,351	15,644	17,617	18,573	19,616	20,145	19,688	18,182
0.85	13,255	15,592	17,607	18,600	19,675	20,230	19,790	18,290
0.9	13,165	15,541	17,594	18,621	19,725	20,303	19,879	18,386
0.95	13,081	15,492	17,579	18,637	19,767	20,368	19,959	18,472
1	13,001	15,444	17,563	18,650	19,805	20,426	20,030	18,549
1.05	12,926	15,399	17,546	18,659	19,837	20,477	20,094	18,619
1.1	12,855	15,355	17,529	18,666	19,865	20,523	20,152	18,682
1.15	12,789	15,313	17,511	18,671	19,890	20,564	20,205	18,739
1.2	12,726	15,273	17,494	18,675	19,911	20,601	20,252	18,792
1.25	12,667	15,234	17,476	18,677	19,931	20,634	20,296	18,841
1.3	12,611	15,198	17,459	18,678	19,948	20,665	20,336	18,885
1.35	12,558	15,163	17,442	18,679	19,963	20,692	20,373	18,926
1.4	12,507	15,129	17,426	18,678	19,977	20,718	20,406	18,964
1.45	12,460	15,098	17,410	18,677	19,989	20,741	20,438	19,000
1.5	12,415	15,067	17,394	18,676	20,000	20,763	20,467	19,033
1.55	12,372	15,038	17,379	18,674	20,010	20,783	20,494	19,064
1.6	12,331	15,010	17,364	18,672	20,019	20,801	20,519	19,092
1.65	12,293	14,983	17,350	18,670	20,027	20,818	20,543	19,119
1.7	12,256	14,958	17,336	18,667	20,034	20,834	20,565	19,145
1.75	12,220	14,933	17,322	18,665	20,041	20,849	20,585	19,168
1.8	12,187	14,910	17,309	18,662	20,047	20,862	20,605	19,191
1.85	12,155	14,887	17,297	18,659	20,053	20,875	20,623	19,212
1.9	12,124	14,865	17,284	18,656	20,058	20,887	20,640	19,232
1.95	12,095	14,845	17,273	18,653	20,063	20,899	20,656	19,251
2	12,067	14,825	17,261	18,650	20,067	20,909	20,672	19,269

Table 23. Catch-rates (number caught per net-day) of lake whitefish caught in trap nets from five sample areas of Lake Pend Oreille, Idaho over 11 weeks of sampling from 3 October 2005 through 15 December 2005.

	Sample Area					
Sample Week	North	Midwest	Mideast	Midsouth	South	Average
10/03/05	-	92.67	3.00	152.50	-	54.6364
10/10/05	-	14.06	3.25	51.13	1.06	17.375
10/17/05	-	26.62	14.86	63.50	1.00	25.0943
10/24/05	64.40	23.90	3.50	28.91	2.00	20.5778
10/31/05	45.29	11.43	2.86	26.19	0.64	18.1846
11/07/05	34.93	25.86	17.79	23.53	2.43	20.5556
11/14/05	67.00	46.86	15.07	25.13	1.13	21.5263
11/21/05	33.76	10.00	3.08	4.57	-	16.7381
11/28/05	15.12	35.00	15.23	10.65	0.50	11.4487
12/05/05	27.67	33.44	20.28	39.38	-	30.8169
12/12/05	32.79	58.71	22.21	31.88	3.81	20.7733
Average	33.99	29.04	12.50	33.35	1.76	

Table 24. Catch-rates (number caught per net-day) of lake whitefish caught in trap nets at 11 net locations in Lake Pend Oreille, Idaho over 11 weeks of sampling from 3 October 2005 through 15 December 2005. Abbreviated names of tagging locations are as defined in Table 18.

