Estimating the number of walleye in Mille Lacs, Minnesota in 2008, 2013 and 2014.

Prepared for the Minnesota Department of Natural Resources
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1. Introduction

The Minnesota Department of Natural Resources conducted a mark-recapture experiment to estimate the number of walleye in Mille Lacs, Minnesota in separate surveys run in spring/summer of 2008, 2013 and 2014. The study protocol is fully described in Jones (2013).

Briefly, walleye were captured on the spawning grounds in late April and early May (Tables 1a, 1b, 1c). These fish were sexed, tagged, fin clipped (with the position of the fin clip dependent upon the sex), and released[1]. Other variables (such as location of the spawning ground, length of the fish, etc.) were also recorded. Some these clipped fish were recovered by the Tribes prior to the gillnet sample (below). The Tribes also removed 46,311/ 6512/ 4624 in 2008/ 2013/ 2014 walleye.

Sampling gillnets were set between late-May to late-June. Walleye were captured, of some of which recaptures from the tagging period as determined by the presence of the fin clip and/or tag from a fish tagged in that year. The sex of the recaptured fish was known, but the sex of the fish without fin clips was not known.[2] Other variables (such as location of the gillnet, length of the fish, etc.) were also recorded.

A random sample of unclipped walleye from the gillnet sample was then selected for sex determination.

Population estimates will be computed for two population. First, the population of interest are walleye greater than 14" in length at the time of tagging (spawning) excluding

[1] Some of the fish captured on the spawning grounds were tagged from previous years' studies. These were treated as "newly" marked in the that year.
[2] Some of the fish captured in the gillnet were tagged from previous years' studies and the sex would be known based on determination at the earlier studies. In these cases, the sex determination from the previous years' studies was not used.

removals by the Tribes. Second, because of the very low catchability of smaller walleye, the population of walleye >17"(M) and >19"(F) is also computed.

Because the time interval between the tagging/clipping and the gillnet sample is short, the population is assumed to be closed with negligible deaths or recruitment to the population. The usual assumptions for a closed population capture-recapture study are made, including

- Marks are not lost between sampling occasions. Because fish are fin-clipped and the time interval is short, this assumption seems reasonable.
- Marked fish can be correctly identified. The examination of fish was done by MDNR members so this again seems reasonable. No other fin-clips were applied in previous studies.
- Mixing of tagged and untagged fish. Tagging/clipping was done at many spawning locations around the lake as was the gillnet survey. However, there was only a short period of time between the end of the marking and the start of the gillnet sampling. If tagged/clipped fish have not fully mixed with other fish from spawning grounds not sampled, there is the potential for substantial bias.

Several estimation methods will be applied to this experiment. All estimation was performed using R 3.1.1 (R Core Team 2013)

2. Pooled-Petersen Estimator

A breakdown of the number of fish clipped, recaptured, and newly recaptured is found in Table 2a. The simple Petersen estimates, combined over both sexes are

2008 14+	678 (SE 57) thousand fish
2013 14+	299 (SE 33) thousand fish
2014 14+	265 (SE 17) thousand fish
2008 17/19+	580 (SE 53) thousand fish
2013 17/19+	271 (SE 31) thousand fish
2014 17/19+	237 (SE 16) thousand fish

The simple Petersen estimates are likely biased upwards because of the heterogeneity in catchability between the two sexes and the change in catchability between the two sampling occasions for the two sexes. Seber (1982) showed that the bias in a simple-Petersen is related to the negative correlation of the catchability between the first and second sampling occasion. In this case, males/females are more/less catchable on the spawning grounds and less/more catchable in the gillnet sample. This creates a negative correlation in catchability between the two sampling occasions and so will lead to a positive bias.

The extent of the bias can be examined using a spreadsheet[3]. For example, suppose that the total population was 300 thousand with a 2:1 sex ratio (F:M); that males/females have a capture probability of 5%/1% on the spawning grounds; and that males/females have a 1%/2% capture probability in the gillnet sample. The expected value of the pooled-Petersen estimate is close to 390 thousand – a bias of almost +30% in the estimated population size.

A stratified estimator is almost certainly required on the basis of sex for these years. There may also heterogeneity in catchability by length and other attributes.

Not unexpectedly, the estimates for the sub-population (>17/19") is smaller than the estimate for 14+". The intent of the using the 17/19" estimator was to exclude immature (smaller) fish. The sexual maturity of the fish was recorded for all fish at the time of tagging. Not unexpectedly, in all years, all but a handful of the tagged fish were mature fish. This implies that recaptures were also all mature fish. The maturity status was not recorded in the gillnet samples for any years, and only recorded in the sex sample in 2008. In that year, 357/407= 88% of the sexed-fish were mature. If this ratio was applied to the gillnet sample, and a revised pooled-Petersen estimator computed, the estimate of the 14+ fish would be reduced by 12% from 678 thousand to 595 thousand fish which is very close to the estimate from the 17/19+ portion of the study of 580 thousand fish.

3. Stratified-Petersen on the basis of sex alone

If sex was measured for all fish at both sampling occasions, then it is relatively simple to compute a stratified-Petersen estimator by finding the Petersen for each sex separately, and then adding the two estimates together.

However, sex was only fully determined in the first sample on the spawning grounds. Of course, any recaptured fish's sex is known. A random sample of the newly captured fish in the gillnet sample was sexed as shown in Tables 1a -1c.

Intuitively, the sex ratio in the sex-sample can be used to impute the approximate numbers of each sex of the unsexed fish. These imputed values could be directly in a fully stratified Petersen estimator (i.e. a separate estimate for each sex),but the resulting standard errors will underestimate the actual uncertainly because the actual number of fish in the 3 classes will vary around these imputed values.

A specialized likelihood function was created (see Appendix A and Table 2b) to deal with proper estimation for this case.[4] The estimates are

2008 14+ 651 (417 F; 233 M) thousand fish with estimated standard errors of

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[3] Refer to the BiasInPooling tab in the PetersenWorkBook2013.xls file.

[4] All fish that received a caudal clip (sex recorded as "u") were dropped for this analysis (< 1% of fish handled). As long as these fish occurred at random with respect to the actual sex, then no biases are introduced.

		72 (70 F; 27 M).
2013	14+	196 (130 F; 66 M) thousand fish with estimated standard errors of 24 (22 F; 13 M).
2014	14+	227 (146 F; 81 M) thousand fish with estimated standard errors of 16 (13 F; 9 M).

2008	17/19+	454 (283 F; 170 M) thousand fish with estimated standard errors of 52 (50 F; 22 M).
2013	17/19+	167 (114 F; 53 M) thousand fish with estimated standard errors of 21 (20 F; 11 M).
2014	17/19+	195 (130 F; 65 M) thousand fish with estimated standard errors of 14 (13 F; 8 M).

The Partially-Stratified-Petersen estimates are considerably smaller than the pooled-Petersen estimate in 2013 and 2014. The estimate in 2008 is smaller, but the uncertainty is very large so the difference may not be real. The stratification by sex appears to have removed considerable bias caused by the heterogeneity in catchability by sex.

4. Stratification by sex and length - I

Catchability also varies by length within each sex at both samples because of gear selectivity. Pure heterogeneity in catchability (e.g. gear selectivity with the same shape in both samples) implies that there is a positive correlation in catchability between the two samples which leads to a negative bias in the estimates of population size.

In this case, it is not clear if the heterogeneity is different in the two gear types, but Figures 1a-1c show that the distribution of lengths does differ between males and females in all the samples, but appears to have the same distribution across samples in a year for each sex.

A stratification by length and sex could be computed in a similar fashion to the partial-stratification by sex as seen earlier.. Because of the relatively small number of recaptures, three length strata were defined 14-20", 20-24", and 24+". The summary statistics are shown in Tables 3a-3c. Few male fish were captured in the upper stratum (24+") in any year.

Estimates of the abundance for males and females for each stratum and the overall total were obtained (Tables 4a-4c). The overall population estimates are

2008	14+	722 (482 F; 240 M) thousand fish with standard errors of 103 (102 F; 29 M)
2013	14+	215 (134 F; 81 M) thousand fish with standard errors of 29 (25 F; 17 M)
2014	14+	232 (149 F; 81 M) thousand fish with standard errors of 18 (16 F; 9 M).

2008	17/19+	481 (290 F; 191 M) thousand fish with standard errors of	
		63 (59 F; 25 M)	
2013	17/19+	192 (109 F; 82 M) thousand fish with standard errors of	
		25 (20 F; 19 M)	
2014	17/19+	197 (125 F; 72 M) thousand fish with standard errors of	
		14 (12 F; 9 M).	

The estimates in 2008 and 2013 is larger than the estimate without length stratification indicating that some bias caused heterogeneity in catchability due to length may have been removed, but the estimates in 2014 is very close in both cases. The estimate of abundance for male fish 24+ inches in length is very close to zero – this is no unexpected as few males grow larger than 24" in length.

5. Stratification by sex and length - II

The previous section required that the length be divided into a small number of strata. Chen and Lloyd (2000) developed a method where no stratification is needed – a smoothed estimate over all lengths is used to estimate a Petersen estimate based on a moving window.

Chen and Lloyd (2000) only considered stratification by a single covariate. In this problem we have the additional complexity that not all fish are sexed and so the Chen and Lloyd (2000) method cannot be used directly for males and females separately and the results combined. Instead, we adopted a two-stage process.

First, a logistic regression was applied to the sample taken from the gillnet sample for sex determination where the probability of being a male was modeled as a function of length (Figure 2). All the data were pooled so the same relationship was used in in 2008, 2013, and 2014. As noted earlier, few males above 24+ inches were captured and the probability that a fish captured in the gillnet sample is male declines rapidly as a function of length. As expected, the curves for each year were similar (not shown) so this common curve is justified.

Second, we used this fitted model to classify an unsexed-fish as male/female depending on the predicted probability of being male. If a fish for a given length had a predicted probability of being male of 0.33, then the fish was classified as 0.33 of a male and 0.67 of a female. This is similar to the naïve estimator for sex stratification where the distribution of the sex in the sexed-sample was used to allocate fish to the two sexes. These fractional fish in each sex were then used in the usual Chen and Lloyd (2000) method. As in the separation by sex, the estimated standard errors computed using the expected counts will be underestimates of the actual standard error. The corrected standard error, allowing for random assignment of fish to sex based on the probability of being male at a given length in the gillnet sample, was computed by computing the Chen and Lloyd (2000) estimate over 100 simulated (random) datasets and then adding the additional the variability of the estimates around the average to the average estimated variance of the estimator. The increase in the se was less than 5%, similar to the small increase over the naïve standard error found in the previous section. The small correction to the naïve se is again a consequence of the large number of fish sexed and captured in the gillnet sample so that the random variation around the expected values is small.

The estimated abundance (by length) is shown in Figures 3a-3c based on all walleye 14+" and in Figures 3d-3f for walleye 17/19+". Plots are similar (but not shown) when the truncated data set is used. The estimated total population size using the modified Chen and Lloyd method are

2008	14+	736 (514 F; 222 M) thousand fish with estimated (corrected) SE of 117 (115 F; 24 M)
2013	14+	256 (134 F; 122 M) thousand fish with estimated (corrected) SE of 37 (23 F; 29 M)
2014	14+	249 (158 F; 91 M) thousand fish with estimated (corrected) SE of 18 (16 F; 9 M)
2008	17/19	415 (294 F; 121 M) thousand fish with estimated (corrected) SE of 53 (51 F; 14 M)
2013	17/19	186 (111 F; 75 M) thousand fish with estimated (corrected) SE of 23 (20 F; 12 M)
2014	17/19	192 (129 F; 63 M) thousand fish with estimated (corrected) SE of 14 (13 F; 6 M)

The estimated total abundance is slightly larger than that from the stratified sex and length method with 3 length classes. However, the estimated abundance curve shows an apparent increase at the very smallest length class – this may be an artefact of the data and may have increased the estimated total. The cause for this apparent increase appears to be an artefact of very small sample sizes at the two smallest length intervals (14-16", Tables 5a-5c and Tables 5d-5f) where no recaptures were obtained (and so the selectivity is very difficult to estimate). The estimated length distribution for males appears to indicate that virtually no males are present at 24+" length.

The estimated selectivity curves for the two sexes in the two samples are presented in Figures 4a-4c based on using all sampled walleye 14+" and Figures 4d-4f for walleye 17/19+". The curves are similar for the truncated data and not shown. The estimated selectivity curves for the two sexes in the gillnet sample are similar but the females have a higher capture rate at all lengths. The estimated selectivity curves in the spawning ground survey are quite different for the two sexes with males having a much higher selectivity than females for most lengths. There are very few males present in the population with lengths 24+". Both sexes have a quite low selectivity at the lower length bound of the population making it difficult to estimate abundance for these smaller fish.

6. Movement and mixing

Another potential source of heterogeneity in catchability is the lack of mixing between the two sampling events because of geographic distance. As shown in Figures 5a-5c, tagging/clipping and gillnet sampling occurred around the lake.

6.1 East vs West

The tag number on the recaptured fish was used to link the recapture zone with the tagging zone. However, in 2013, 11/73 recaptured fish were clipped (indicating tagged previously) but missing the tag number and so could not be classified by place of release. Virtually all of the recaptured fish in 2008 and 2014 had tag numbers.

To investigate if the recapture probabilities differ depending on where tagged, the tagging and recapture zones were classified into two broad geographic strata – east or west based on UTM easting 450000. The summary data are presented in Tables 6a-6c. A formal test for differential gross recapture rates failed to find evidence of a difference for both sexes, but the small number of recaptures likely implies that the power is low to detect anything but gross differences. The mean time at large for recaptured fish was also compared (Tables 6a-6c). There was no evidence of a difference in the mean time at large depending on where initially tagged except for males in 2008.

An investigation of the degree of potential bias due to geographical stratification being ignored is presented in Tables 7a-7c. The tagging/clipping, recaptures, and gillnet recoveries were stratified into the two strata East or West as noted earlier. Recoveries missing the tag number could not be linked back to their location of tagging and so were dropped. This implies that estimates of abundance presented in Tables 7a-7c will be biased upwards because the assumed number of recaptures is too small. The data were also pooled over sex to avoid having to model the sex distribution of the sample in each geographic stratum as was done earlier. This will also bias the estimates in Tables 6a and 6b upwards because of the heterogeneity in catchability between the two sexes in the two samples as seen earlier. The pattern of recaptures in Tables 7a-7c shows that fish are recaptured about twice as often in their stratum of releases (diagonal elements of the movement matrix) than in the other stratum and so mixing does not appear to be complete around the lake.

The key message from Tables 7a-7c is to see the extent of possible bias introduced by ignoring the geographical stratification. In this case the difference between the stratified and unstratified estimates is negligible given the standard errors seen on the earlier estimates. Therefore at a gross level, there does not seem to be any reason to develop an estimator stratified by sex, length, and geographical stratum.

6.2 Inshore vs. offshore - I

All of the tagged fish were released from the spawning grounds which are all on shore. Gillnets were set throughout the lake. Is there a differential marked fraction inshore vs offshore potentially indicating a lack of mixing?

Angling zones 15, 16, 22, 23, and 41 were classified as "off-shore", while the remaining angling zones were classified as "in-shore". Summary statistics are shown in Tables 8a-8c. Data was very sparse in 2013 with only about 2% of new captured fish captured in off-shore gillnets with no recaptured fish. There was no evidence of a differential marked fraction in 2008 and 2013 but power to detect a difference is low. In 2014, about 5% of fish were newly captured offshore and the marked fraction was only about ¼ of the marked fraction in shore (p=.002). So there is evidence in 2014 that marked fish don't mix with inshore/offshore fish.

Unfortunately, the data is far too sparse to stratify by inshore/offshore in both years so no formal estimates can be made with this stratification.

Tables 9a-9c summarize information on the sex ratio in the gillnet samples from those fish selected for sex determination. These fish were a random sample from all newly captured fish (where sex was not recorded) so reflect a combination of the sex ratio in the population and the differential selectivity for males and females in the gear. No fish were captured and sexed from offshore in 2008. Data was again very sparse in 2013, but in neither year was there evidence that the sex ratio in fish selected for sex-determination differed between inshore and offshore areas.

Figure 6 compared the length distribution of newly captured fish in the gillnets in the inshore and offshore zones. Again, data is very sparse for the offshore catches in 2013. A qqplot (not shown) and a chi-square test of the hypothesis of equal length distributions failed to detect any difference in the length distribution in either year except for 2008 where the large sample size detected trivial differences.

6.3 Inshore vs offshore - II

There is evidence that the marked fraction (i.e. the proportion of fish that are tagged) varies with the depth of the gillnet. Differential marked fractions are usually an indication of incomplete mixing of tagged and non-tagged fish. Because the depth of the gillnets tends to increase in the offshore areas, this section examines potential biases due to non-mixing of tagged and non-tagged fish.

The sampling metadata was extracted from the database and the mean depth of the gillnet was computed as the average of the recorded depth at the shallow and deep end of the net. The mean depth was divided into depth classes as shown in Table 10 and the observed marked fraction was computed for each depth interval (Figure 9). A simple regression was fit to the marked-fractions by depth for each year and there was evidence of a decline in the marked-fraction with depth ($p < .001$ for each year).

This decline in the marked fraction suggests that mixing of the tagged fish is incomplete among inshore/offshore areas. This can lead to bias in the estimates if catchabilitity also varies among the areas. In order to investigate the potential size of the bias in a Pooled-Petersen estimator, hypothetical scenarios were constructed for the three years in the study.

Inshore and offshore net sets were defined using the mean depth of the net with a mean depth of 0-15' being defined as onshore, and 15+' defined as offshore (Table 11).

Parameters for the scenarios are summarized in Table 12. Estimated population sizes were based on the results of the previous analyses. Fish are tagged on the spawning ground which are inshore, and the number of tagged-fish released were based on the number of tags released in each year. These tagged fish distribute themselves between the inshore and offshore areas. The untagged population also distributes itself between the inshore and offshore areas. This gives rise to two equations in two unknowns:

$$\frac{n_1 b}{n_1 b + Ua} = f_{inshore}$$

$$\frac{n_1(1-b)}{n_1(1-b) + U(1-a)} = f_{offshore}$$

where n_1 and U are the number of fish tagged and number of fish unmarked; a and b are the (unknown) proportion of the unmarked and marked fish that find themselves in the inshore stratum, and f is the observed marked fraction from Table 11. These equations can be solved for a and b which then allows computation of the expected number of tagged and untagged fish in each stratum during the gillnet survey that are available for capture.

