

YEAR CLASS STRENGTH AND CATCHABILITY OF MOUNTAIN LAKE BROOK TROUT

by

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Abstract

Increased gillnet catch per effort (cpe) of juvenile salmonids occurred following intense exploitation of the adult population, for several studies conducted in mountain and arctic small lakes. Higher cpe may reflect increased catchability or greater numbers, so behavioral or numerical responses cannot be inferred from changes in cpe alone. I used age structured estimation methods, and gillnet depletion data from 1986 to 1992 for seven Sierra Nevada small lake brook trout populations, to reconstruct year class strength and prerecruit (age 1) gillnet catchability prior to and during the experimental removals. I made Walters-Collie (1988) estimates of year class strength for the seven study lakes across the years of the removals. The within-year depletions and available models consistently underpredicted the number of fish remaining in the lake, so estimates did not use the within-year structure of the data. Ageing error correction provided little change in the estimated strength of cohorts produced during the mid- to late 1980's. Estimates showed an inverse relationship between year class strength and adult population size, for cohorts from 1984 to 1990. Prerecruit \hat{q} also appeared inversely related to adult population density for most lake populations. This may have been either a direct effect of adult density, or indirectly mediated through the effect of adult density on prerecruit length at age. Year and cohort-specific adult \hat{q} 's showed little evidence for density dependence in adult \hat{q} . The vulnerable proportion of the adult population appeared insensitive to population density. I developed a modification of the WC fitting to adjust for between-lake variation in encounter probability which estimated a relative activity parameter, \hat{k} . Relative to \hat{q} , variation in \hat{k} was reduced and showed little apparent between-lake density dependence.

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Chapter 1. General Introduction

Prior to 1860, more than 95% of 16,000 western North American mountain lakes were fishless (Bahls 1991). In the following century, extensive stocking programs driven primarily by the outdoor recreation industry led to the introduction of trout and char to most of the lakes. One widely introduced species was eastern brook trout, *Salvelinus fontinalis* (Mitchill), which often establishes self-sustaining stunted populations. Concern for the status of native aquatic organisms has led ecologists to reconsider the wisdom of widespread salmonid introductions, since many other species do not appear to coexist with introduced trout and char (Bahls 1991). As well, fishery managers generally consider stunted populations undesirable because of the small adult body size attained. It is clear that an ability to effectively manipulate the density of such populations would be desirable. Freshwater salmonids grow indeterminately, and their life history parameters are generally size- and thus density-dependent. As a result, the dynamics of self-sustaining populations are often characterized by strong interactions between size or age groups. Predicting the response of such populations to manipulation will likely hinge upon better understanding of recruitment dynamics and the interaction between age classes.

This study grew directly from Donald L. Hall's (1991) investigation of size-density relationships and the potential alleviation of stunting of Sierra Nevada brook trout. Hall began his work in 1985 with a survey of more than 50 small lake populations. He made experimental removals of hundreds of fish from each of twelve lakes in 1987, repeating ten of the lakes in 1988 and eight in 1989. The removals were intended to accomplish three tasks simultaneously: reduce density, allow population estimation, and provide samples for evaluating growth and reproductive responses. Population estimation was fundamental, since without it the response to density reduction could only be evaluated qualitatively. Density reduction was apparently difficult to achieve (Hall 1991). Depletion of adult populations appeared to have been matched by new cohort recruitment to the catchable population. Minimal growth response of the remaining adults was observed (Hall 1991).

Nevertheless, the apparent recruitment response to removals was an intriguing hint of strong population regulation, and the primary motivation for this thesis. In 1991 and 1992, I redepleted eight of Hall's study lakes. Additional removals have had two distinct benefits. First, the additional data have allowed me to follow the fate of cohorts produced during the original depletions, which were not yet fully vulnerable at the end of Hall's study in 1989. More fundamentally, the additional data have allowed me to use powerful estimation procedures to reconstruct population abundance and year class strength before and during the experiment. This in turn has allowed me to examine the numerical and catchability responses to removals in greater detail.

Arrangement of the thesis

I have organized this thesis into three chapters. Each chapter is intended to stand independently, structured around the questions which I approached. Wherever possible I have used simulation in parallel with analysis of data from field experiments. This has been an important method of validating computational algorithms, as well as allowing me to examine the potential performance of the models and estimators I have used.