	Net Location											
Lift Week	BB	CH	GB	IB	PI	SP	SYB	SB	TP	WI	WB	Average
10/3/05	-	-	152.50	-	-	1.00	-	-	5.00	92.67	-	54.64
10/10/05	-	0.75	85.38	1.38	4.38	1.25	-	-	5.25	23.75	16.88	17.38
10/17/05	-	0.75	82.67	1.33	19.50	24.43	-	-	5.29	32.71	44.33	25.09
10/24/05	-	3.29	43.50	0.50	20.00	4.33	64.40	-	2.67	29.75	20.57	20.58
10/31/05	-	0.71	23.56	0.57	-	4.29	84.29	6.29	1.43	11.43	29.57	18.18
11/7/05	-	3.29	10.88	1.57	-	33.80	60.57	9.29	6.36	25.86	38.00	20.56
11/14/05	-	1.38	20.88	0.88	-	25.29	67.00	-	4.86	46.86	29.38	21.53
11/21/05	33.33	-	4.57	-	-	5.33	-	34.00	0.83	10.00	-	16.74
11/28/05	12.89	0.42	14.00	0.58	-	24.33	-	17.63	7.43	35.00	9.25	11.45
12/5/05	36.00	-	14.31		-	21.00	-	19.33	19.56	33.44	64.46	30.82
12/12/05	36.71	6.69	12.40	0.94	-	12.29	-	28.86	32.14	58.71	64.33	20.77
Average	28.94	2.55	32.99	0.94	13.60	16.37	69.74	20.41	8.88	32.95	33.73	

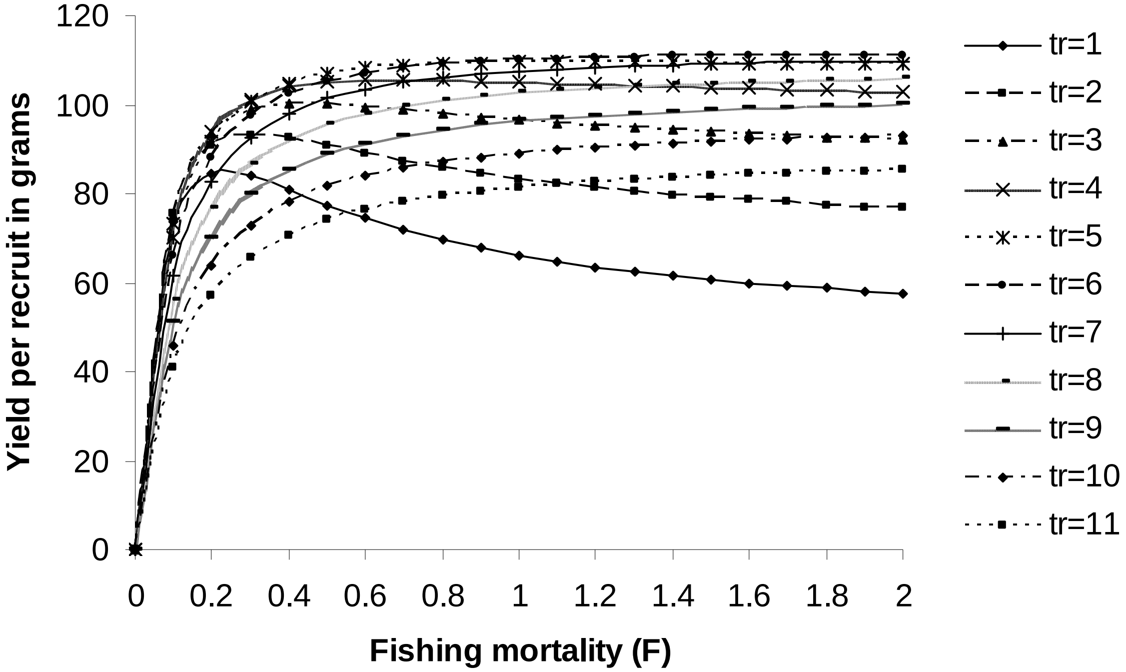

Figure 25. Yield per recruit (grams per recruit) as a function of instantaneous fishing mortality rate (*F*) and age at full recruitment ($t_r = 1 - 11$) for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

Figure 26. Yield per recruit (grams per recruit) as a function of age at full recruitment (t_r = 1 – 12) and instantaneous fishing mortality rate (*F* = 0.1 – 1.0) for lake whitefish caught in trap nets in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