We assumed that the number of nets set in each stratum is proportional to the effort to capture fish, with equal efficiency assumed for all nets. We also assumed that inshore comprises 20% of the lake and offshore 80% of the lake based on a simple ratio of observed area. Furthermore, assuming that fish are uniformly spread within each stratum, the product of these two ratios gives the ratio of catchability in each stratum (Table 12). For example, putting twice as many nets in the inshore area compared to the offshore area with the inshore area ¼ the size of the offshore area gives a ratio of 8:1 for catchability. If the ratio of catchabilites is 1:1, the no bias would exist due to unequal mixing because all fish are equally catchable regardless of stratum. We arbitrarily set the catchability in the off-shore stratum at .01 which then fixes the catchability in the inshore stratum to match the ratios of catchability shown in Table 12.

A spreadsheet was created to computed expected number of fish captured in the gillnets along with the expected number of recaptures. These and the initial number of fish tagged were used in a Pooled-Petersen estimator to estimate the bias due to incomplete mixing. Solutions are shown in Figures 9 and the estimated potential bias due to incomplete mixing is

Year	2008	2013	2014
%bias	-9%	-15%	-28%

It is surprising at first glance that the absolute bias in 2013 is less than that in 2014 when the ratio of catchabilities is greater. [All else being equal, ratios closer to 1:1 should lead to lower biases.] The ratio of the marked fractions in 2013 is also larger than in 2014 which implies less mixing. [All else being equal, more mixing leads to less bias.] However, in the 2013 scenario, most of the fish are in the inshore stratum, so that the few fish in the off-shore stratum where relatively little effort occurs only has a small effect on the estimate.

6.4 Inshore vs. offshore – III

If the ratio of catchabilities in the inshore/offshore area were known, then it is possible to "correct" the Pooled-Petersen estimator by reweighting the statistics from each stratum. For example, from Table 12, the ratio of catchabilities in 2008 is 6.1:1 (inshore:offshore). If we multiply the number recaptured and number captured in the gillnets in the offshore stratum by 6.1, this would remove the bias due to unequal catchability:

$$\hat{N} = \frac{n_1 \times \left(n_{2,i} + 6.1 n_{2,o}\right)}{\left(m_{2,i} + 6.1 m_{2,o}\right)} = \frac{20000 \times \left(33829 + 6.1(1714)\right)}{\left(1083 + 6.1(31)\right)} = \frac{20000 \times (44800)}{(1280)} = 700000$$

The statistics from the Pooled-Petersen were adjusted using the ratio of catchabilities from Table 12 and presented in Table 13. The estimated %bias in the original Pooled-Petersen estimates is:

Year	2008	2013	2014
%bias	-21%	-40%	-27%

The estimate bias from this method in 2013 is considerable – the actual number of fish could almost be 70% larger than the Pooled-Petersen![5] However, the number of recaptures in the offshore area in 2013 is very small (4) and small changes in this number have a large influence on the bias. For example, if 6 fish were recaptured rather than 4, the estimated bias changes to -33%.

7. Using both years of data

An attempt was made to use both years of years in a single Jolly-Seber model. The initial attempts pooled over both sexes. Four capture time were defined corresponding to the tagging and gillnet samples in 2013 and 2014. The following capture histories (first row) and counts (second row) were obtained

0001	0010	0011	0100	0101	0110	1000	1001	1010	1100	1111
3700	14169	213	3170	48	78	6803	33	7	65	1

For example, history 0011 corresponds to fish captured and tagged in 2014 and then recaptured in the gillnets in 2014. Losses on capture (e.g. fish removed for sex sampling or otherwise dead) are accounted for another field not shown.

[5] A -40% bias from the corrected estimate implies that the pooled-Petersen is 0.6 of the adjusted estimate, or that the adjusted estimate is 1/0.6=1.67 times larger than the pooled-Petersen.

The within year histories look reasonable. For example

History	Count	Interpretation
1000	6803	Number tagged in 2013
1100	65	Number recaptured in gillnets in 2013
0100	3170	Number newly captured in 2013

(and similar histories for 2014) match fairly well the summary statistics in Table 1a and 1b. [The above histories include all fish (even those <14" in length) and fish that are clipped but lost their tag and recovered are exclude.

However, there appears to be a problem with tag loss or behavioral changes between years. Population abundance is around 200,000. There were a total of 10,000 fish tagged and released in 2013 (spawning and gillnet samples). About 15,000 fish were tagged in 2014 representing about 7% of the population. About 7% of 10,000 or 700 fish from 2013 would be expected to be captured in 2014, but less than 200 fish were captured from 2013 (histories of the form 1010, 1011, 0110, 0111, 1101, 1110, or 1111). Consequently, no estimates were computed pending further investigation of this matter.

It should be noted that most fish captured in the gillnets in 2014 and released were NOT given individual tag numbers and so extending this attempt in the future is not feasible even if the above problem is resolved.

8. Discussion

A summary of the estimates from the three years, the different estimators, and the different length cutoffs is presented in Figure 8.

Heterogeneity in catchability is usually the weak point in any mark-recapture study. There are several sources of heterogeneity in catchability in the current study.

- Sex. There is differential catchability of males and females both at the time of tagging (males more catchable) and in the gillnet survey (females more catchable). This negative correlation in catchability leads to a positive bias in the pooled-Petersen estimator .If the sex was measured for all fish at all capture occasions, the correction is trivial; however, not all fish were sexed at all occasions and a specialized estimator, the partially-Stratified estimator, was developed.

  In all years, the partially-stratified estimator was lower than the pooled-Petersen estimate with substantial differences in 2013 and 2014. There is a clear near for stratification by sex.

- Length. There is evidence of selectivity by length at both sampling occasions. Smaller fish are much less catchable than larger fish in both sampling occasions. This may be due to immature fish not appearing in the spawning grounds and the size of the mesh in the gillnets. This positive correlation in catchability between the two sampling occasions leads to a negative bias in estimates of abundance if ignored. In particular, because fish with lengths close to 14" have very low catchability, this segment of the population is effectively invisible and stratification cannot provide good estimates for these smaller fish.

In all years, the estimates tend to increase as additional stratification by length is imposed. Two sex-and-length-stratified estimator showed only a small change in abundance estimates relative to adjusting only for stratification by sex. Based on this analysis, the estimates from the sex + length stratified model or the sex + Chen and Lloyd analysis are to be preferred, however, the confidence intervals on all of the stratified estimates are wide enough that there really isn't a clear cut choice. Ideally, a partially-stratified estimator using length as a individual covariate could adjust for both simultaneously – this is currently under development by a Ph.D. student at SFU.

A key unresolved issue with these models for the 14"+ is the low selectivity for fish around 14-16 inches. Here the data are very sparse, and no good estimate of the abundance of this segment of the population is available – the estimates from the 14" cutoff are likely underestimates of the actual abundance of the 14+" segment of the population. Because these smaller fish are essentially invisible, statistical modelling based only on mark-recapture data is unlikely to resolve this problem. Auxiliary information such as harvest information by length class of tagged and untagged fish may provide some information about the relative sizes of these smaller age classes which can then be used to augment the results of the tagging study.

A truncated population (17/19+") definition was also used to remove the more serious differential catchabilities due to length. As expected, these estimates are smaller than the 14+" estimates, and showed less effects of dealing with length heterogeneity. If estimates of abundance for these smaller fish are needed, gear must be modified at both sampling occasions to catch more of these fish, especially in the gillnet sample.

- Geographical. There was no evidence of differential catchability based on geographical stratification and so this stratification was not applied.

- Inshore/Offshore. There is evidence of unequal mixing of tagged fish in the two strata during the gillnet survey because the marked-fraction generally declines with the depth of the gillnet and deeper nets are generally set in offshore areas. This would not be a concern if the catchability in the two strata were equal at either sampling occasion. Heterogeneity in catchability during the tagging phase may exist if, for example, non-spawners or skip-spawners did not move inshore and were not available for tagging. Heterogeneity in catchability during the gillnet phase may be due to the study design. More nets were generally placed in the inshore areas which form a small fraction of the lake. This would generally lead to a positive correlation in catchability between the two sampling occasions;

spawners are more catchable on the spawning areas than non-spawner; tend to be in the inshore areas at the time of the gillnet phase (incomplete mixing) and are subject to higher catchability because more effort is placed in the inshore areas. This positive correlation in catchability leads to a negative bias in estimates that ignore this stratification.

A simple model to assess the potential degree of bias shows that it ranges from about -10 to -30%. However, this model made a number of simplifying assumptions which may not accurately reflect reality. A model where the relative effort and area of the inshore/offshore areas was used to estimate the ratio of catchabilities in the strata was used to "correct" the pooled-Petersen estimator for unequal catchability. Estimates of bias ranged from -20 to -40%, but the larger (absolute) bias may be an artefact of a very small number of fish recaptured in the gillnets in the offshore stratum.

It currently is not possible to correct for this incomplete mixing/differential catchability using data based methods because it is not possible to measure the differential catchability with the current study design. The differential catchability could be estimated by augmenting the current design with radio tagged fish released on the spawning grounds which are then tracked for their movement and then obtaining direct measures of the different catchability in the inshore/offshore areas. The catchability by depth of the net in the gillnet survey could also be constructed leading to a finer stratification as well. Knowledge of the differential catchability could then be used to correct the various estimators considered in this report.

If the incomplete mixing is related to maturity (e.g. immature fish tend to remain offshore and are not tagged), it may be possible to exclude immature fish from the population estimate with some changes to the study design. Maturity status is measured when the fish are tagged, so that immature fish can be excluded from the tagging effort. Recapture then would necessarily be mature fish. The gillnet sample captures both mature and immature fish, but the sex-sample in 2013 and 2014 did not record the maturity status of the selected fish. If this attribute was also recorded, the proportion of mature fish in the sex-sample could be used to impute the proportion by maturity class for the remaining gillnet sample. The estimated obtained would then refer only to the abundance of mature fish in the population. A finer resolution may also be possible when both length and the maturity status in the sex-sample are used in a model that predicts maturity status as a function of length and may be an alternative to the simple length truncation currently employed. Furthermore, if this change lead to an equal marked fraction inshore and offshore, then the unequal catchability inshore/offshore would not introduce any bias in the estimates of abundance. Conceivably, effort could be concentrated only in the inshore areas assuming that tagged and untagged fish mature fish mix on the spawning grounds and have similar movement patterns about the lake

If incomplete mixing persists, a reallocation of the nets could also be used to try and ensure that catchability is roughly equal for all fish across the lake. For example, nets could be randomly placed throughout the lake. This would assume that nets have the same selectivity curve in all areas of the lake.

Lastly, if the number of nets and area assumptions are approximately valid indicators of differential catchability, it may be possible to correct the estimates as by reweighting the statistics. A range of differential catchabilities can by used in a simulation study with any of the proposed estimators to see the range of bias that could be expected. The limiting factor for this approach is the need to estimate the marked fraction by both sex and/or length for both inshore and offshore strata which may not be feasible because of the low number of recaptures. Bayesian methodology would allow specification of the approximate ratio in catchability without having to be ``certain'' about the ratio and would automatically incorporate the uncertainty in the ratio into the estimates.

Ignoring the problem of inshore/offshore, the estimators that would appears to be the most reliable in reflecting their underlying population would be the 17/19+ estimates adjusted for differential catchability by sex. Any of the three estimators could be used as they are all very similar. The extent of the bias caused by heterogeneity in catchability/incomplete mixing in the inshore/offshore area was estimated based on very simple models, but shows that the bias in abundance estimates could range from -10% to -40%.

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Table 1a. Summary statistics for the 2008 survey.				
	Female (adipose clip)	Male (dorsal clip)	Unknown (caudal clip)	Total
Gross Tagged/clipped 2008-04-01 -> 2008-05-17	**4611**	**15157**	**146**	**19914**
(less than 14”)		-532	-19	-551
(less band removals)	-28	-519	-2	-549
Net Tagged/clipped >14”	**4583**	**14106**	**125**	**18814**
(less 17”(M)/19”(F)	-1019	-4067	-52	-5138
Net Tagged/clipped >17/19	**3564**	**10039**	**73**	**13676**
Recaptured in gillnet >14” 2008-05-19 -> 2008-06-30	36	100	0	136
Recaptured in gillnet >17/19	33	82	0	115
Gross newly captured in gillnet			4927	4927
(less than 14”)			-162	-162
Net newly captured in gillnet >14”			4765	4765
(less 17”(M)/19”(F)			-880	-880
Net newly captured in gillnet > 17/19”			3885	3885
Gross selected for sex sample from gillnet sample	292	149	0	441
(less than 14”)	-17	-17	-0	-34
Net selected for sex sample >14”	275	132	0	407
(less 17/19”)	-79	-33	-0	-112
Net selected for sex sample >17/19”	196	99	0	295

Database did not contain information about fish selected for sexing; only summary data was available without length information.

Table 1b. Summary statistics for the 2013 survey.				
	Female (adipose clip)	Male (dorsal clip)	Unknown (caudal clip)	Total
Gross Tagged/clipped 2013-04-19 -> 2013-05-17	**1598**	**5253**	57	**6908**
(less than 14")		-25	-13	-38
(less band removals)	-10	-117		-127
Net Tagged/clipped >14"	**1588**	**5111**	44	**6743**
(less 17"(M)/19"(F)	-156	-781	-9	-946
Net tagged/clipped > 17/19	**1432**	**4330**	35	**5797**
Recaptured in gillnet >14" 2013-05-23 -> 2013-06-21	35	41	1	77
Recaptured in gillnet >17/19"	33	39	1	73
Gross newly captured in gillnet			3355	3355
(less than 14")			-19	-19
Net newly captured in gillnet			3336	3336
(less 17"(M)/19"(F)			-274	-274
Net newly captured in gillnet > 17/19"			3062	3062
Gross selected for sex sample from gillnet sample	239	42	1	282
(less than 14")	-2	-1	-0	-3
Net selected for sex sample >14"	237	41	1	279
(less 17/19")	-37	-7	-0	-44
Net selected for sex sample >17/19"	200	34	1	235

Table 1c. Summary statistics for the 2014 survey.				
	Female (adipose clip)	Male (dorsal clip)	Unknown (caudal clip)	Total
Gross Tagged/clipped 2014-04-16 -> 2014-05-14	**5286**	**9097**	**78**	**14,462**
(less than 14")	-7	-70	-4	-81
(less band removals)	-16	-157	0	-173
Net Tagged/clipped >14"	**5263**	**8871**	**74**	**14,208**
(less 17"(M)/19"(F)	-212	-2108	-26	-2346
Net Tagged/clipped >17/19	**5051**	**6763**	**48**	**11,862**
Recaptured in gillnet >14" 2014-05-20 -> 2014-06-13	109	104	1	214
Recaptured in gillnet >17/19"	108	90	1	199
Gross newly captured in gillnet >14"			3817	3817
(less than 14")			-46	-46
Net newly captured in gillnet >14"			3771	3771
(less 17"(M)/19"(F)			-313	-313
Net newly captured in gillnet > 17/19"			3458	3458
Gross selected for sex sample from gillnet sample	379	109	13	501
(less than 14")	-6	-1	-0	-7
Net selected for sex sample >14"	373	108	13	494
(less 17/19")	-50	-15	-0	-65
Net selected for sex sample >17/19"	323	93	13	429

Table 2a. Summary statistics used for the Pooled-Petersen estimators.

Summary statistics for Pooled-Petersen estimator >14"

	2008	2013	2014
n_1 (marked)	18,814	6,743	14,208
m_2 (recaptured)	136	77	214
n_2 (sample 2)	4,901	3,413	3,985

Summary statistics for Pooled-Petersen estimator >17/19"

	2008	2013	2014
n_1 (marked)	13,659	5,797	11,862
m_2 (recaptured)	115	73	199
n_2 (sample 2)	4,880	3,409	3,970

Table 2b. Summary statistics used for the Partially-Stratified Petersen estimator.

Summary statistics for Partially-Stratified Petersen estimator >14"

History	2008 Count	2013 Count	2014 Count
U0	125	43	73
UU	0	1	1
0U	4358	3057	3227
M0	14006	5070	8767
MM	100	41	104
0M	132	41	108
F0	4547	1553	5154
FF	36	35	109
0F	275	237	373

Summary statistics for Partially-Stratified Petersen estimator >17/19"

History	2008 Count	2013 Count	2014 Count
U0	73	34	47
UU	0	1	1
0U	3478	2827	3029
M0	9957	4291	6673
MM	82	39	90
0M	132	34	93
F0	3531	1399	4943
FF	33	33	108
0F	275	200	323

For example, history MM refers to fish identified as male on the spawning ground and then recaptured. History 0U refers to fish captured in the gillnet sample, but sex was not determined. History 0F refers to fish captured on the gillnet sample, selected for sex determination, and it was determined it was female.

Table 3a. Summary statistics used for stratification by length and sex in 2008 for 14+" (before the slash) and 17/19" after the slash for the 14-20" category.[6]				
	Female (adipose clip)	Male (dorsal clip)	Unknown (caudal clip)	Total
Tagged/clipped				
14-20 in	1857/ 838	10123/ 6056	101/ 49	
20-24 in	1384	3897	21	
24+ in	1335	76	3	
Recaptured in gillnet				
14-20 in	10/ 7	62/ 44	0/ 0	
20-24 in	18	38	0	
24+ in	8	0	0	
Newly captured in gillnet				
14-20 in				2551/ 1671
20-24 in				1427
24+ in				786
Selected for sex sample				
14-20 in	120/ 41	84/ 51	0	
20-24 in	86	44	0	
24+ in	69	4	0	

[6] Numbers do not total to Table 1a because a small number of fish did not have length measurements taken.

Table 3b. Summary statistics used for stratification by length and sex in 2013 for 14+" (before the slash) and 17/19" after the slash for the 14-20" category [7]

	Female (adipose clip)	Male (dorsal clip)	Unknown (caudal clip)	Total
Tagged/clipped				
14-20 in	280/ 124	2710/ 1929	23/ 14	
20-24 in	810	2336	14	
24+ in	498	64	6	
Recaptured in gillnet				
14-20 in	5/ 3	16/ 14	1/ 1	
20-24 in	17	21	0	
24+ in	12	3	0	
Newly captured in gillnet				
14-20 in				1034/ 760
20-24 in				1547
24+ in				755
Selected for sex sample				
14-20 in	49/ 12	19/ 12	0/ 0	
20-24 in	106	21	0	
24+ in	82	1	1	

[7] Numbers do not total to Table 1b because a small number of fish did not have length measurements taken.