In this general introduction, I review the reported experimental thinning of small lake salmonid populations and reinterpret the results with regard to year class strength and catchability. I summarize the general methods and terminology used for the current experimental study. For the experimental populations, environmental conditions likely influenced year class strength and might have impacted the shape of the catch curves used for survival estimates. I examine weather time series for suggestions about mechanisms that may drive variation in year class strength. This information is also useful in the evaluation of the response of year class strength to removals, since the treatments for this study were not staggered with respect to time. I conclude with a preview of the material of Chapters 2 to 4.

Literature Review: response of salmonid lake populations to experimental thinning

Exploitation experiments on arctic and mountain lake salmonid populations have provided tantalizing suggestions of density dependence in reproduction and population regulation. Donald and Alger (1986) suggest that montane, subalpine, alpine and arctic lakes have dominant characteristics in common. These features include simple fish communities, low productivity, minimal human exploitation or other disturbance, and a long annual period of ice cover which may buffer the lakes from interannual environmental variability (Johnson 1980). Manipulation of the fish populations of these lakes has been characterized by two motives: a practical desire to determine the potential production and appropriate management of exploitation for such lakes, and the notion that such lakes might serve as simple, self-contained homogeneous systems to test population regulation theory (Johnson 1983, citing Holling 1973). A common design has been several years' removals by gillnets. Removals provide samples to characterize the population before and during the experiment. Size and growth, relative abundance, maturity schedules and fecundity have all been monitored, usually with respect to age. Here I review the reported results of studies which have manipulated small lake salmonid populations through exploitation. I confine my review to studies with age specific results.

Lindstrom et al. (1970) and Fagerström (1972) report on a removal experiment in 10 ha Lake Långbjörnsjön, Jämtland Mountains, Sweden. From 1958 through 1966 they removed, primarily by gillnetting, 147 - 556 brown trout (*Salmo trutta*) aged 1+ to 8+ and 83 - 479 arctic char (*Salvelinus alpinus*) per year from the lightly sportfished populations. They reported only the results for brown trout. They observed an increase in length at age of 4 to 18 % after the removals. Mark-recapture estimation failed due to small sample size and tag loss/mortality. This left relative abundance at age as the interpretable result, complicated by year to year changes in netting procedure. The 1959 year class recruited strongly to the nets at age 2, a year earlier than other cohorts, and was still strong at age 4 and 5. Subsequent cohorts did not appear strong, either at age 2 or later. From relative abundance data, they inferred that the pre-removal 1953 and 1954 cohorts were larger than the 1959 and later

cohorts, produced after removals. The study does not appear to document a consistent response, either in terms of year class strength or earlier recruitment to the nets, although the lack of population estimation makes interpretation difficult and the concurrent removal of char confounds the result.

From 1971 to 1978, Healey (1978, 1980) gillnetted age 1+ to 12+ lake whitefish (*Coregonus clupeaformis*) from four previously unexploited lakes of 305 - 547 ha in the Canadian Northwest Territories. Small survey samples were taken in 1971 and 1972 to establish preremoval characteristics, and in 1975, 1976 and 1978 to monitor the response. Exploitation was approximately 0, 10, 20 and 30% annually in the four lakes during 1973 and 1974. Healey recorded that age 3+ and older fish were longer by 5 to 10% following the exploitation. Removal estimates for 1973 were possible for the two lakes subject to heavy exploitation, using ages 3+ and older. Otherwise, relative year class strength and recruitment were inferred from survey catch per effort (cpe). High cpe for the 1973 and 1974 cohorts in 1975 and later surveys in the most heavily exploited lake, compared to cpe's for the same ages prior to exploitation, led Healey to conclude that he had observed increased recruitment due to exploitation of adult whitefish. However, higher cpe's of young fish occurred principally in the most heavily exploited lake, where most of the adult population had been removed. Catchability of the younger fish presumably increased in response to the removal of larger adults (Healey 1980), so that comparisons of cpe between years provide weak inference concerning abundance. The gillnetting concurrently removed hundreds of predaceous lake trout from the exploited lakes (Healey 1978) which might be expected to have a large impact on both catchability and abundance of young whitefish. His cpe-based estimates of year class strength for the unexploited lake showed that the 1973 and 1974 cohorts were also the most abundant of the period 1961-75. In light of these details, Healey's conclusion that he observed a recruitment response to adult whitefish exploitation appears weakly justified.