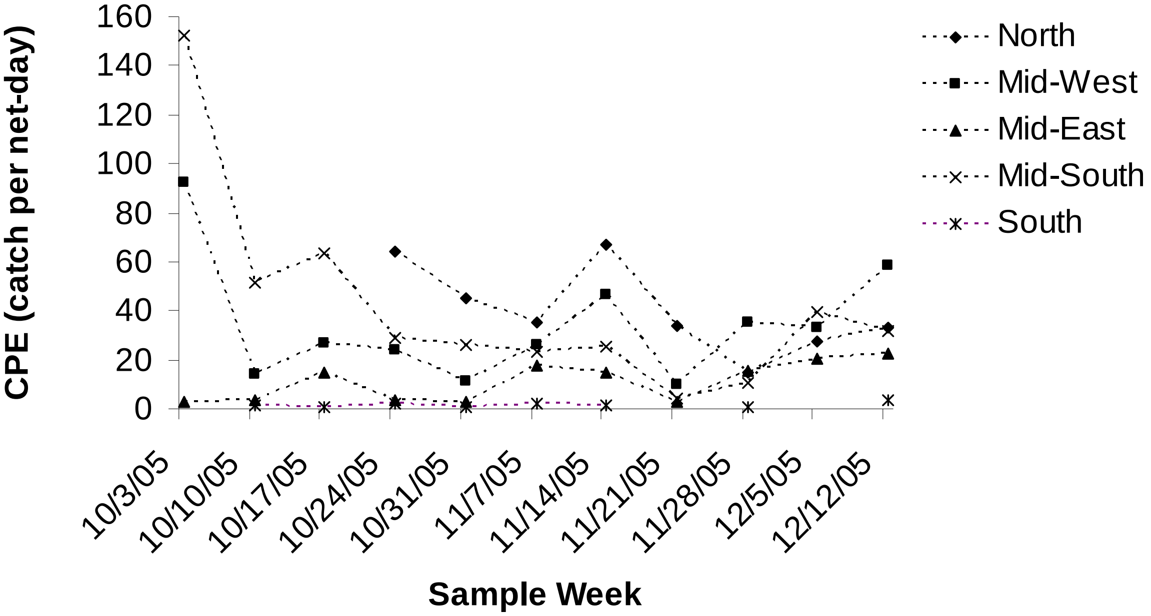

Figure 27. Catch per net-day of lake whitefish in trap nets from five sample areas over 11 weeks of sampling in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

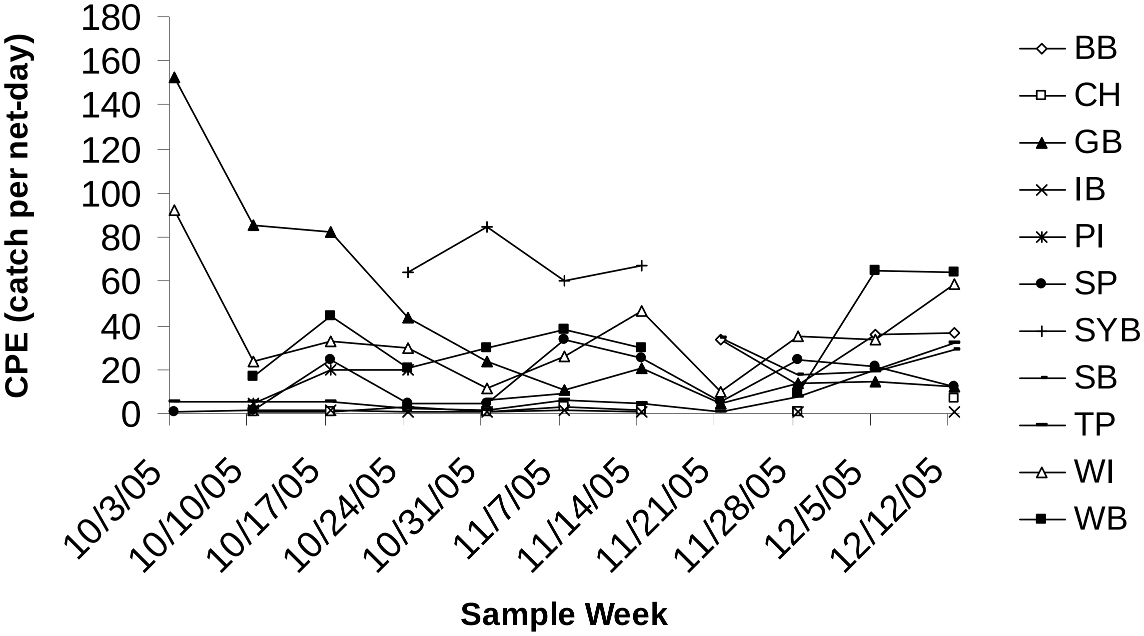

Figure 28. Catch per net-day of lake whitefish in trap nets from Bottle Bay (BB), Cape Horn (CH), Garfield Bay (GB), Idlewilde Bay (IB), Pearl Island (PI), Sheepherder Point (SP), Sunnyside Bay (SYB), Sunrise Bay (SB), Thompson Point (TP), Warren Island (WI), and Whiskey Bay (WB) over 11 weeks in Lake Pend Oreille, Idaho from 3 October 2005 through 15 December 2005.

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