Table 3c. Summary statistics used for stratification by length and sex in 2014 for 14+" (before the slash) and 17/19" after the slash for the 14-20" category [8]				
	Female (adipose clip)	Male (dorsal clip)	Unknown (caudal clip)	Total
Tagged/clipped				
14-20 in	584/ 372	6411/ 4303	49/ 23	
20-24 in	3243	2410	22	
24+ in	1430	45	3	
Recaptured in gillnet				
14-20 in	11/ 10	62/ 48	0/ 0	
20-24 in	77	41	1	
24+ in	21	1	0	
Newly captured in gillnet				
14-20 in				1236/ 923
20-24 in				2020
24+ in				515
Selected for sex sample				
14-20 in	89/ 39	60/ 45	2/ 2	
20-24 in	231	46	8	
24+ in	53	2	3	

[8] Numbers do not total to Table 1c because a small number of fish did not have length measurements taken.

Table 4a. Abundance Estimates for 14+" from sex and length stratified model in 2008 (thousands) before slash and 17/19" after the slash..						
Stratum	M+F Est	M+F SE	F Est	F SE	M Est	M SE
14-20"	466/ 244	92/ 39	283/ 91	90/ 35	183/ 134	27/ 23
20-24"	128	19	74	18	54	11
24+"	128	44	125	44	3	4
ALL	722/ 481	103/ 63	482/ 290	102/ 59	240/ 191	29/ 25

Table 4b. Abundance Estimates for 14+"from sex and length stratified model in 2013 (thousands)						
Stratum	M+F Est	M+F SE	F Est	F SE	M Est	M SE
14-20"	90/ 67	22/ 17	40/ 15	18/ 9	50/ 50	15/ 15
20-24"	93	17	63	15	31	8
24+"	32	9	32	9	.3	.2
ALL	216/ 192	29/ 25	135/ 109	25/ 20	81/ 81	17/ 17

Table 4c. Abundance Estimates for 14+" from sex and length stratified model in 2014 (thousands)						
Stratum	M+F Est	M+F SE	F Est	F SE	M Est	M SE
14-20"	98/ 65	14/ 9	40/ 16	12/ 5	58/ 48	8/ 8
20-24"	96	9	74	8	22	4
24+"	36	8	35	8	.9	1
ALL	232/ 197	18/ 14	149/ 125	16/ 12	81/ 72	9/ 9

Table 5a. Summary data for 2008 for modified Chen and Lloyd method for walleye 14+".

Length Centre (inches	Female Tagged/ Clipped	Female Recap	Female Imputed Unclipped	Male Tagged/ Clipped	Male Recap	Male Imputed Unclipped	Smoothed Population Estimates F pop est ('000 s)	M pop est ('000 s)	F+M pop es ('000s
14.5				1451	10	295		43	
15.5				1000	4	132		32	
16.5	83	0	86	1893	5	78	67	25	9[illegible]
17.5	277	0	190	3242	19	132	71	26	9[illegible]
18.5	750	3	410	1876	17	218	71	25	9[illegible]
19.5	747	7	465	661	7	190	61	20	8[illegible]
20.5	319	1	320	1092	14	101	43	13	5[illegible]
21.5	226	3	253	1544	14	60	28	9	3[illegible]
22.5	324	7	284	961	9	51	24	7	3[illegible]
23.5	515	7	325	300	1	44	30	7	3[illegible]
24.5	571	2	346	64	0	36	37	7	4[illegible]
25.5	421	2	258	12	0	21	37	7	4[illegible]
26.5	260	3	124				25		
27.5	67	1	36				13		
28.5	15	0	9				6		
29.5	1	0	1				2		

Note that there was insufficient data for males with lengths 26"+ or females 16"- to use in the analysis.

Table 5b. Summary data for 2013 for modified Chen and Lloyd method for walleye 14+".

Length Centre (inches	Female			Male			Smoothed Population Estimates		
	Tagged/ Clipped	Recap	Imputed Unclipped	Tagged/ Clipped	Recap	Imputed Unclipped	F pop est ('000 s)	M pop est ('000 s)	F+M pop es ('000s
14.5				61	0	33		19	
15.5				234	0	57		15	
16.5	26	0	60	525	2	55	6	12	1
17.5	35	1	100	550	5	69	7	12	1
18.5	95	1	154	486	2	81	9	12	2
19.5	124	3	247	854	7	98	10	13	2
20.5	156	7	316	944	9	97	12	12	2
21.5	203	4	313	726	3	73	15	10	2
22.5	231	3	333	475	5	59	18	8	2
23.5	220	3	323	191	4	44	18	5	2
24.5	196	4	310	55	2	32	15	3	1
25.5	169	5	226	6	1	18	11	1	1
26.5	90	2	106				7		
27.5	34	0	45				4		
28.5	6	1	8				2		
29.5	3	0	2				1		

Note that there was insufficient data for males with lengths 26"+ or females 16"- to use in the analysis.

Table 5c. Summary data for 2014 for modified Chen and Lloyd method for walleye 14+”.

Length Centre (inches	Female Tagged/ Clipped	Female Recap	Female Imputed Unclipped	Male Tagged/ Clipped	Male Recap	Male Imputed Unclipped	Smoothed Population Estimates F pop est (‘000 s)	M pop est (‘000 s)	F+M pop es (‘000s
14.5				379	1	51		10	
15.5				734	7	77		9	
16.5	31	0	47	1053	6	42	8	9	1
17.5	39	0	106	1528	11	73	9	10	1
18.5	142	2	176	1740	16	92	10	10	2
19.5	372	10	328	977	20	131	13	10	2
20.5	591	23	446	861	11	136	15	9	2
21.5	828	29	475	902	21	111	18	8	2
22.5	980	14	423	475	5	76	20	6	2
23.5	844	13	326	172	2	44	20	5	2
24.5	734	10	237	35	1	25	17	3	2
25.5	424	6	140	9	0	11	13	2	1
26.5	183	4	73				8		
27.5	74	1	17				4		
28.5	11	0	5				2		
29.5	3	0	1				1		

Note that there was insufficient data for males with lengths 26”+ or females 16”- to use in the analysis.

Table 5d. Summary data for 2008 for modified Chen and Lloyd method for walleye 17/19+".

Length Centre (inches	Female Tagged/ Clipped	Female Recap	Female Imputed Unclipped	Male Tagged/ Clipped	Male Recap	Male Imputed Unclipped	Smoothed Population Estimates F pop est ('000 s)	M pop est ('000 s)	F+M pop es ('000s
14.5									
15.5									
16.5									
17.5				3519#	20	132		25	
18.5				1876	17	218		25	
19.5	838#	7	465	661	7	190	53	20	7
20.5	319	1	320	1092	14	101	40	14	5
21.5	226	3	253	1544	14	60	27	9	3
22.5	324	7	284	961	9	51	24	7	3
23.5	515	7	325	300	1	44	30	7	3
24.5	571	2	346	64	0	36	37	7	4
25.5	421	2	258	12	0	21	37	7	4
26.5	260	3	124				25		
27.5	67	1	36				13		
28.5	15	0	9				6		
29.5	1	0	1				2		

Note that there was insufficient data for males with lengths 26"+ or females 16"- to use in the analysis.

Counts in this class may differ from the corresponding counts in the 14"+ analysis because fish exactly on the class boundary (e.g. exactly 17") are included in this class in this table, but would have belonged to the previous class in the 14+" analysis.

Table 5e. Summary data for 2013 for modified Chen and Lloyd method for walleye 17/19+".

Length Centre (inches	Female Tagged/ Clipped	Female Recap	Female Imputed Unclipped	Male Tagged/ Clipped	Male Recap	Male Imputed Unclipped	Smoothed Population Estimates F pop est ('000 s)	M pop est ('000 s)	F+M pop es ('000s
14.5									
15.5									
16.5									
17.5				589[#]	5	69		11	
18.5				486	2	81		12	
19.5	124[#]	3	247	854	7	98	9	13	2[illegible]
20.5	156	7	316	944	9	97	11	12	2[illegible]
21.5	203	4	313	726	3	73	14	10	2[illegible]
22.5	231	3	333	475	5	59	18	8	2[illegible]
23.5	220	3	323	191	4	44	18	5	2[illegible]
24.5	196	4	310	55	2	32	15	3	1[illegible]
25.5	169	5	226	6	1	18	11	1	1[illegible]
26.5	90	2	106				7		
27.5	34	0	45				4		
28.5	6	1	8				2		
29.5	3	0	2				1		

Note that there was insufficient data for males with lengths 26"+ or females 16"- to use in the analysis.

[#] Counts in this class may differ from the corresponding counts in the 14"+ analysis because fish exactly on the class boundary (e.g. exactly 17") are included in this class in this table, but would have belonged to the previous class in the 14+" analysis.

Table 5f. Summary data for 2014 for modified Chen and Lloyd method for walleye 17/19+".

Length Centre (inches	Female			Male			Smoothed Population Estimates		
	Tagged/ Clipped	Recap	Imputed Unclipped	Tagged/ Clipped	Recap	Imputed Unclipped	F pop est ('000 s)	M pop est ('000 s)	F+N pop es ('000s
14.5									
15.5									
16.5									
17.5				1586#	11	73		10	
18.5				1740	16	92		10	
19.5	372#	11	328	977	20	131	12	10	2[illegible]
20.5	591	23	446	861	11	136	15	9	2[illegible]
21.5	828	29	475	902	21	111	17	8	2[illegible]
22.5	980	14	423	475	5	76	20	6	2[illegible]
23.5	844	13	326	172	2	44	20	5	2[illegible]
24.5	734	10	237	35	1	25	17	3	2[illegible]
25.5	424	6	140	9	0	11	13	2	1[illegible]
26.5	183	4	73				8		
27.5	74	1	17				4		
28.5	11	0	5				2		
29.5	3	0	1				1		

Note that there was insufficient data for males with lengths 26"+ or females 16"- to use in the analysis.

Counts in this class may differ from the corresponding counts in the 14"+ analysis because fish exactly on the class boundary (e.g. exactly 17") are included in this class in this table, but would have belonged to the previous class in the 14+" analysis.

Table 6a. Geographical stratification in 2008 to investigate if there is evidence of a difference in recapture rates, depending on where tagged.						
	Females			Males		
Geographical Stratum	E	W	Total	E	W	Total
Tagged	2976	1600	4576	8108	5988	14096
Recaptured#	21	13	34	51	42	93
Gross recapture probability#	.0070	.0081		.0062	.0070	
Pearson test	$X^2 = 0.04$, p-value = .82.			$X^2 = 0.17$, p-value = .67.		
Mean days at large	26.5	31.4		26.4	32.1	
SD days at large	7.3	8.8		6.8	8.4	
ANOVA	$F = 3.06$, $p = 0.09$			$F=14.4$, $p < .001$		

Table 6b. Geographical stratification in 2013 to investigate if there is evidence of a difference in recapture rates, depending on where tagged.						
	Females			Males		
Geographical Stratum	E	W	Total	E	W	Total
Tagged	842	746	1588	2198	2911	5110
Recaptured#	21	13	34	18	22	40
Gross recapture probability#	.025	.017		.0082	.0076	
Pearson test	$X^2 = 0.730$, p-value = .40.			$X^2 = 0.01$, p-value = .92.		
Mean days at large	31.9	28.8		30.8	28.6	
SD days at large	8.5	8.5		8.2	7.5	
ANOVA	$F = .94$, $p = 0.34$			$F = 0.65$, $p = .42$		

11 fish lost their tags and could not be linked back to stratum of tagging. Consequently, the reported recapture probabilities are underestimates of the actual recapture probabilities.

Table 6c. Geographical stratification in 2014 to investigate if there is evidence of a difference in recapture rates, depending on where tagged.						
	Females			Males		
Geographical Stratum	E	W	Total	E	W	Total
Tagged	4296	961	5257	5946	2920	8866
Recaptured#	88	18	106	75	29	104
Gross recapture probability#	.020	.019		.013	.010	
Pearson test	$X^2 = 0.05$, p-value = .83.			$X^2 = 0.97$, p-value = .32.		
Mean days at large	28.5	30.3		26.6	25.8	
SD days at large	6.1	5.2		6.7	7.0	
ANOVA	F = 1.4, p = 0.23			F= .24, p = 0.63		

10 fish lost their tags and could not be linked back to stratum of tagging. Consequently, the reported recapture probabilities are underestimates of the actual recapture probabilities.

Table 7a. Summary statistics to investigate the potential bias from ignoring an E/W geographical stratification in 2008. Both sexes are also pooled so biases from heterogeneity in catchability between sexes is also present. No standard error presented because of the clear problems with the estimates – the question of interest is the degree of potential bias.

	Tagged	E	W
E	11164	60	16
W	7633	8	49
Gillnet recoveries		1791	2014

Pooled Petersen estimate 557 thousand fish.
Stratified Petersen (Darroch) $\hat{N}_{Darroch} = 553$ thousand fish.

Table 7b. Summary statistics to investigate the potential bias from ignoring an E/W geographical stratification in 2013. The 11/72 recaptured fish that could not be linked back to the original place of recapture are ignored which implies that estimates of abundance will be biased upwards. Both sexes are also pooled so biases from heterogeneity in catchability between sexes is also present. No standard error presented because of the clear problems with the estimates – the question of interest is the degree of potential bias.

	Tagged	E	W
E	3073	22	7
W	3668	5	30
Gillnet recoveries		1449	1088

Pooled Petersen estimate 273thousand fish.
Stratified Petersen (Darroch) $\hat{N}_{Darroch} = 274$ thousand fish.

Table 7c. Summary statistics to investigate the potential bias from ignoring an E/W geographical stratification in 2014. There were 10 recaptured fish that could not be linked back to the original place of recapture and are ignored which implies that estimates of abundance will be biased upwards. Both sexes are also pooled so biases from heterogeneity in catchability between sexes is also present. No standard error presented because of the clear problems with the estimates – the question of interest is the degree of potential bias.

	Tagged	E	W
E	10,268	122	44
W	3,929	10	38
Gillnet recoveries		1939	1174

Pooled Petersen estimate $\hat{N}_{pp} = 221$ thousand fish.

Stratified Petersen (Darroch) $\hat{N}_{Darroch} = 220$ thousand fish.

Table 8a. Summary statistics to investigate if the marked-fraction is different in inshore vs offshore angling zone in 2008. Angling zones 15, 16, 22, 23, 41 were classified as "off-shore"; all other angling zone were classified as inshore. Both sexes were pooled.

Location	Newly captured fish	Recaptured fish	Marked Fraction
Inshore	4027	125	.030
Offshore	737	11	.015

Fisher's Exact test p-value of equal marked fraction: .15

Table 8b. Summary statistics to investigate if the marked-fraction is different in inshore vs offshore angling zone in 2013. Angling zones 15, 16, 22, 23, 41 were classified as "off-shore"; all other angling zone were classified as inshore. Both sexes were pooled.

Location	Newly captured fish	Recaptured fish	Marked Fraction
Inshore	3281	75	.022
Offshore	55	0	.000

Fisher's Exact test p-value of equal marked fraction: .63

Table 8c. Summary statistics to investigate if the marked-fraction is different in inshore vs offshore angling zone in 2014. Angling zones 15, 16, 22, 23, 41 were classified as "off-shore"; all other angling zone were classified as inshore. Both sexes were pooled.

Location	Newly captured fish	Recaptured fish	Marked Fraction
Inshore	3573	212	.056
Offshore	198	2	.010

Fisher's Exact test p-value of equal marked fraction: .002

Table 9a. Summary statistics to investigate if the sex-ratio is different in inshore vs offshore angling zones from fish selected for sex-determination in 2008. Angling zones 15, 16, 22, 23, 41 were classified as "off-shore"; all other angling zone were classified as inshore.

Location	Female	Males	Unknown
Inshore	275 (67%)	132 (32%)	0 (0%)
Offshore	0	0	0

Fisher's Exact test p-value of equal sex ratio cannot be computed.

Table 9b. Summary statistics to investigate if the sex-ratio is different in inshore vs offshore angling zones from fish selected for sex-determination in 2013. Angling zones 15, 16, 22, 23, 41 were classified as "off-shore"; all other angling zone were classified as inshore.

Location	Female	Males	Unknown
Inshore	232 (85%)	39 (14%)	1 (0%)
Offshore	5 (71%)	2 (28%)	0 (0%)

Fisher's Exact test p-value of equal sex ratio: .29

Table 9c. Summary statistics to investigate if the sex-ratio is different in inshore vs offshore angling zones from fish selected for sex-determination in 20143. Angling zones 15, 16, 22, 23, 41 were classified as "off-shore"; all other angling zone were classified as inshore.

Location	Female	Males	Unknown
Inshore	326 (74%)	100 (23%)	13 (3%)
Offshore	47 (85%)	8 (14%)	0 (0%)

Fisher's Exact test p-value of equal sex ratio: .17

Table 10. Summary statistics on the impact of depth of gillnet on the marked fraction. Note that a simple chi-square test cannot be used to test the hypothesis of equal marked fraction because the sampling unit is the gillnet and not the fish.

Depth Class (feet)	Number Net sets#	Total Fish	Marked	Marked Fraction
		2008		
00-10&	496	1214	44	0.036
10-15	767	1546	47	0.030
15-20	303	456	9	0.020
20-25	147	250	3	0.012
25-30	246	753	16	0.021
30+	88	231	3	0.013
		2013		
00-10&	773	1086	32	0.029
10-15	1203	1663	39	0.023
15-20	509	434	3	0.007
20-25	159	93	1	0.011
25-30	103	30	0	0.000
30+	91	33	0	0.000
		2014		
00-10&	719	1527	98	0.064
10-15	890	1383	84	0.061
15-20	432	531	20	0.038
20-25	196	148	2	0.014
25-30	243	181	5	0.028
30+	214	180	2	0.011

Includes sets with no fish captured.

& Depth class on left boundary included in class. For example, if the mean depth was exactly 10 feet, this data would be included in the 10-15' depth class.

Table 11. Summary statistics and other information used to investigate the potential bias from incomplete mixing between inshore and offshore fish.

Depth Class (feet)	Number Net sets[#]	Total Fish	Marked	Marked Fraction
		2008		
00-15[&] (in-shore)	1263	2760	91	0.033
15+ (off-shore)	784	1690	31	0.018
		2013		
00-15[&] (in-shore)	1976	2749	71	0.026
15+ (off-shore)	862	590	4	0.0068
		2014		
00-15[&] (in-shore)	1609	2910	182	.063
15+ (off-shore)	1085	1040	29	0.028

[#] Includes sets with no fish captured.