Johnson (1976, 1983, 1994) documents studies on stunted arctic char populations in small lakes of the Canadian Northwest Territories. Two lake populations, Little Nauyuk (44.6 ha) and Gavia (17.4 ha)

were subject to heavy exploitation of age 1+ to 17+ fish by gillnetting, beginning in 1975. Johnson interpreted the results of the experiment through length and age frequency distributions and overall cpe. After initial removals of cannibalistic larger fish, small fish of variable age began to appear in the gillnet catch later in the first year's removals and appeared in both early and late removals of the following years.

I reworked Johnson's published results to examine cpe by age and cohort. In Little Nauyuk Lake following the 1975 exploitation, cpe for younger ages (1+ to about 8+) increased slightly from 1976 to 1977 and then declined through 1981. Abruptly in 1983, cpe for the same ages increased fourfold and was high again in 1985, declining in 1988 (Table 1.1). Data for *Gavia* shows a similar pattern except the abrupt increase occurred in 1981. Johnson's results are difficult to explain, moreso without population estimation. In both cases (*Gavia* in 1981, Little Nauyuk in 1983) the cpe increase was abrupt across many age classes, which is difficult to interpret in terms of recruitment. Perhaps cpe is too variable to infer abundance and recruitment from the available data; ageing error is also a strong possible accomplice (Johnson 1983).

Langeland (1986) gillnetted age 1+ to 11+ arctic char from 7m deep 163 ha Lake Øvre Stavåtjønn, central Norway, during 1979 to 1984. Population estimation was age/size aggregated using mark-recapture in 1979 (ages 3+ and older) and 1981 (ages 2+ and older), and the removal method in 1983 (ages 2+ and older). Langeland did not estimate numbers at age but inferred from aggregated estimates and age frequency distributions that "recruitment of young fish was also reduced by the intense fishing. However, the high fraction of one-year-old fish in 1984 indicated increased recruitment and a strong 1983 year class." Without a population estimate, any conclusion regarding the numerical strength of the 1983 cohort is suspect.

Donald and Alger (1989) removed 321 to 423 brook trout aged 1+ to 7+ from 3.5 m deep 2 ha Olive Lake, Rocky Mountains, British Columbia each year during 1982-84. Population estimation was

Table 1.1 . Estimated catch per effort for Little Nauyuk Lake gillnet removals. Estimates are based upon Table 1 and Figure 5 in Johnson (1994) . Catch from 1982 and 1984 was not sampled for age composition. Catch per effort increased abruptly from 1982 to 1983, apparently across many cohorts.

	Year											
	75	76	77	78	79	80	81	82	83	84	85	88
Catch	2724	855	506	754	544	362	501	602	713	1571	691	542
Effort	26.0	11.3	6.2	9.4	13.2	12.0	11.8	11.8	6.0	12.0	4.0	6.1
Total cpe	104.8	75.7	82.1	80.5	41.3	30.2	42.5	51.0	118.8	130.9	172.8	88.9
Cohort												
87												0
86												0
85												3
84											0	11
83											25	7
82									1		21	10
81									17		13	7
80							0		11		4	7
79						0	1		5		8	10
78					0	0	3		11		16	11
77				3	0	4	3		13		19	8
76			1	2	6	3	1		19		14	4
75		2	4	6	2	1	2		9		13	4
74	0	7	9	3	3	3	7		6		18	2
73	3	8	7	2	3	2	4		7		9	3
72	3	2	4	5	4	2	4		4		4	1
71	5	4	7	9	4	4	5		6		3	0
70	3	7	8	13	7	3	4		3		3	0
69	4	6	11	13	4	4	3		3		1	1
68	4	7	8	11	4	2	1		2		1	0
67	6	5	5	7	1	1	2		2		1	0
66	8	6	7	3	3	0	0		1		0	0
65	8	5	2	1	0	1	0		0		0	0
64	7	5	4	1	0	1	0		1		0	0
63	12	4	3	1	0	1	0		0		0	0
62	10	2	1	1	0	0	0		0		0	0
61	6	1	0	0	0	0	0		0		0	0
60	6	2	0	0	0	0	0		0		0	0
59	4	1	0	0	0	0	0		0		0	0
58	5	1	0	0	0	0	0		0		0	0
57	4	1	0	0	0	0	0		0		0	0
56	2	2	0	0	0	0	0		0		0	0
55	2	0	0	0	0	0	0		0		0	0
	75	76	77	78	79	80	81	82	83	84	85	88
	Year											

age/size aggregated by the mark-recapture method using gillnets for marking and electrofishing for recapture. In 1985, mean weight at age had increased by 30% (age 1+) to 250% (age 6+) compared to a 1981 pre-exploitation sample. Donald and Alger inferred increased recruitment at age 1+ from the increased proportion of age 1+ in the catch following 1981, and population estimates which did not decline during the study despite removals. However, they did not account for changing catchability of age 1+ fish as adults were removed, and its effect on population and recruitment estimates. Neither did they attempt to estimate year class strength for cohorts produced before removals, to rectify recruitment estimates with later years' abundance estimates for the same cohorts, or to examine year class strength for the same period for a comparison population not subject to exploitation.

Hall's work on density reduction of small lake brook trout populations was conducted in single-species lakes and used replication. The treatments were not effectively staggered; of the experimental units continued through 1989, one was begun in 1986 and seven in 1987 (Hall 1991). Cohorts produced during the experiments were only beginning to recruit to the sampling gear at the end of the study, so interpretation was incomplete. Again, increased size and catchability of young cohorts was apparent as the removals proceeded (Hall 1991). Population estimation was incomplete for the large cohorts suspected to have resulted from the removals.

Borgstrom (1992) manipulated the stunted brown trout population of 49 ha 40m deep Lake Løyning, western Norway from 1985 to 1989. The population spawns in a river above and below the lake, as well as in inlet streams; juveniles begin to join the lake population at age 3+ with complete recruitment to the lake by 5+. Borgstrom removed about 2000 age 3+ to 11+ fish per year, corresponding to an approximate annual exploitation of 20 to 40%. Population estimation was accomplished by size-structured mark recapture (seining and gillnetting, respectively) with the exception of the estimates for the 9-14 cm class, mostly 3+ fish. This class was not recaptured in sufficient numbers to allow an estimate, so Borgstrom assumed equal seine catchability for this class and the next larger class, and estimated numbers of 9-14 cm fish based on the population estimate for the larger class and the two

classes' proportional representation in the seine catch. He noted an inverse relationship between the estimated number of age 3+ fish in the lake, and the estimated number of 5+ and older fish in the lake. He inferred that recruitment of 3+ fish from the river and stream nursery grounds had responded to the removal of adults and deduced the same result from the work of Jensen (1977). If catchability for 3+ fish in the lake was lower relative to the next larger class in the early years of the study when adult densities were still relatively high, then bias across years in the recruitment-at-age-3+ estimates would have resulted. Still, such bias would probably only exaggerate the trend of earlier recruitment from nurseries as adult densities were lowered. Borgstrom notes other evidence that juvenile fish make two-way movements between streams and the lake as they approach recruitment to the lake population, possibly assessing lake conditions (Lien 1978). Presumably earlier recruitment would lead to higher relative year class strength because mortality rates in the stream and river nurseries are assumed higher than for recruited adults in the lake (Borgstrom 1992). However, Borgstrom did not report any attempt to reconstruct year class strength for cohorts produced before the experiment, or follow cohorts produced during the experiment to assess their eventual total contribution to the lake population.

Summary

Increased cpe for young cohorts was observed following the initial removal of adults from small lake salmonid populations, in six of seven studies reviewed. Cpe increases have been interpreted as a recruitment response to exploitation. Authors have generally been unclear about whether they are referring to recruitment to the sampling gear or recruitment to the adult population. The term "recruitment" remains loosely defined in the fisheries literature and it is not my intent to criticize its use. Nevertheless the distinction is necessary, especially when attempting to deduce the mechanisms of population regulation (Healey 1980; Johnson 1983, 1994; Borgstrom 1992) from exploitation experiments. Interpretation of the results of these experiments has been hampered by one or more of the following:

- (1) lack of control / replication / staggering of treatments;
- (2) other confounding manipulations - most notably, significant removals of other fish species;

(3) insufficient population estimation and short abundance time series; no estimate of pre-exploitation recruitment levels; no attempt to follow cohorts produced during experiments, to rectify abundance estimates across years and as adults.