[&] Depth class on left boundary included in class. For example, if the mean depth was exactly 15 feet, this data would be included in the 15+' depth class.

Table 12. Scenarios used to investigate the potential bias from incomplete mixing of fish in- and off-shore.

	2008	2013	2014
Population size	700,000	300,000	300,000
Total fish tagged (inshore)	20,000	6,000	12,000
Observed marked fraction – inshore	0.032	0.026	0.062
Observed marked fraction - offshore	0.018	0.007	0.028
Net sets Inshore:offshore	1.6:1	2.3:1	1.5:1
1/Area Inshore:offshore	4.0:1	4.0:1	4.0:1
Ratio of catchabilities	6.4:1	9.1:1	6.0:1
n1	20,000	6,000	12,000
m2= inshore+offshore	1113=1082+31	511=507+5	436=379+57
n2=inshore+offshore	35540=33829+1714	21812=21106+706	7865=5838+2027
Pooled Petersen	638,473	255,865	216,357
Estimated bias in Pooled-Petersen due to non-mixing	-9%	-15%	-28%

Table 13. Correcting the pooled-Petersen for 14+" fish using the estimated ratio of catchabilities from Table 12 to estimate the potential bias from incomplete mixing by depth.

	2008	2013	2014
n1 (Table 2a)	18814	6743	14208
m2=inshore+offshore (Table 11)[#]	122 =91+31	75 =71+4	211 =182+29
n2=inshore+offshore (Table 11)	4450 =2760+1690	3339 =2749+590	3950 =2910+1040
Pooled Petersen estimate ('000s)[a]	686	300	266
Corrected m2	280 =91+(6.1)(31)	107 =71+9.1(4)	356 =182+6.0(29)
Corrected n2	13069 =2760+(6.1)(1690)	8118 =2749+9.1(590)	9150 =2910+6.0(1040)
Corrected Petersen ('000s)	878	509	365
Estimated % bias	-22%	-41%	-27%

[#] Differs slightly from Table 2a because some fish were captured in nets where the depth was unknown.
[a] Differs slightly from previous Pooled-Petersen estimates because statistics slightly different due to missing depth data from some net sets.

Figure 1a. Summary of distribution of lengths in the various samples in 2013.

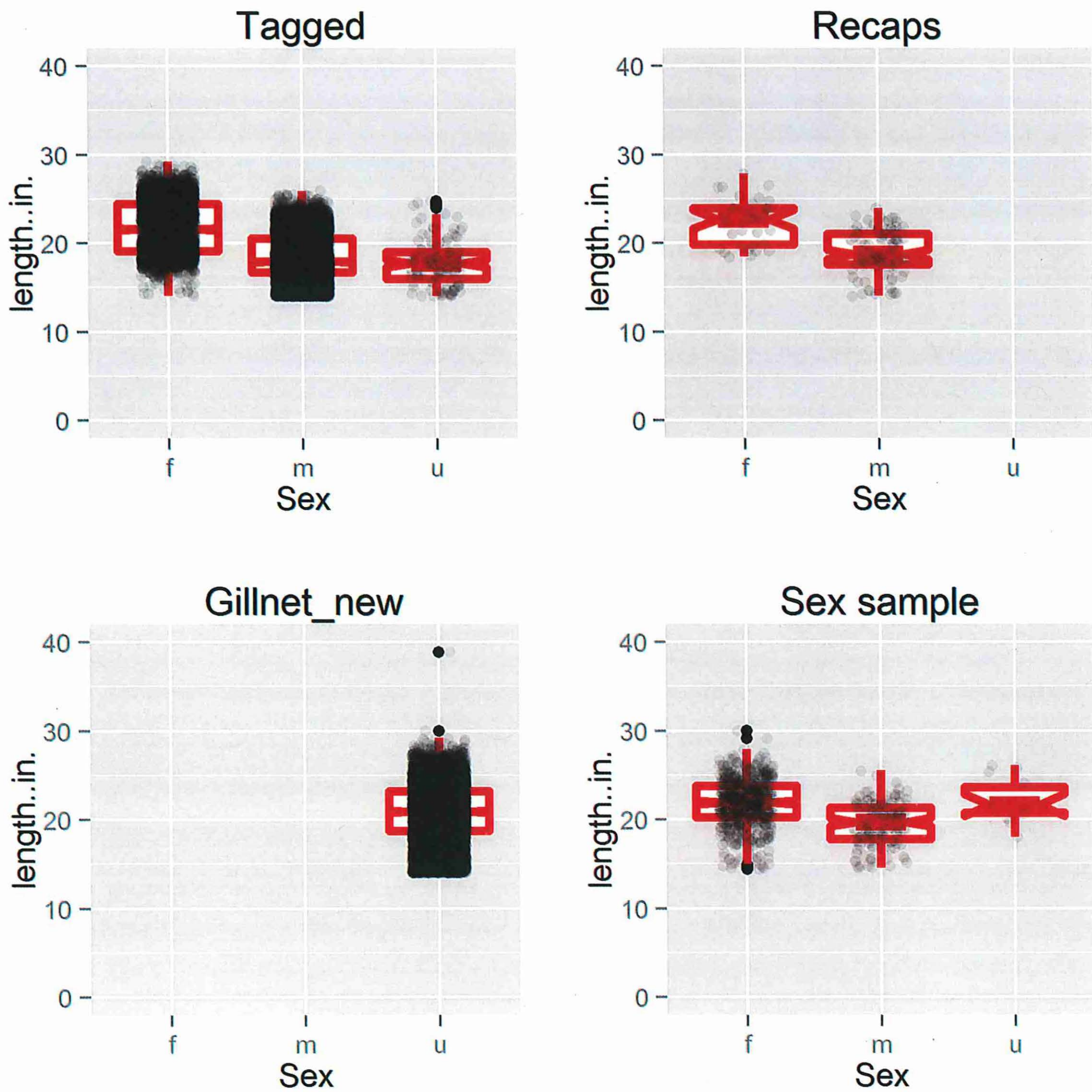

Figure 1b. Summary of distribution of lengths in the various samples in 2013.

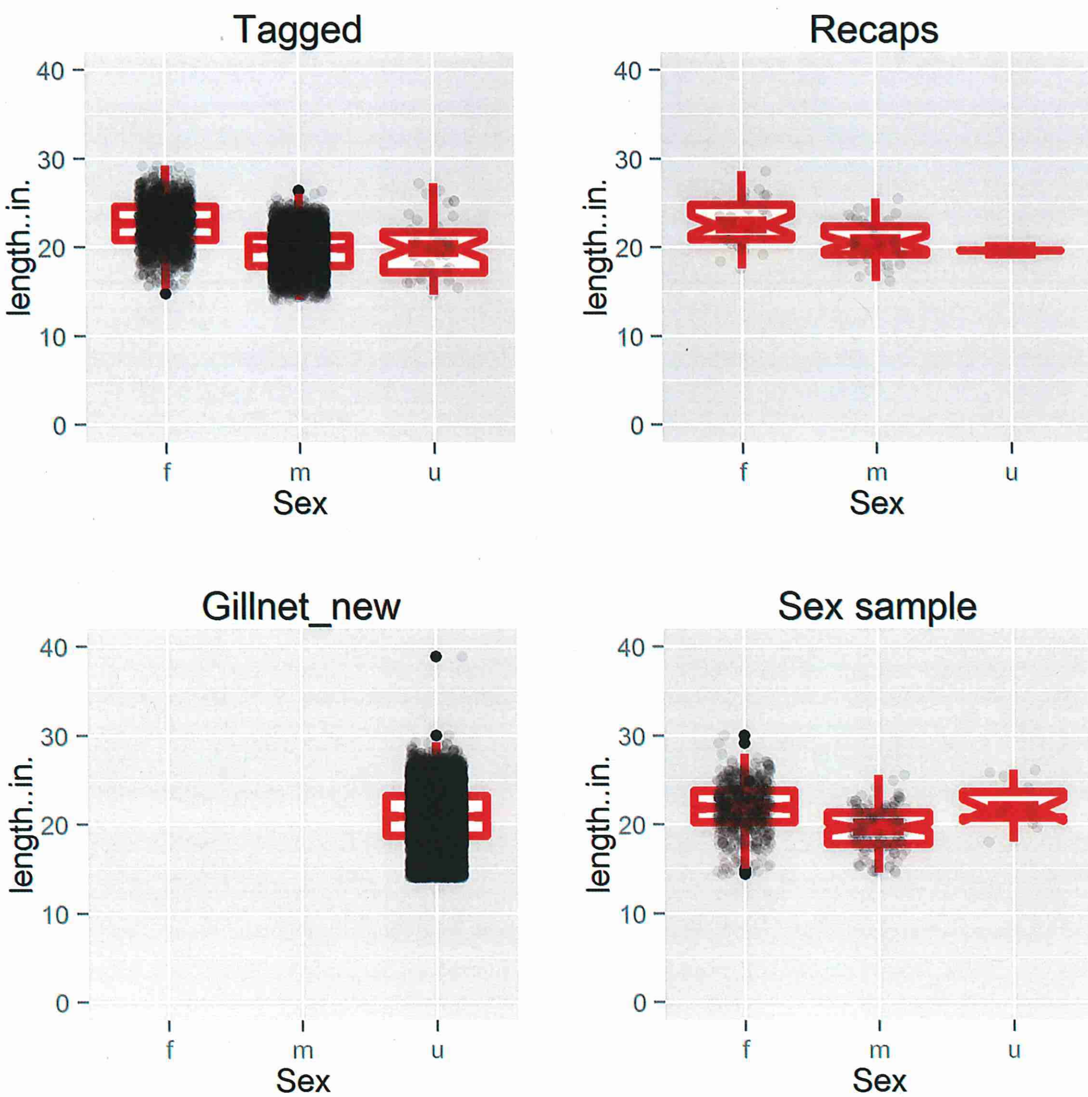

Figure 1c. Summary of distribution of lengths in the various samples in 2014.

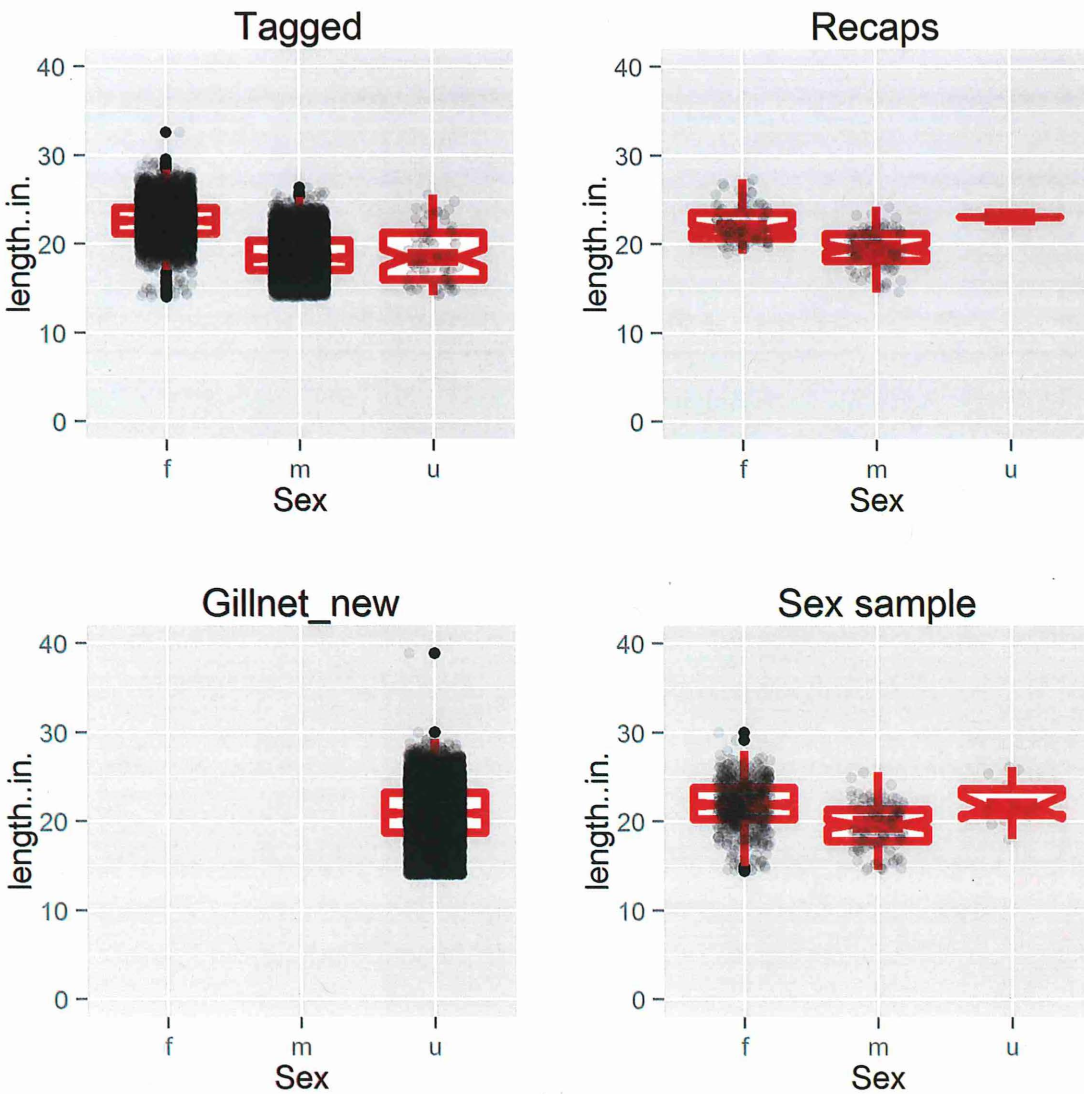

Figure 2. The logistic regression to predict the sex of a fish given its length based on samples taken from the gillnet sample that were selected for sex determination in all years. The fitted model is

$$\text{logit}(p_{male}) = 4.43 - 0.27(length)$$

where $p_{male} = \dfrac{1}{1+\exp(-\text{logit})}$. The markings at the top and bottom refer to the lengths of male and female fish respectively in the sample.

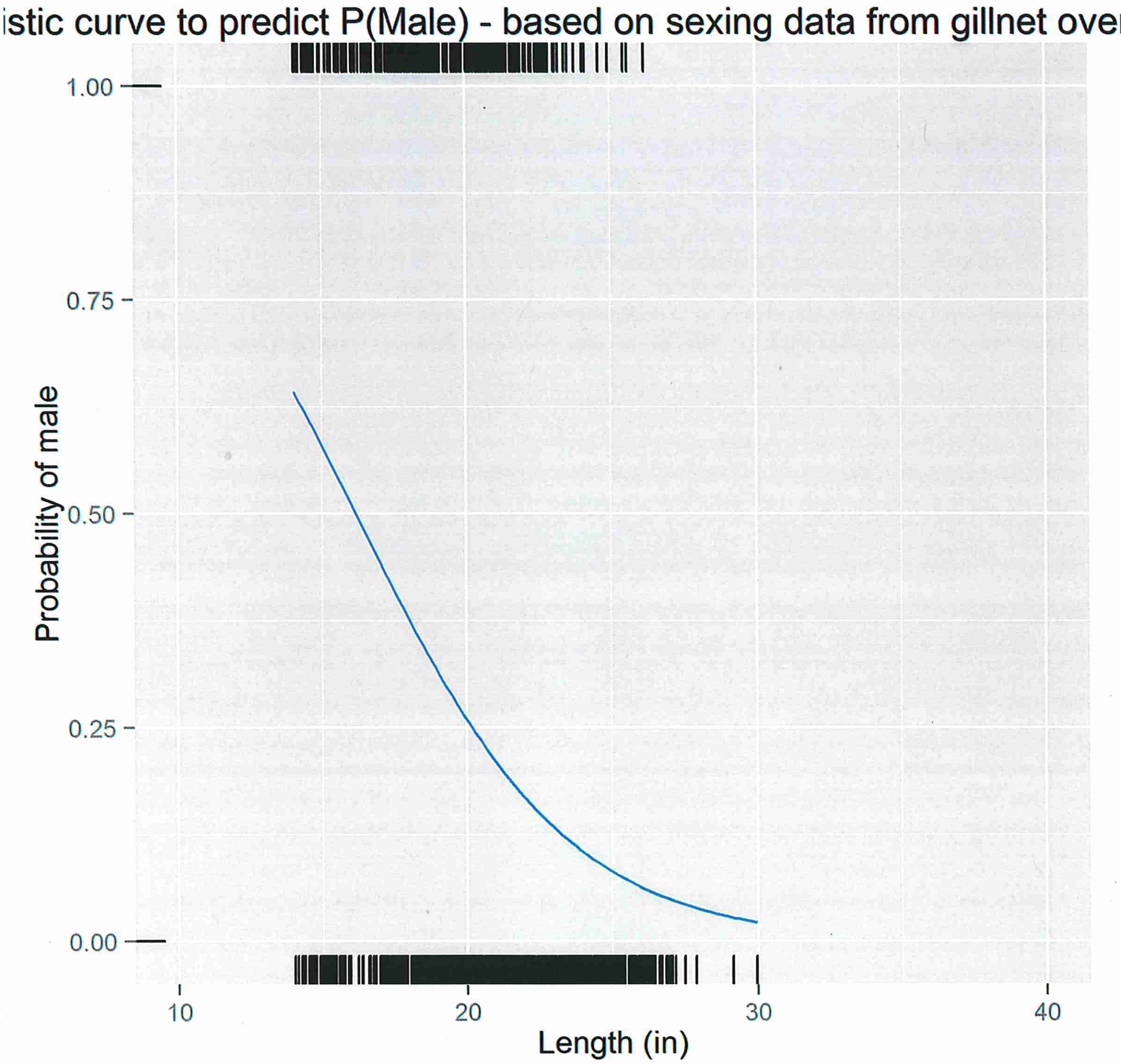

Figure 3a. Estimated abundance in 2008 from the modified Chen and Lloyd method for walleye 14+" Points are the separate estimates computed using statistics from each length interval (Table 5a). The curve is the smoothed estimates. Total abundance estimates at top of figure are derived from smoothed estimates. Standard errors are underestimates of actual variability because the expected number of each sex allocated from the gillnet sample based on the logistic regression of Figure 2 was used.