These difficulties in design have not prevented speculation on the mechanisms of population regulation, inferred from the behavioral or numerical response of young fish to adult removals (Power 1978; Healey 1980; Johnson 1983, 1994; Borgstrom 1992). There is a burgeoning literature on the mortality risk - growth return optimization that presumably governs the behavior of juvenile fish (Walters and Juanes 1993). If the removal of adults changes the risk - return balance for young fish, this might be expected to lead to some combination of faster growth and higher survival to maturity, and thus increased year class strength. Although implied, this has not been convincingly demonstrated in the lake salmonid population studies I reviewed. Increased cpe may reflect either higher catchability or higher numbers. When adults are removed, greater juvenile length at age often occurs and presumably has a positive influence on catchability, because longer fish are believed to have a proportionately higher probability of encountering the gear through increased swimming distance (Rudstam et al. 1984). Increases in cpe of young fish within a single year may simply reflect growth in length during the same time period, possibly accelerated by the removal of adults. As well, however, adult density might have a direct effect on juvenile catchability. Adults may prey upon younger fish or exhibit other aggressive behavior towards juveniles. Juvenile activity or use of some habitats, or both, could thus be increased in response to lower adult density, which might result in higher juvenile gillnet catchability.

In summary, increased juvenile cpe following adult removals suggests population changes which might result in increased year class strength. Increased cpe could be due to higher juvenile numbers in the sampled habitat or higher juvenile catchability. If catchability is higher, it may reflect simply increased length at age, or some additional behavioral response to lower adult density. Such a behavioral response could result from a change in either side of the risk-return balance for juvenile fish. Because

studies have not rigorously estimated both numbers and catchability of juveniles, their results have only been suggestive of suppression of year class strength and juvenile catchability by high adult density.

One or several additional mechanisms might lead to higher abundance for cohorts spawned after the start of adult removals. Among these are changes in population fecundity, egg mortality, and survival of juveniles (Hall 1991). These are all potentially important determinants of year class strength which might respond to adult removals, and represent fascinating topics for further investigation. However, the gillnet data I have collected cannot be used to examine the function of these mechanisms. Instead, my thesis focuses on population estimation methods which allow me to reconstruct the abundance and gillnet catchability of cohorts produced before and during experimental removals. Adult natural mortality is an important parameter of the models I use, so following a brief description of the study area and general methods, I consider how weather might interact with recruitment to impact its estimation.

General study design and methods

Study site and field methods

This study was carried out in eight small lakes east of the crest of the central Sierra Nevada, California (Figure 1.1). While the lakes differ in morphometry, (Table 1.2; Figure 1.2), before manipulation each brook trout population was characterized by maximum fork length of about 200 mm, which is typical of hundreds of Sierra Nevada populations (Hall 1991). Maximum age attained by individuals from these populations is double that attained in the native range. The populations are considered stunted because maximum length is lower than for most lake populations in the native range, and because growth slows or ceases long before maximum age. A 200 mm individual may be from 5 to 15 years of age (Hall 1991). Stunted brook trout resume growth when transplanted to lakes with greater food supply, which distinguishes stunting from dwarfism, a condition believed genetically determined (Hall 1991).

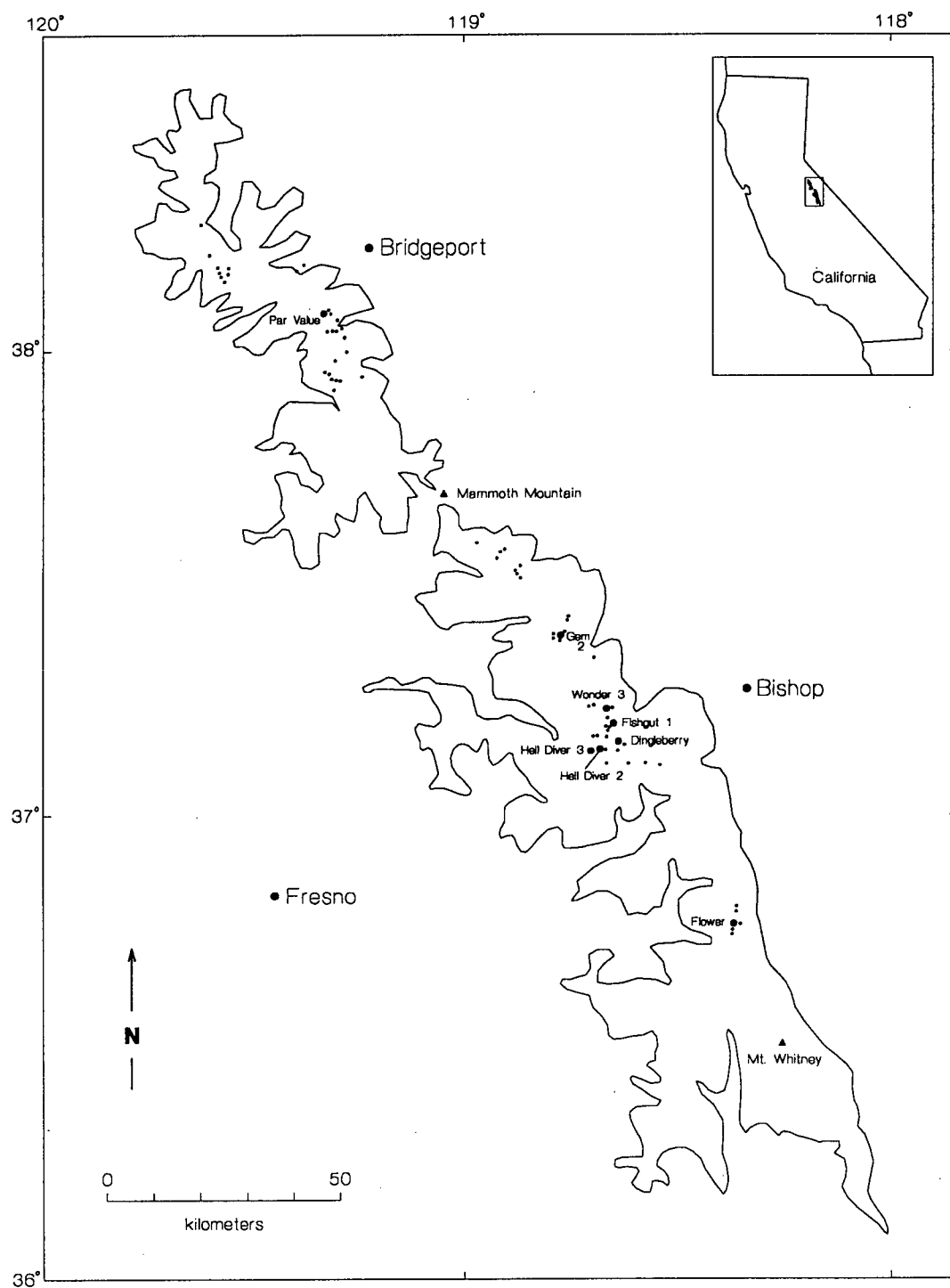


Figure 1.1. Location of the seven study lakes (labelled) along with other brook trout populations sampled in 1986. The contour shown is 3000 m elevation, and the inset shows the location of the study area within the state of California (figure reproduced from Hall 1991).