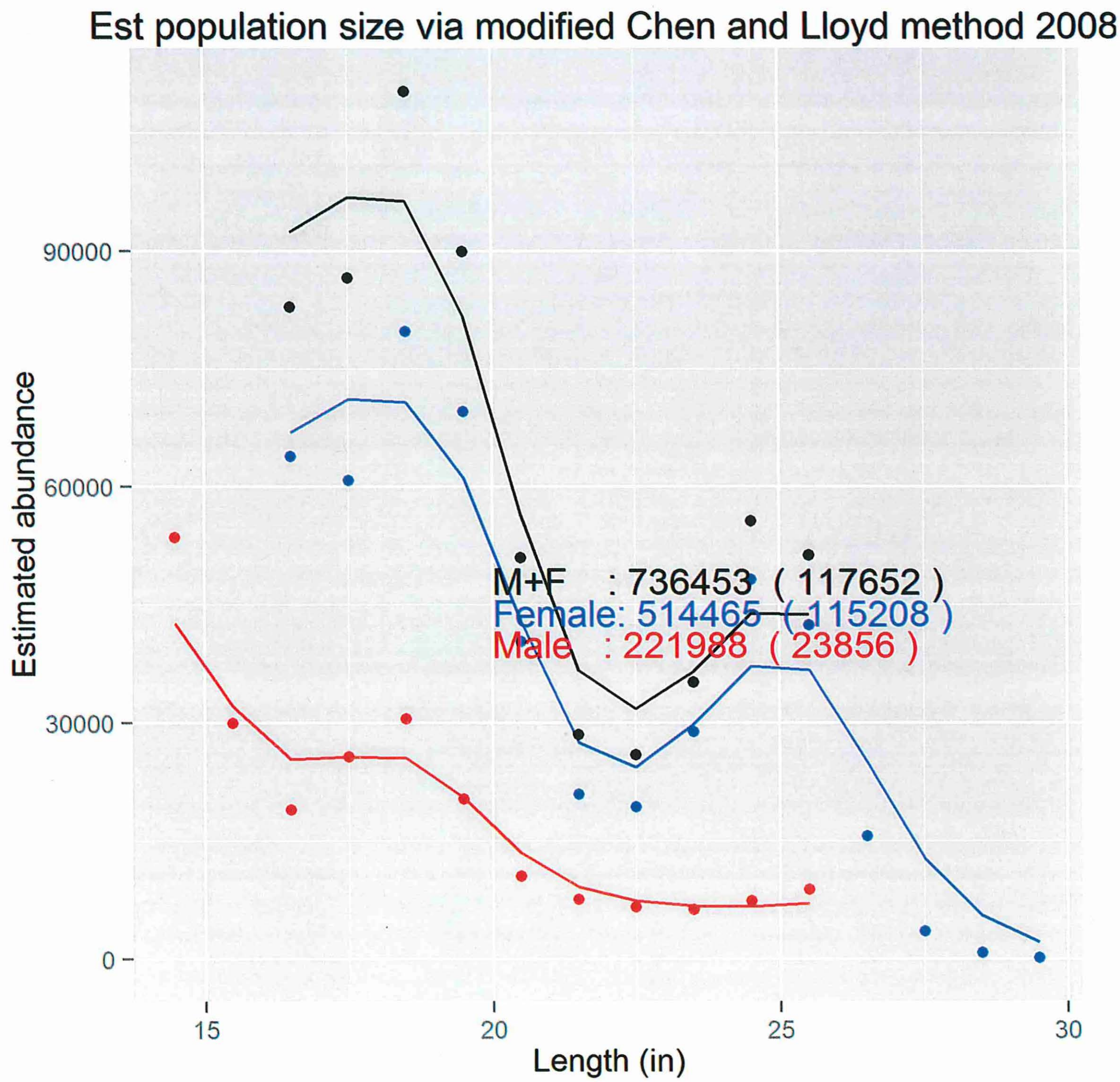

Figure 3b. Estimated abundance in 2013 from the modified Chen and Lloyd method for walleye 14+". Points are the separate estimates computed using statistics from each length interval (Table 5b). The curve is the smoothed estimates. Total abundance estimates at top of figure are derived from smoothed estimates. Standard errors are underestimates of actual variability because the expected number of each sex allocated from the gillnet sample based on the logistic regression of Figure 2 was used.

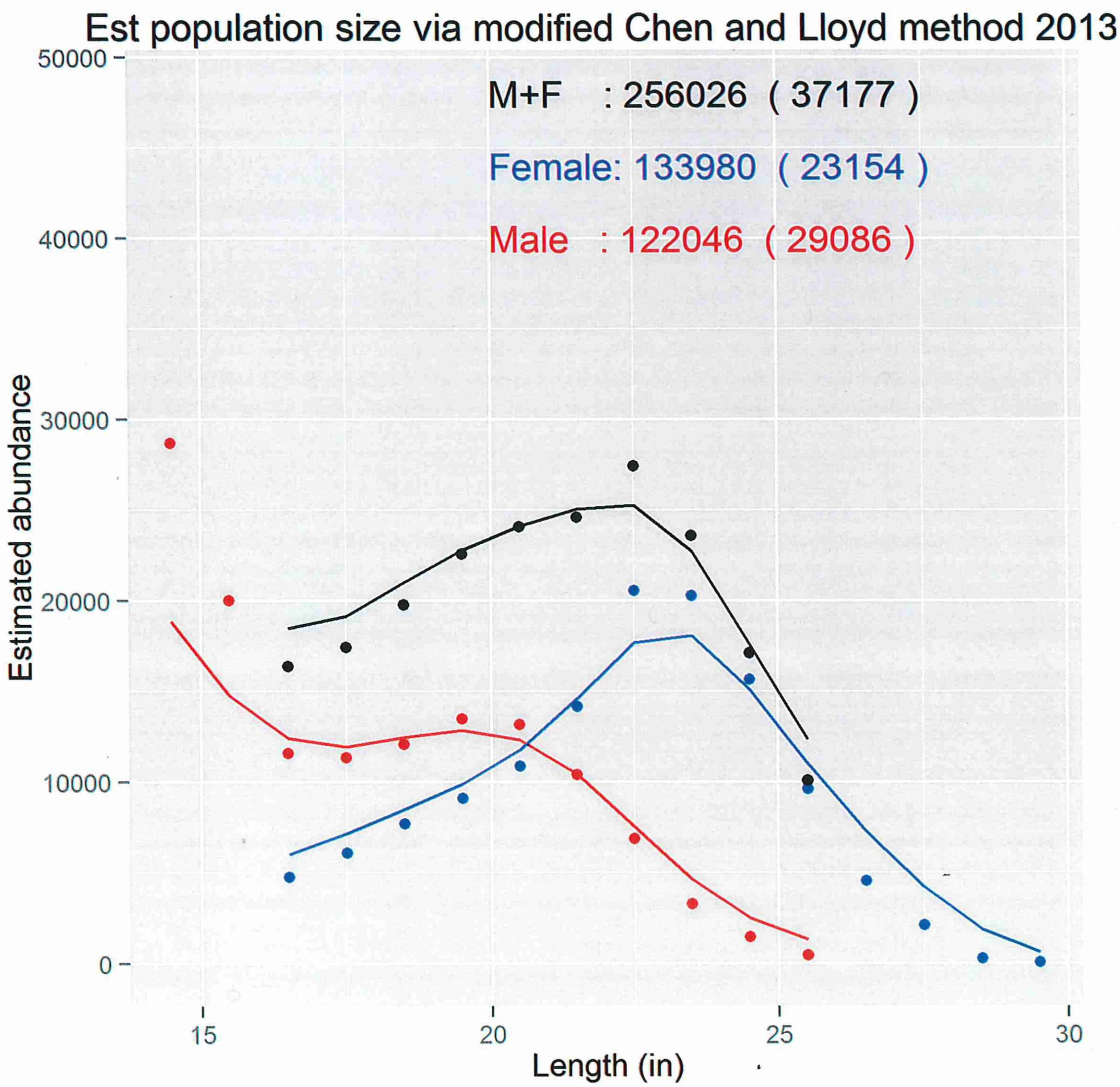

Figure 3c. Estimated abundance in 2014 from the modified Chen and Lloyd method for walleye 14+". Points are the separate estimates computed using statistics from each length interval (Table 5c). The curve is the smoothed estimates. Total abundance estimates at top of figure are derived from smoothed estimates. Standard errors are underestimates of actual variability because the expected number of each sex allocated from the gillnet sample based on the logistic regression of Figure 2 was used.

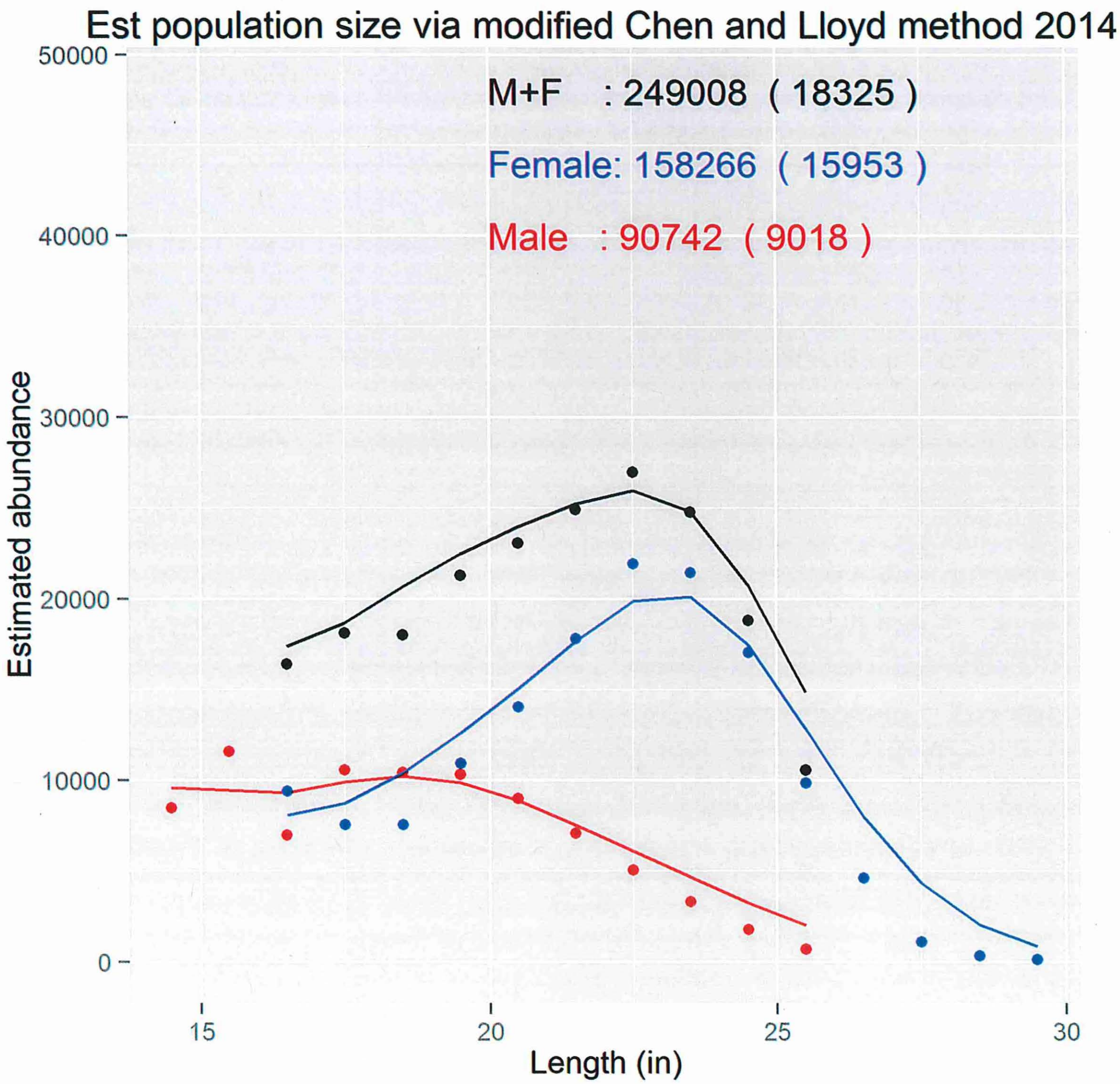

Figure 3d. Estimated abundance in 2008 from the modified Chen and Lloyd method for walleye 17/19+" Points are the separate estimates computed using statistics from each length interval (Table 5d). The curve is the smoothed estimates. Total abundance estimates at top of figure are derived from smoothed estimates. Standard errors are underestimates of actual variability because the expected number of each sex allocated from the gillnet sample based on the logistic regression of Figure 2 was used.

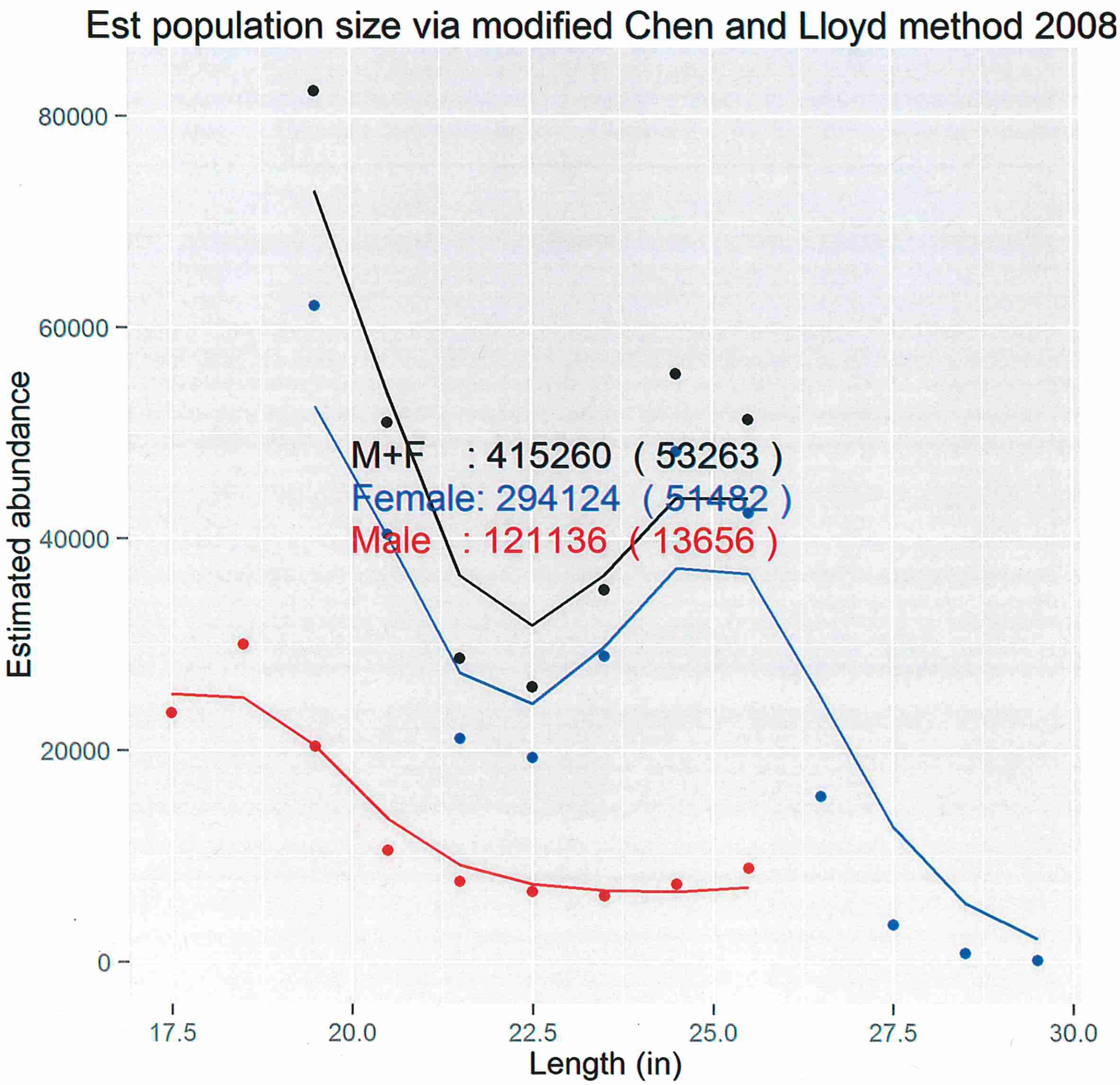

Figure 3e. Estimated abundance in 2013 from the modified Chen and Lloyd method for walleye 17/19+". Points are the separate estimates computed using statistics from each length interval (Table 5e). The curve is the smoothed estimates. Total abundance estimates at top of figure are derived from smoothed estimates. Standard errors are underestimates of actual variability because the expected number of each sex allocated from the gillnet sample based on the logistic regression of Figure 2 was used.