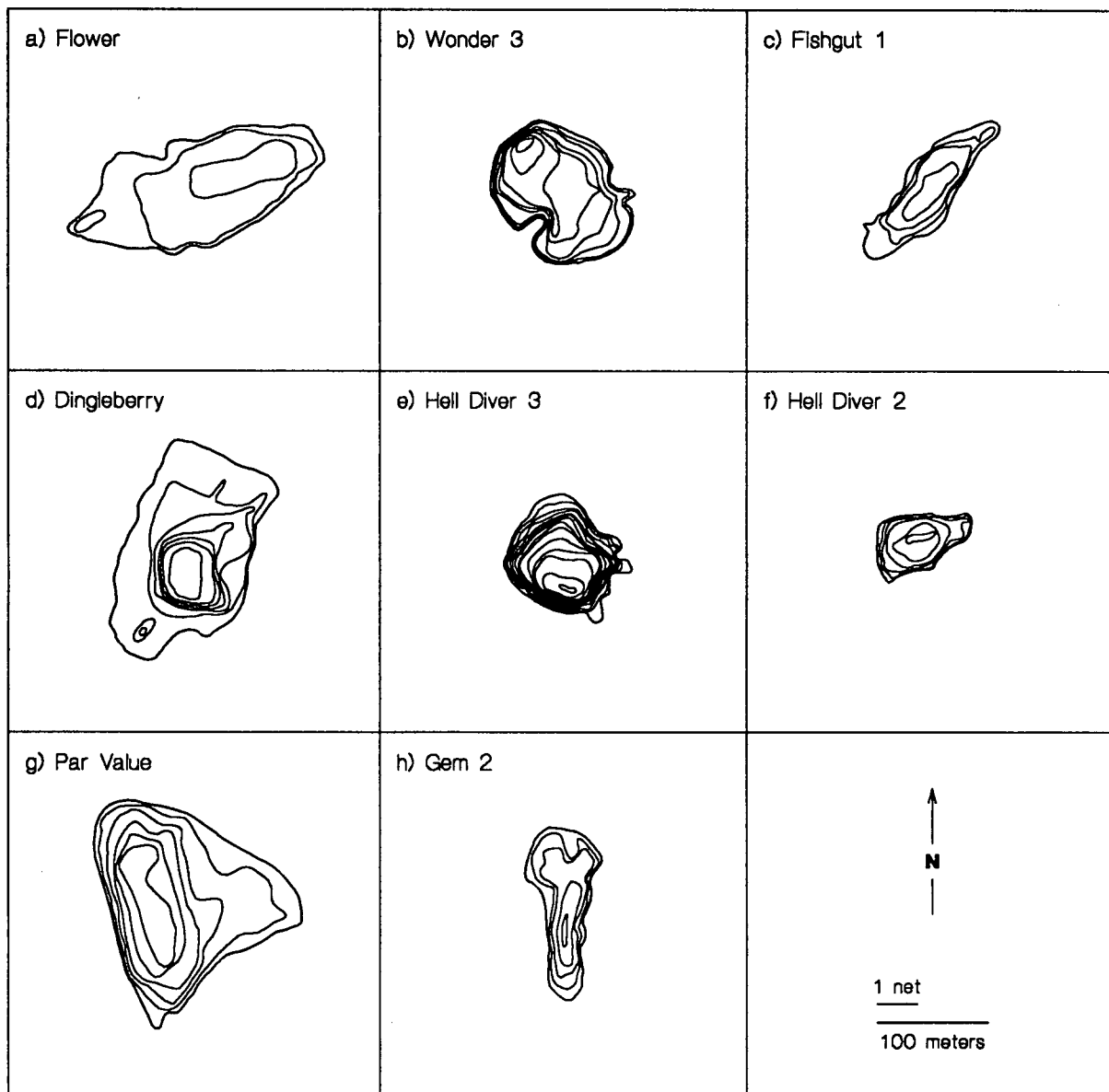


Figure 1.2. Bathymetric maps of the eight study lakes. The contour interval is 1 m except for Par Value where it is 3 m. The length of a study gillnet is also shown, along with the map scale.

Table 1.2. Selected characteristics of the eight study lakes. Given are: elevation, total surface area, shoal area (area above the 3m depth contour), mean depth, maximum depth, and subjective estimates of the angling use and fish accesss to inlet or outlet streams.

Lake	elev (m)	area (ha)	shoal (ha)	\bar{z} (m)	z_{\max} (m)	angling	stream
Gem 2	3335	0.7	0.6	1.8	4.3	mod	none
Hell Diver 2	3480	0.4	0.2	2.8	5.2	light	low
Dingleberry	3195	2.1	1.7	1.8	6.7	heavy	high
Flower	3200	1.9	1.9	1.2	2.4	heavy	high
Fishgut 1	3315	0.6	0.5	1.7	3.7	light	low
Par Value	3135	2.4	0.5	7.5	17.7	mod	low
Wonder 3	3375	1.3	0.5	3.5	7.0	mod	none
Hell Diver 3	3580	0.9	0.2	6.5	13.1	light	low

Removals from the eight lakes were made each year from 1986 or 1987 through 1992, except 1990 (Table 1.3). Fish were captured by gill netting for 3 to 11 consecutive periods of 8 to 16 hours each. We fished Lundgrens (Sweden) light green, nylon, weighted gillnets of length 36 m, height 1.5 m, on bottom. The nets were composed of twelve randomly ordered panels of bar mesh size 4, 6.25, 8, 10, 12.5, 16.5, 18.5, 22, 25, 30, 33 and 38 mm, and were chosen from a pool of ten such nets. Shore anchored nets were usually set perpendicular to shore but we also made sets offshore oriented at random or downwind. Two to 6 nets were fished simultaneously at different locations in the lake. Each removal period ended with lifting and clearing of all nets and a new period began immediately with setting of the nets, usually in different locations than the previous period. At the end of each removal period the catch was weighed and measured and the sagittae removed, labelled and preserved in glycerin. I generally pool the catch at age from all nets fished within a removal period. I also refer to removal periods as netting periods or simply as periods. I use the terms depletion, depletion series, depletion experiment, and multiperiod removal to refer to catch at age and effort data collected for multiple consecutive removal periods and tabulated by period. Estimates which use this level of time resolution of the data are referred to as period-level estimates, since they extract information about population size from the change in cpe at age across periods within a depletion. Methods and estimates which instead aggregate the catch at age and effort for all periods within a depletion, are referred to as depletion-level estimates. Depletion-level estimates extract information solely from the change in cpe at age across years.