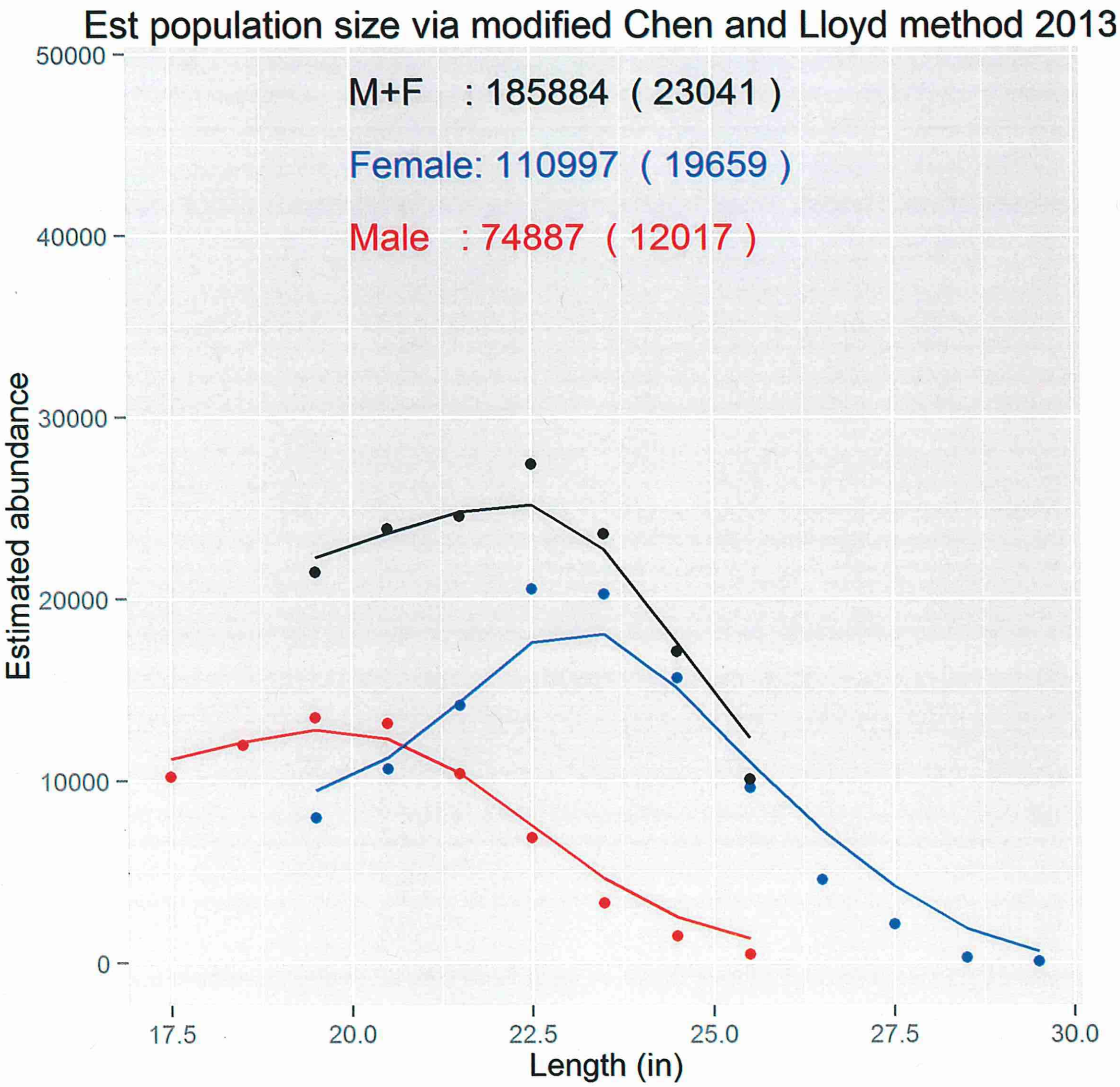

Figure 3f. Estimated abundance in 2014 from the modified Chen and Lloyd method for walleye 17/19+". Points are the separate estimates computed using statistics from each length interval (Table 5f). The curve is the smoothed estimates. Total abundance estimates at top of figure are derived from smoothed estimates. Standard errors are underestimates of actual variability because the expected number of each sex allocated from the gillnet sample based on the logistic regression of Figure 2 was used.

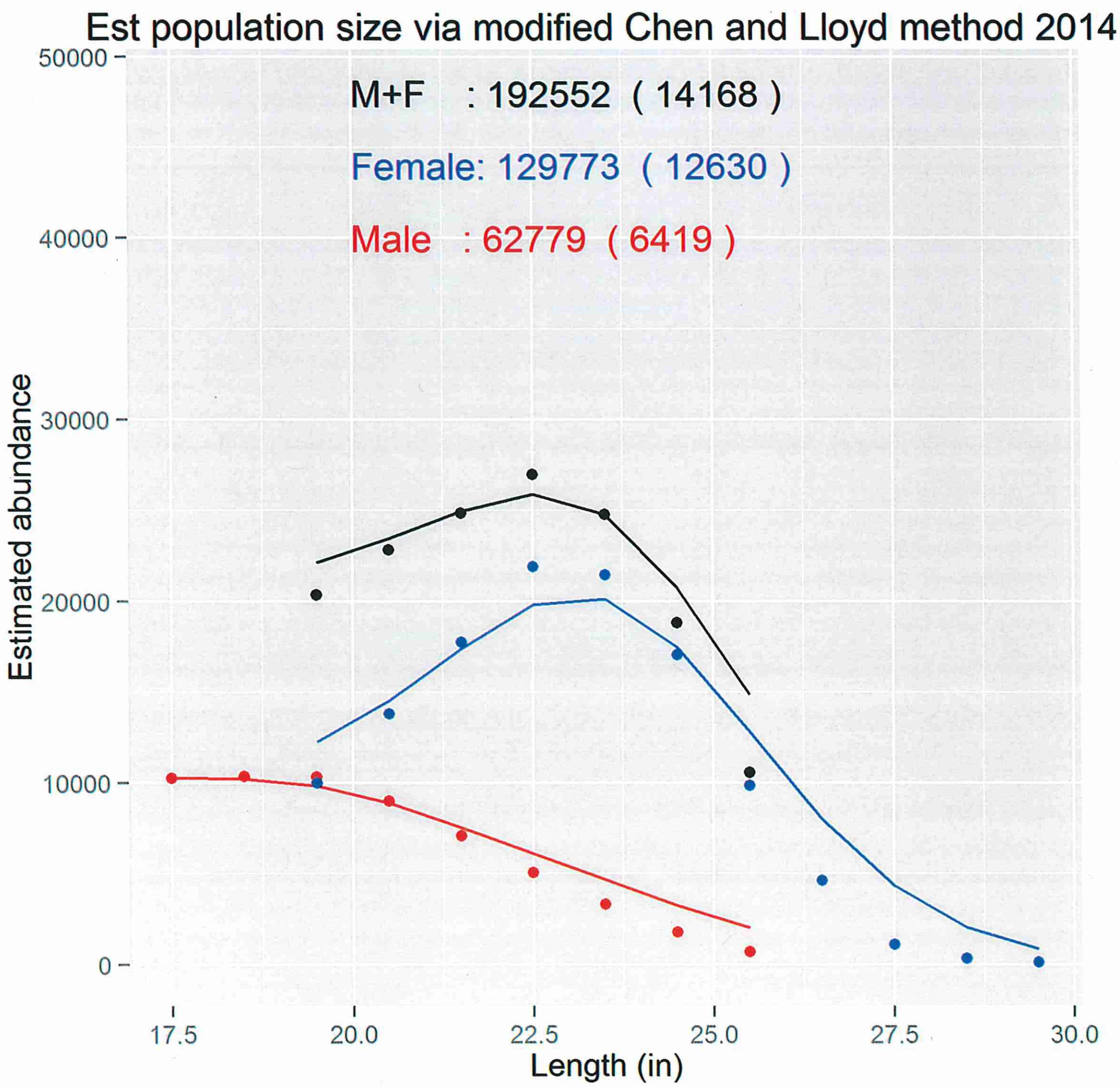

Figure 4a. Estimated gear selectivity for each sex in both samples in 2008 based on the modified Chen and Lloyd (2000) method for walleye 14+".

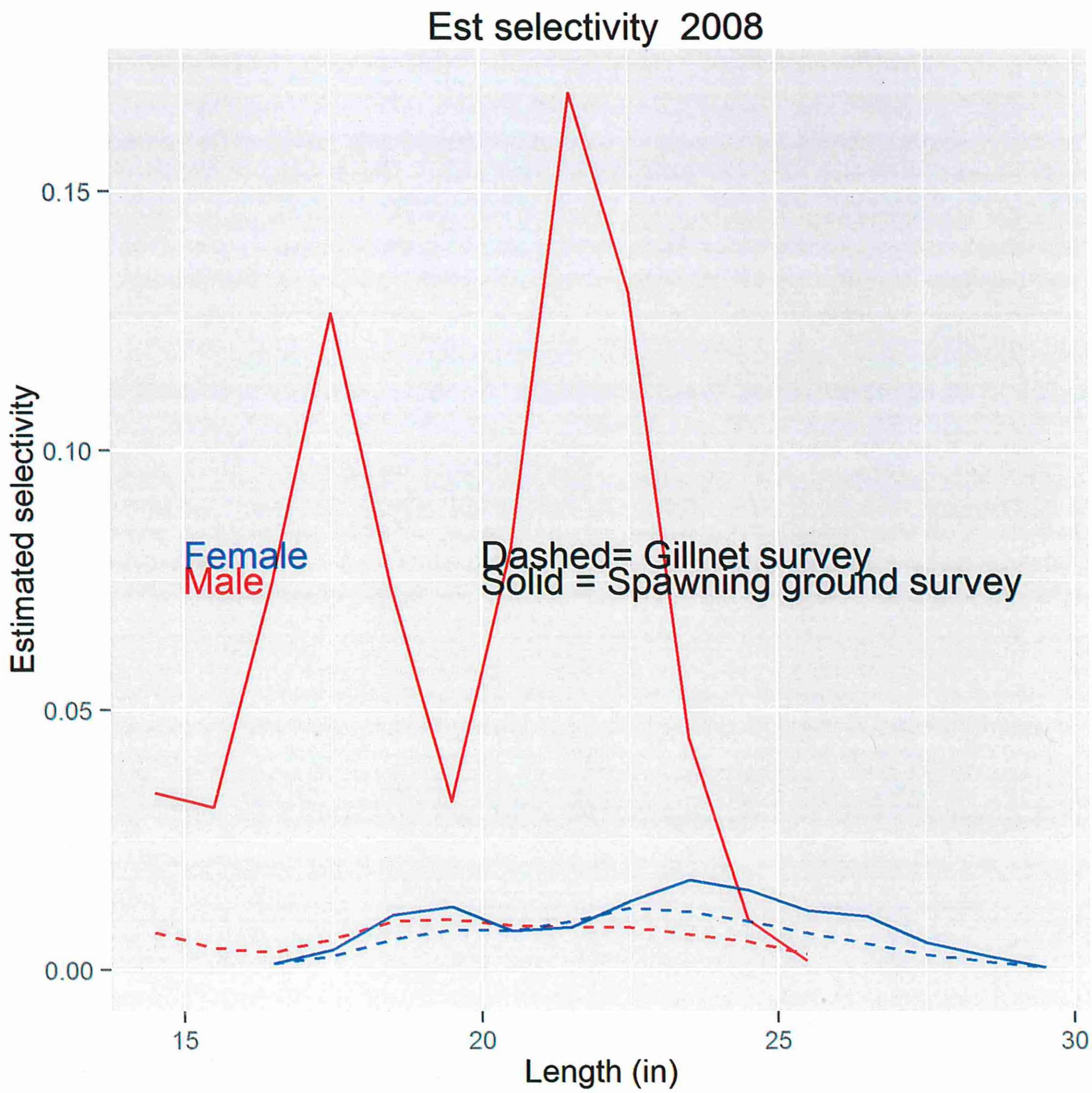

Figure 4b. Estimated gear selectivity for each sex in both samples in 2013 based on the modified Chen and Lloyd (2000) method for walleye 14+".

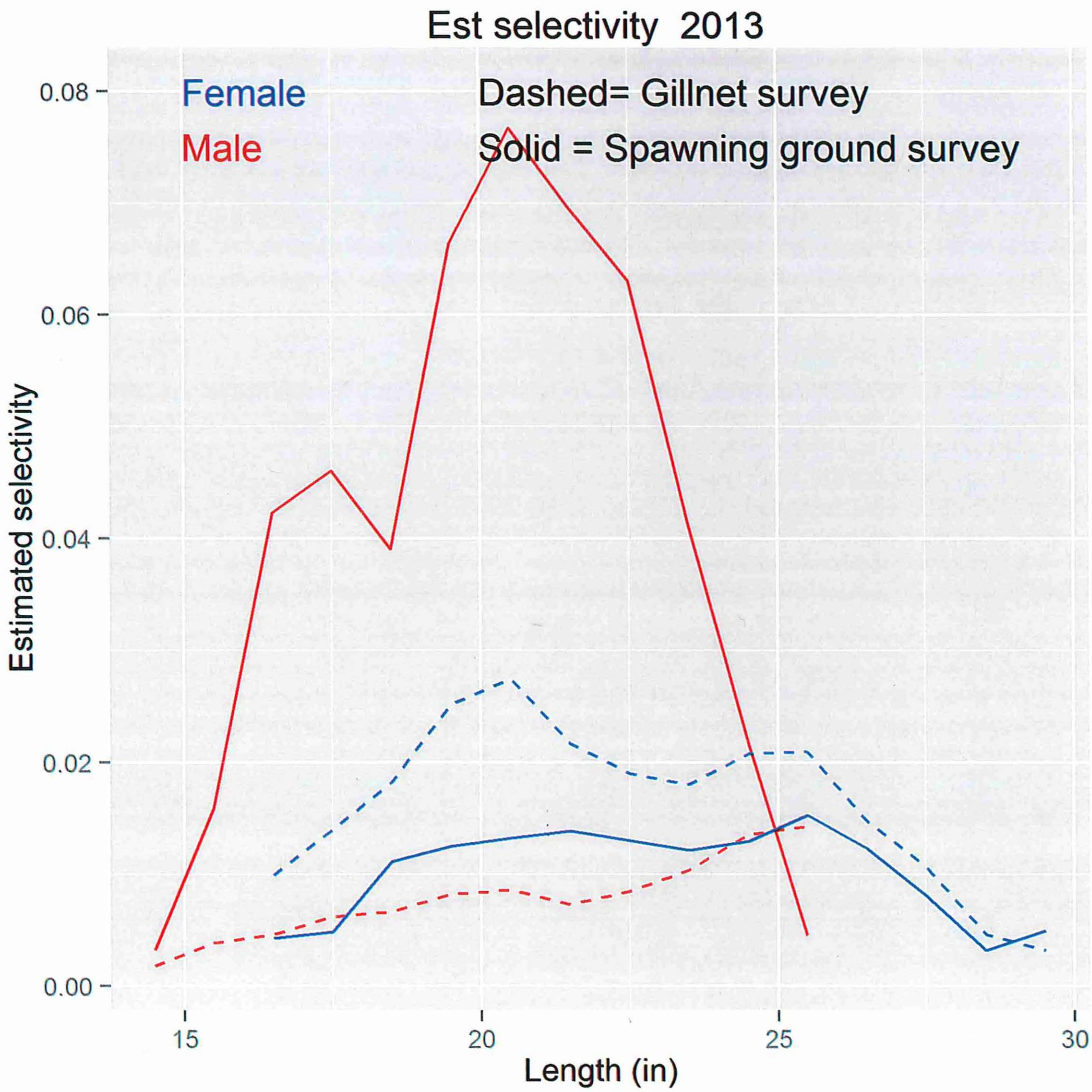

Figure 4c. Estimated gear selectivity for each sex in both samples in 2014 based on the modified Chen and Lloyd (2000) method for walleye 14+".

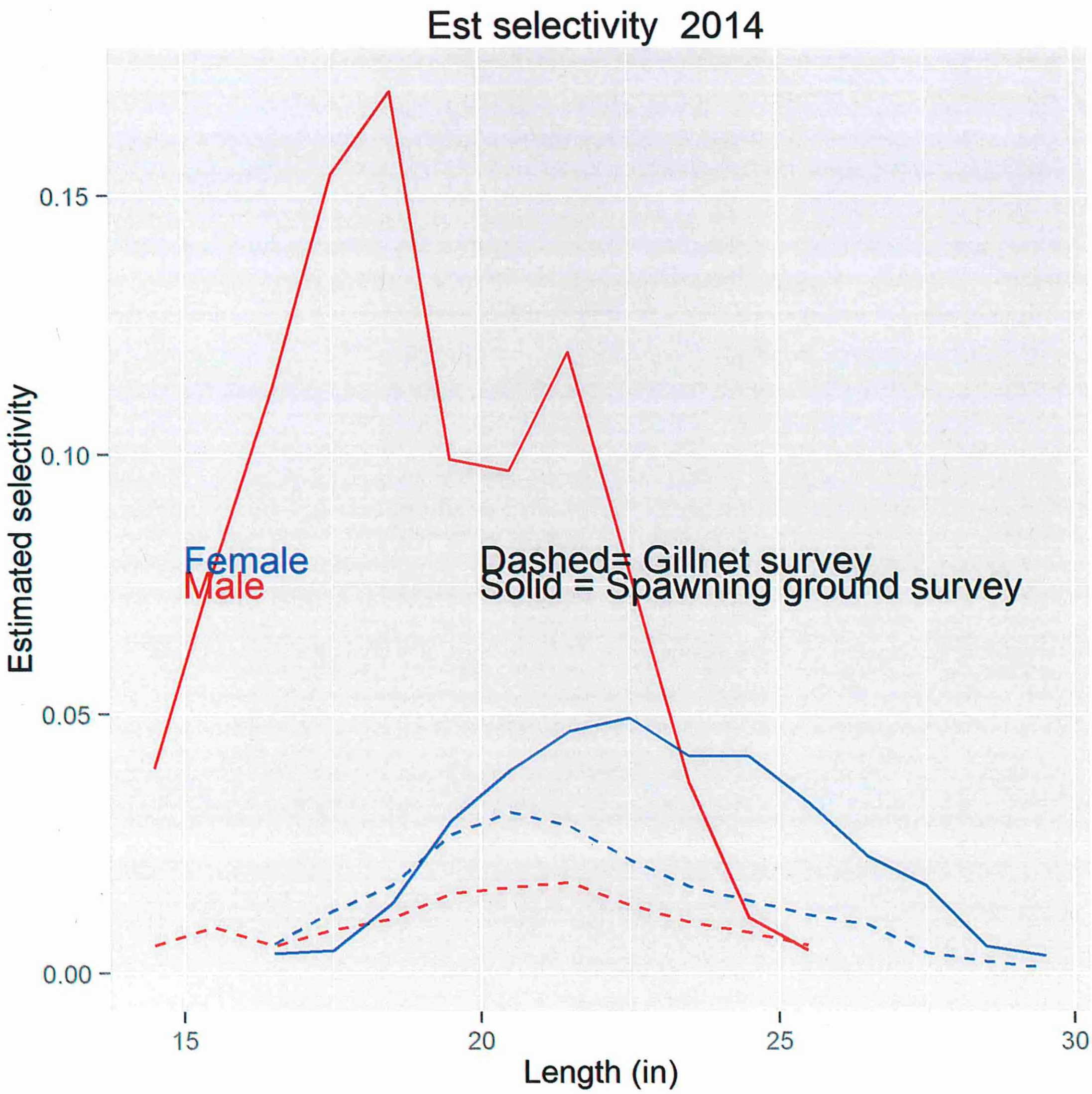

Figure 4d. Estimated gear selectivity for each sex in both samples in 2008 based on the modified Chen and Lloyd (2000) method for walleye 17/19+".

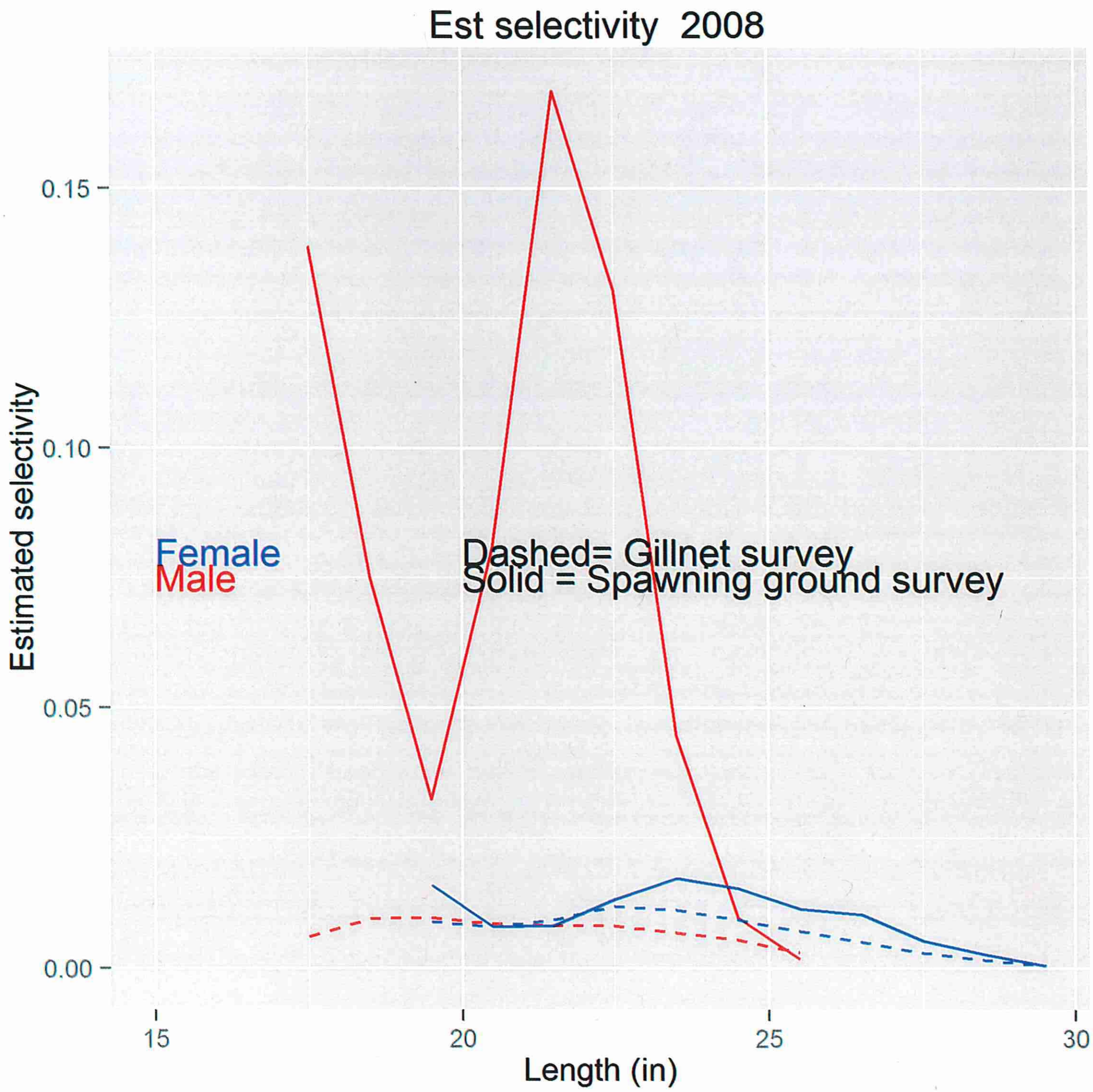

Figure 4e. Estimated gear selectivity for each sex in both samples in 2013 based on the modified Chen and Lloyd (2000) method for walleye 17/19+".

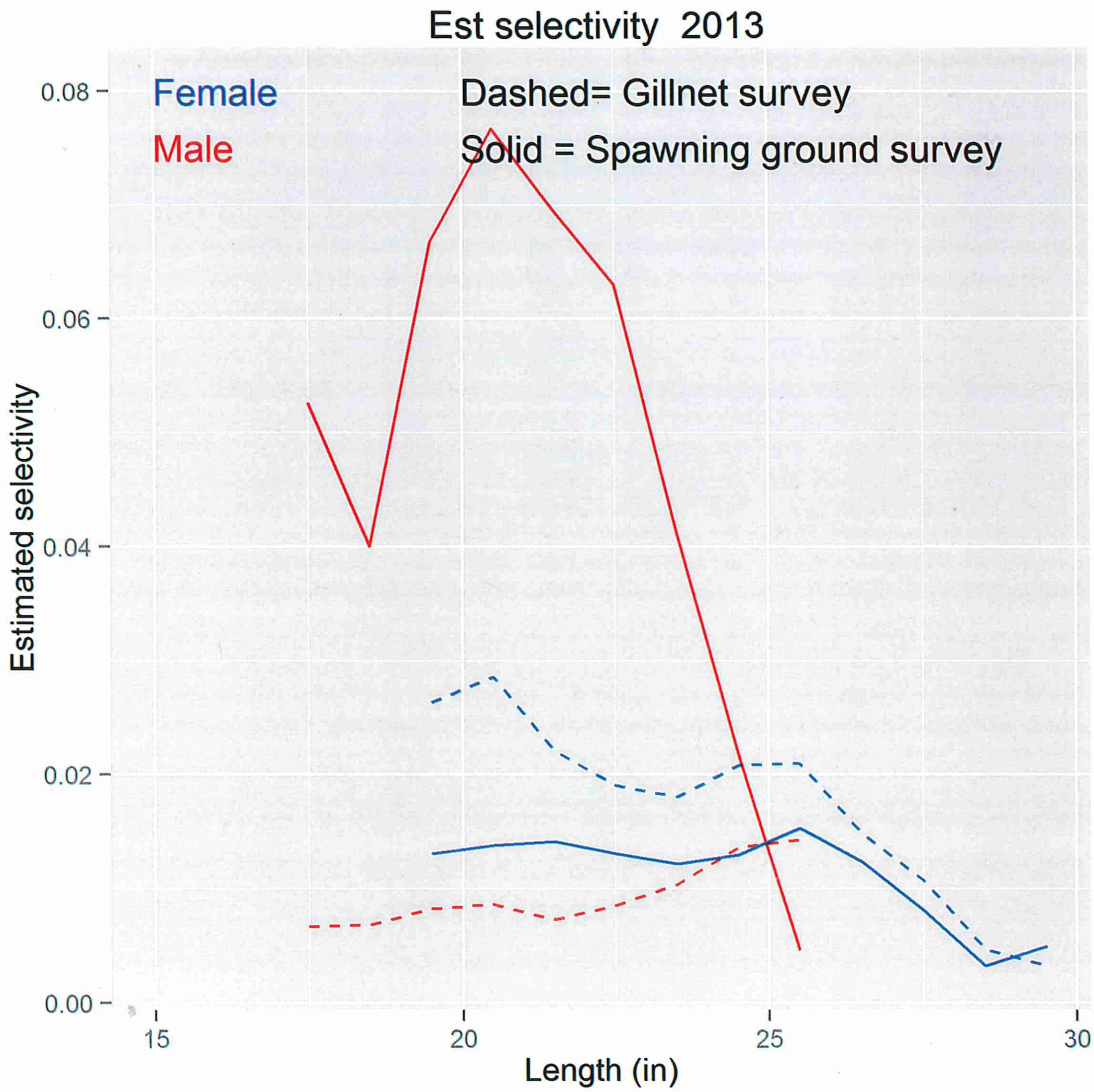

Figure 4f. Estimated gear selectivity for each sex in both samples in 2014 based on the modified Chen and Lloyd (2000) method for walleye 17/19+".

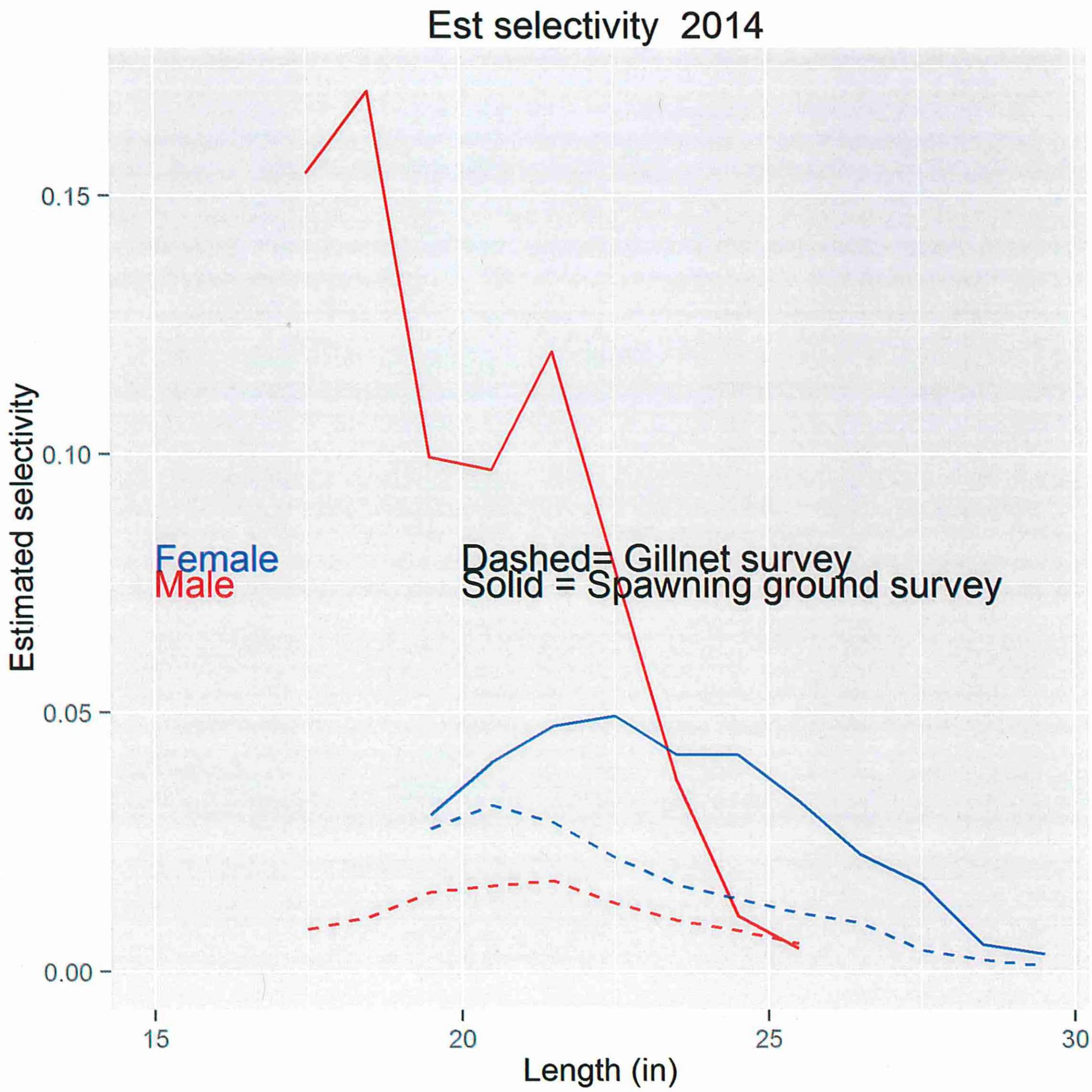

Figure 5a. Illustration of the geographic separation of spawning and gillnet sampling events and movement of recaptures from spawning tagging locations to gillnet sampling locations in 2008. Plotting positions are based on median UTM values in Zone and Angling.Zone fields and jittered to prevent overplotting.

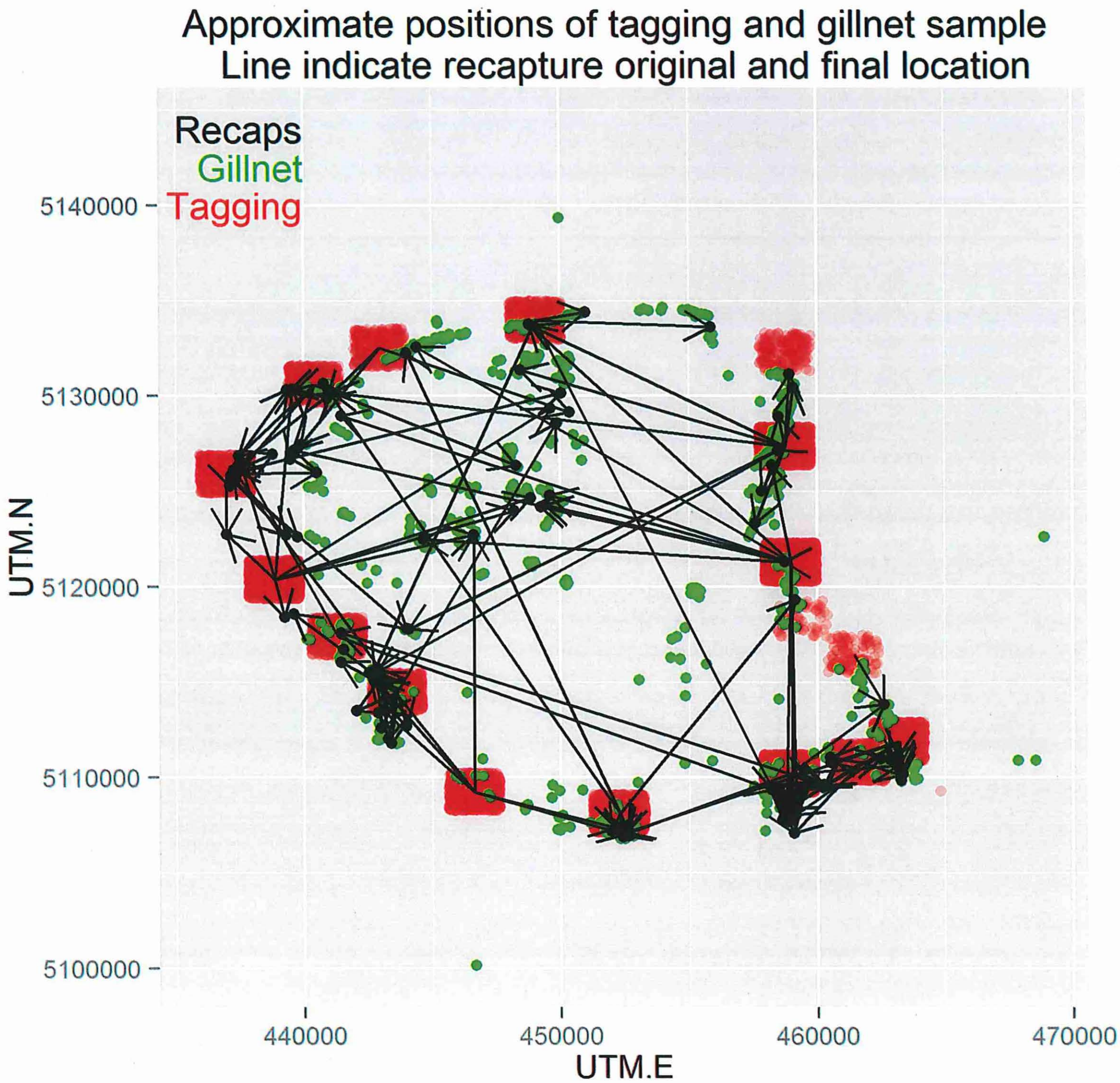

Figure 5b. Illustration of the geographic separation of spawning and gillnet sampling events and movement of recaptures from spawning tagging locations to gillnet sampling locations in 2013. Plotting positions are based on median UTM values in Zone and Angling.Zone fields and jittered to prevent overplotting. 11/73 recaptures were missing tag and so location of release is unknown and not plotted.

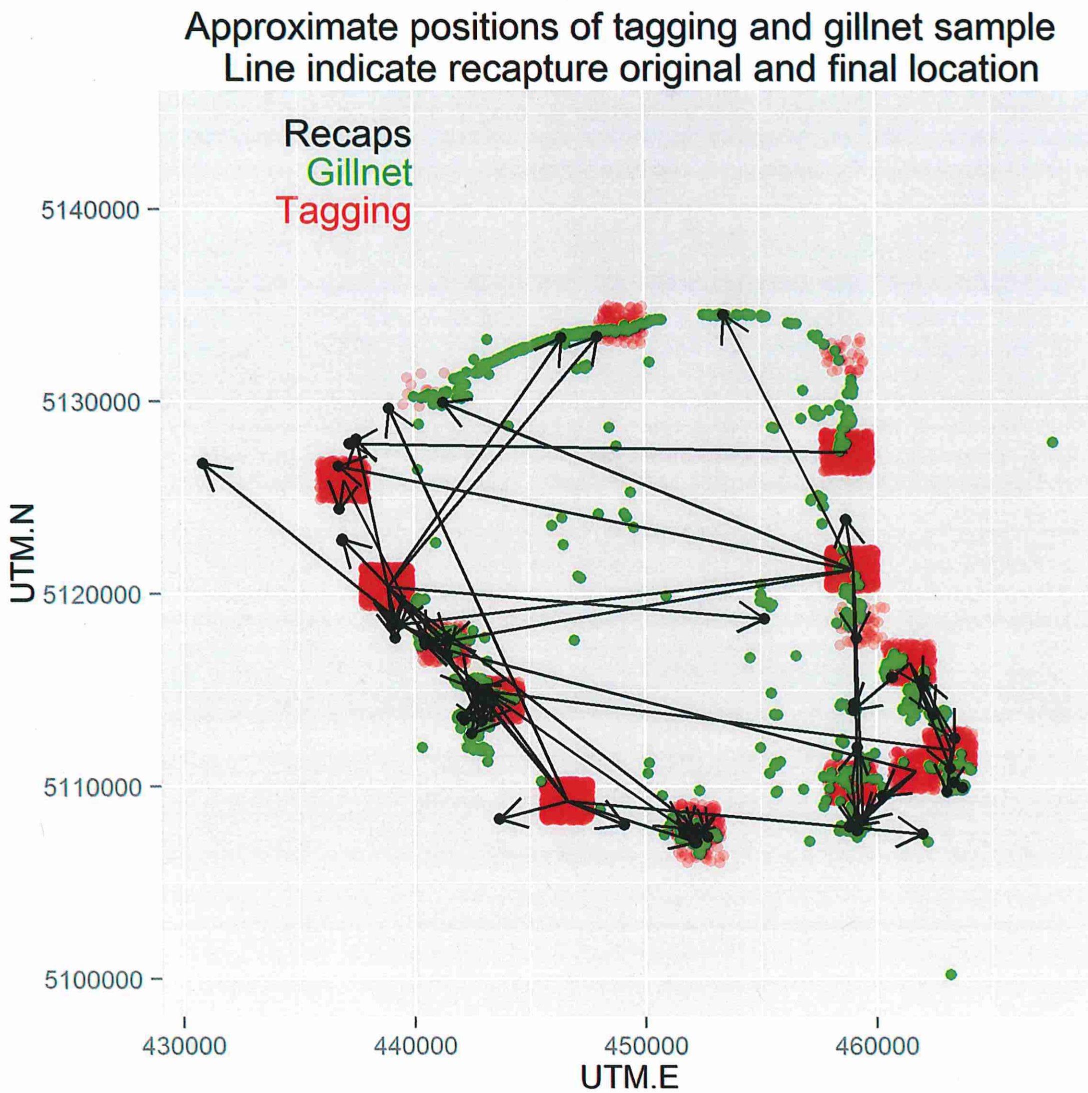

Figure 5c. Illustration of the geographic separation of spawning and gillnet sampling events and movement of recaptures from spawning tagging locations to gillnet sampling locations in 2014. Plotting positions are based on median UTM values in Zone and Angling.Zone fields and jittered to prevent overplotting.

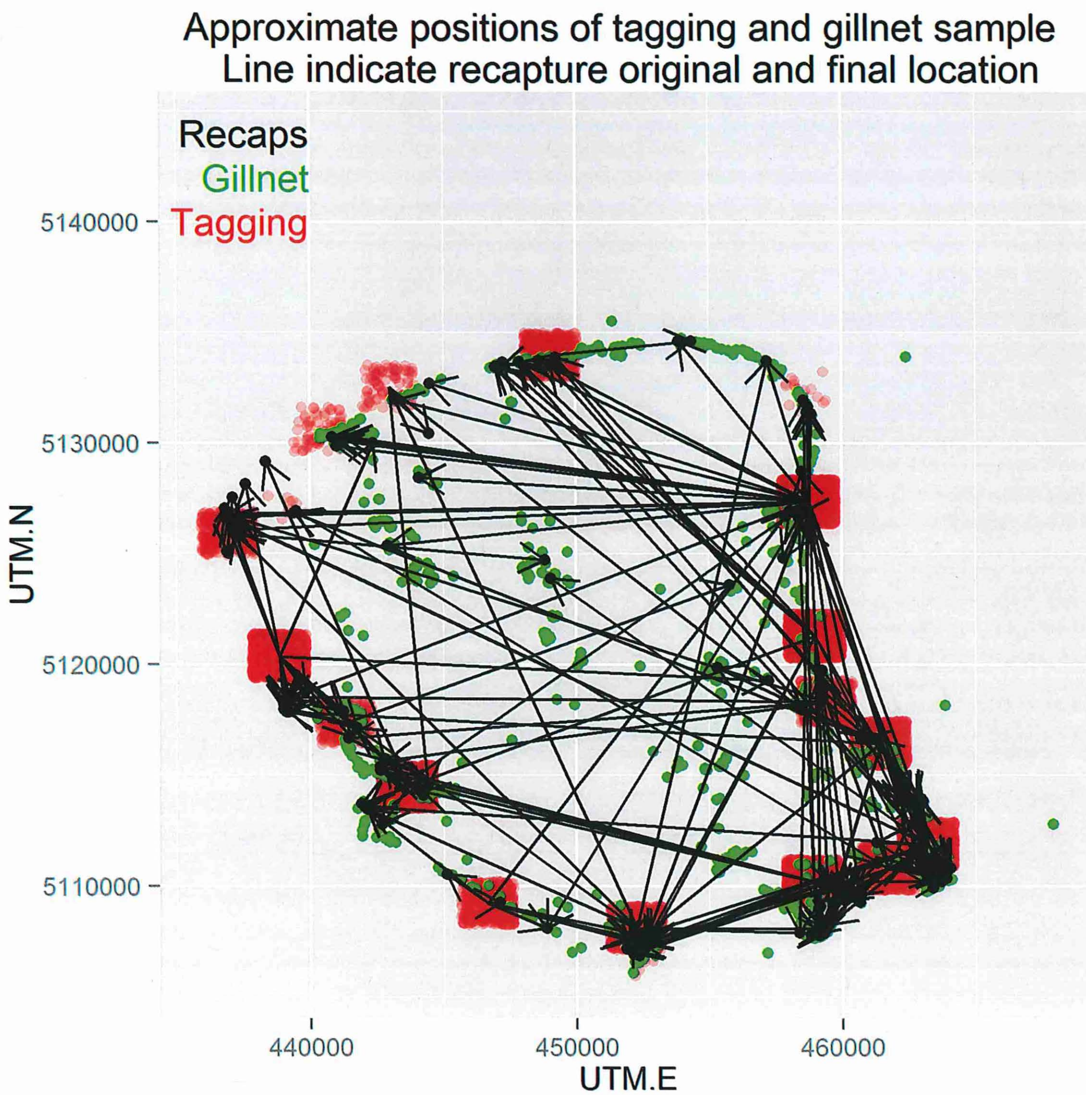

Figure 6. Comparison of length distribution of inshore vs offshore newly captured fish in the gillnets in both years. A qqplot (not shown) and a chi-square test of the hypothesis of equal length distributions failed to detect any difference.

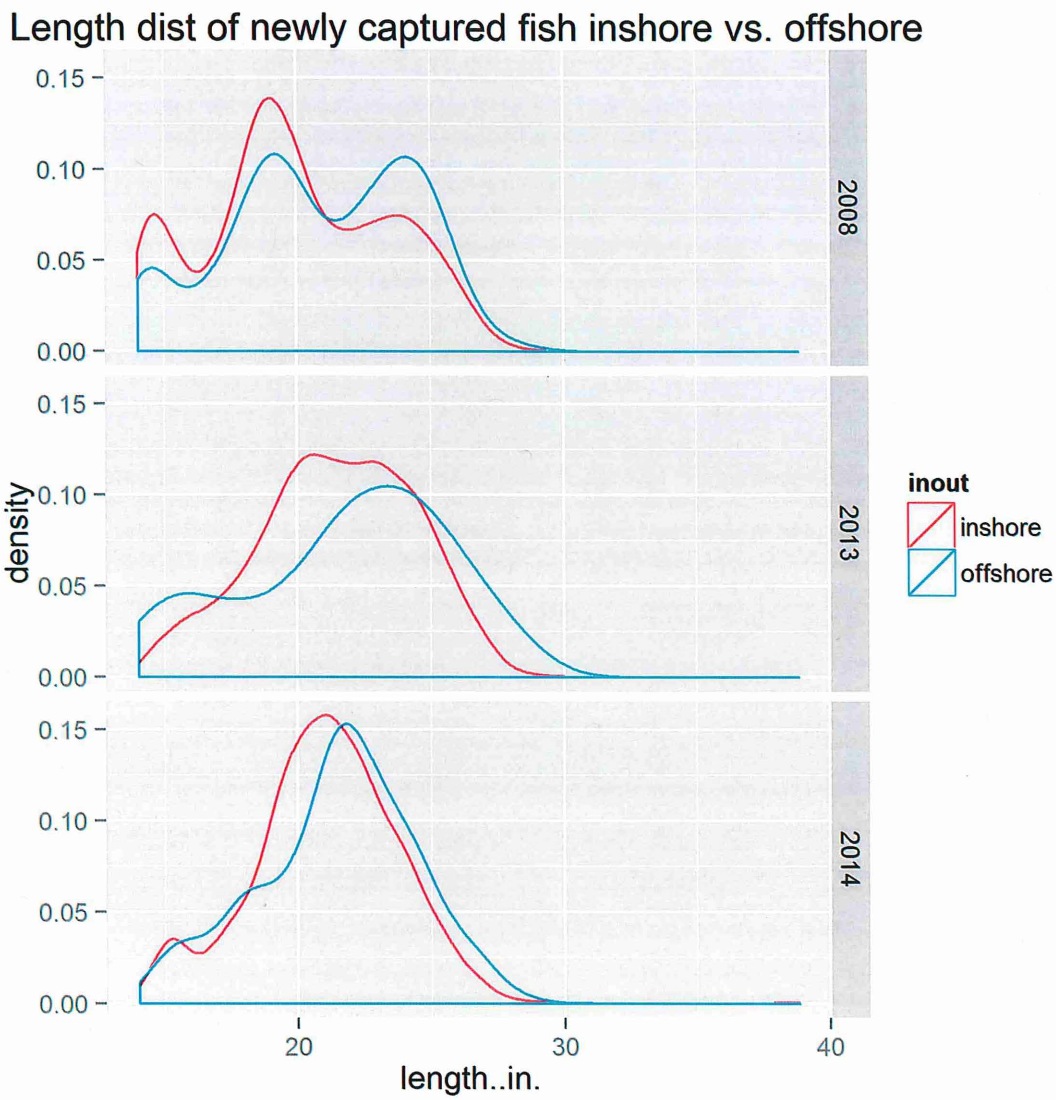

Figure 7. Marked-fraction as function of depth. Each point represents the marked fraction in that depth class. Solid line joins the marked fraction.

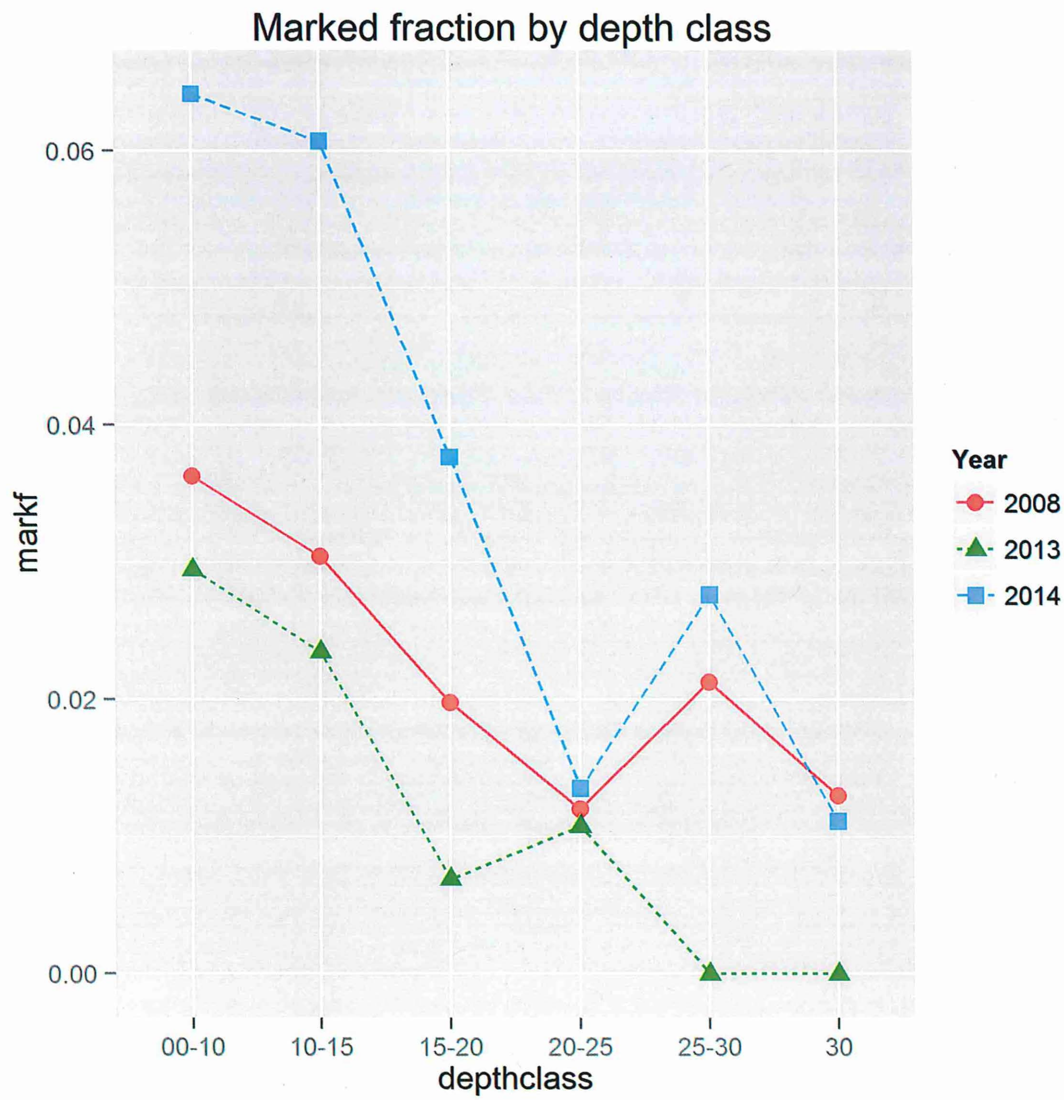

Figure 8. Comparison of estimates of total abundance in both years from the various estimators using all walleye 14+" and walleye greater than 17/19"...

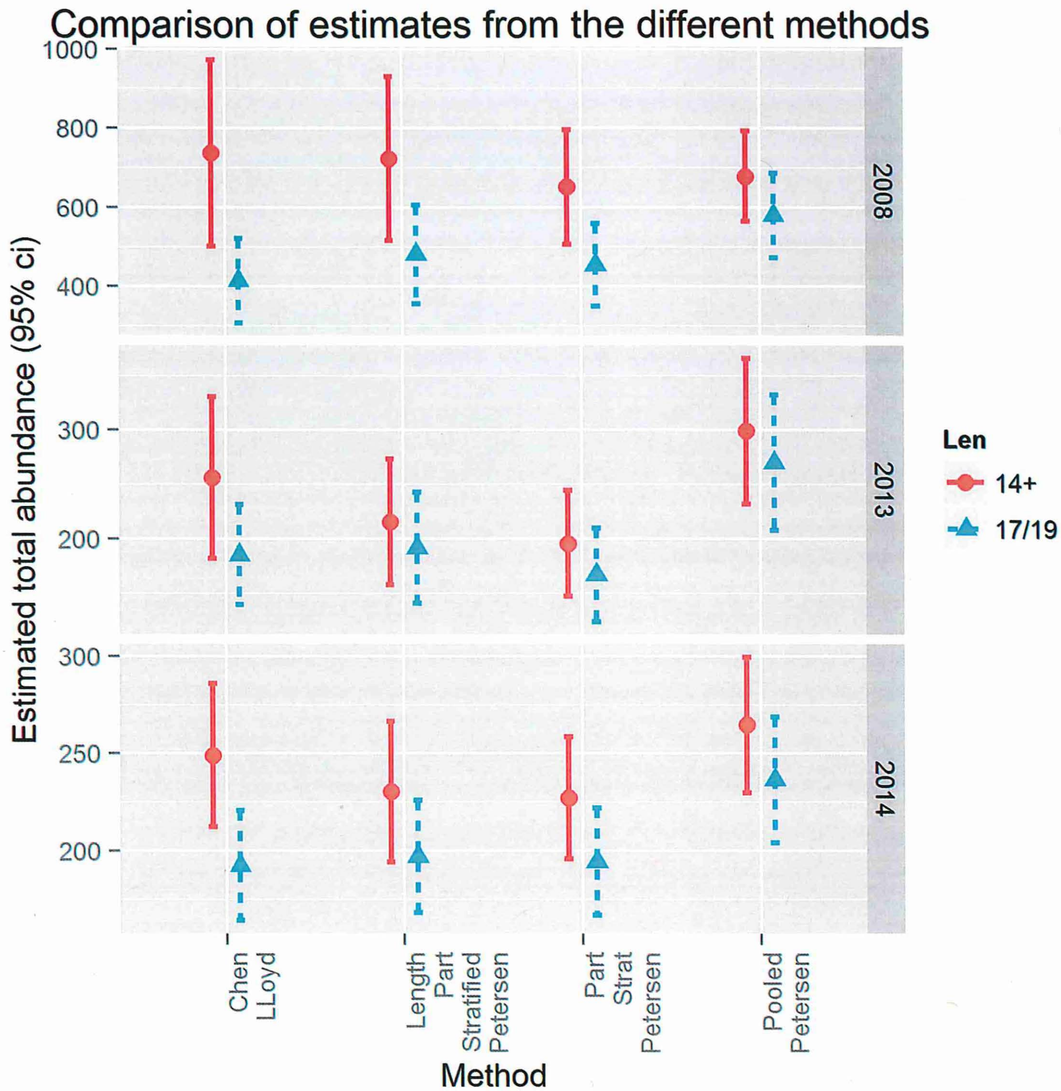

Figure 9. Screenshot of spreadsheet used to investigate the potential bias due to incomplete mixing for all years. The *SimplifiedBias* sheet in the *PetersonWorkbook* is also available.

1 **Simplified Bias Computations for inshore/offshore**

3 It turns out that the previous model is not really needed. Given the population size, number of fish tagged, and the marked
4 fraction in the two strata, there is only one solutions that satisfies the various contraints. From this solution
5 the bias in the pooled Petersen estimator can be estimated

7 Enter values in cells in yellow and computations will automatically update

10		2008				2013				2014			
12	Initial Pop size	700000				300000				300000			
14		Inshore	Offshore			Inshore	Offshore			Inshore	Offshore		
15	Number of tags	20000				6000				12000			
16	applied												
18	Marked fraction	0.032	0.018			0.024	0.007			0.065	0.028		
19	Gillnet catchability	0.064	0.01			0.092	0.01			0.06	0.01		
21	Tagged	20000				6000				12000			
22	Untagged	680000				294000				288000			
24	Fraction of untagged	0.752	0.248			0.762	0.238			0.316	0.684		
25	in strata												
26	Fraction of tags	0.846	0.154			0.918	0.082			0.527	0.473		
27	in strata												
28				Total				Total				Total	
29	Unmarked in each str	511657	168343	680000		223906	70094	294000		90973	197027	288000	
30	Tags in each stratum	16914	3086	20000		5506	494	6000		6324	5676	12000	
31	Total fish i	528571	171429	700000		229412	70588	300000		97297	202703	300000	
33	Computed marked fra	0.032	0.018			0.024	0.007			0.065	0.028		
34				Total	Adjusted total			Total	Adjusted total			Total	Adjusted to
35	n1	20000		20000	20000	6000		6000	6000	12000		12000	12000
36	n2	33829	1714	35543	44800	21106	706	21812	27600	5838	2027	7865	18000
37	m2	1083	31	1113	1280	507	5	511	552	379	57	436	720
39	Pooled Petersen	638473				255865				216357			
40	% bias	-8.8%				-14.7%				-27.9%			
42	Adjusted Petersen	700000				300000				300000			