Table 1. 3. Summary information for depletions made from 1986 through 1992 in seven study lakes. Total effort is in units of net-hours, the number of nets multiplied by the time they were fished. For most depletions, the same number of nets was fished for all periods but if not, the range of number of nets fished is shown.

Lake	Depletion	Starting date	Periods	Nets	Total catch	Total effort
Hell Diver 2	1986	8-23	3	4	106	176
	1987	7-26	5	2	54	105
	1988	7-25	3	2-3	97	89
	1989	8-12	6	4	233	284
	1991	7-07	5	6	207	359
	1992	7-22	5	4	242	245
Dingleberry	1987	7-20	9	2-6	659	531
	1988a	7-16	11	6	827	752
	1988b	7-29	1	4	77	55
	1989	8-6	9	6	913	641
	1991a	7-13	4	5	647	243
	1991b	7-28	9	5	773	535
	1992	8-03	7	5	585	426
Flower	1987	6-17	8	2-4	557	326
	1988	6-13	11	2-6	714	464
	1989	7-11	5	6	921	382
	1991	7-21	10	6	1027	674
	1992	8-24	7	6	866	520
Fishgut 1	1987	7-16	3	2-4	266	115
	1988	7-02	7	2-5	383	312
	1989	8-19	5	6	463	352
	1991	8-05	7	5	440	419
	1992	7-29	6	5	373	343
Par Value	1987	8-17	9	3-6	644	592
	1988a	8-01	9	6	685	638
	1988b	8-20	1	5	79	65
	1989	7-23	11	6	944	763
	1991	8-11	9	6	905	655
	1992	8-17	7	6	815	539
Wonder 3	1987a	6-27	5	2-4	242	180
	1987b	8-28	3	4	287	127
	1988	8-11	6	5-6	429	377
	1989	8-23	9	6	616	636
	1991	8-17	9	5	607	548
	1992	8-11	6	5	342	350
Hell Diver 3	1987	7-28	5	2-4	81	213
	1988	7-25	4	4	68	254
	1989	8-13	3	4	68	148
	1991	8-25	6	4	142	342
	1992	7-25	4	4	54	180

While the Gem Lake 2 population gave no initial indication that it would behave differently, recruitment failed from 1987 through 1991, likely for reasons I discuss later. The population was apparently extirpated in 1991. I have excluded Gem Lake 2 from the analyses made for this thesis.

Age determination

For each fish, the right side saggita was blotted dry and mounted half-embedded, sulcus-side up, in Crystalbond® thermoplastic resin on a standard microscope slide. The slide was inverted and the otolith half-sectioned to the saggital plane by polishing on 1200 grit abrasive paper followed by 9µ lapping paper. Otoliths were examined under reflected and transmitted light at 15-30X magnification, and ages estimated according to criteria presented in Hall (1991b).

Size at age

Demonstration of the effect of removals on size at age was not a primary objective of this study. Gillnets are highly size selective, and it was never established that the fish captured during removals were representative samples for size at age, especially for the younger ages. As well, comparisons are confounded by differences in the seasonal timing of food availability and growth between years, and sampling dates which changed from year to year due to logistics. Nevertheless, gillnet catchability is influenced by size, and size at age may be useful as secondary evidence about population density. For ages 1+ to 3+ in most of the study lakes, mean length at age increased from 1987 to 1989, decreased to near pre-removal levels in 1991 but increased again in 1992 (Figure 1.3). Trends in mean length at age for older age classes were much more variable across years and lakes during the study (Figure 1.3). This is partly due to small sample size, but also may reflect early removal of individuals with the highest growth potential, reduced potential to resume growth at increased age (Reimers 1979), or changing asymmetric competition between age groups (Walters and Post 1993).

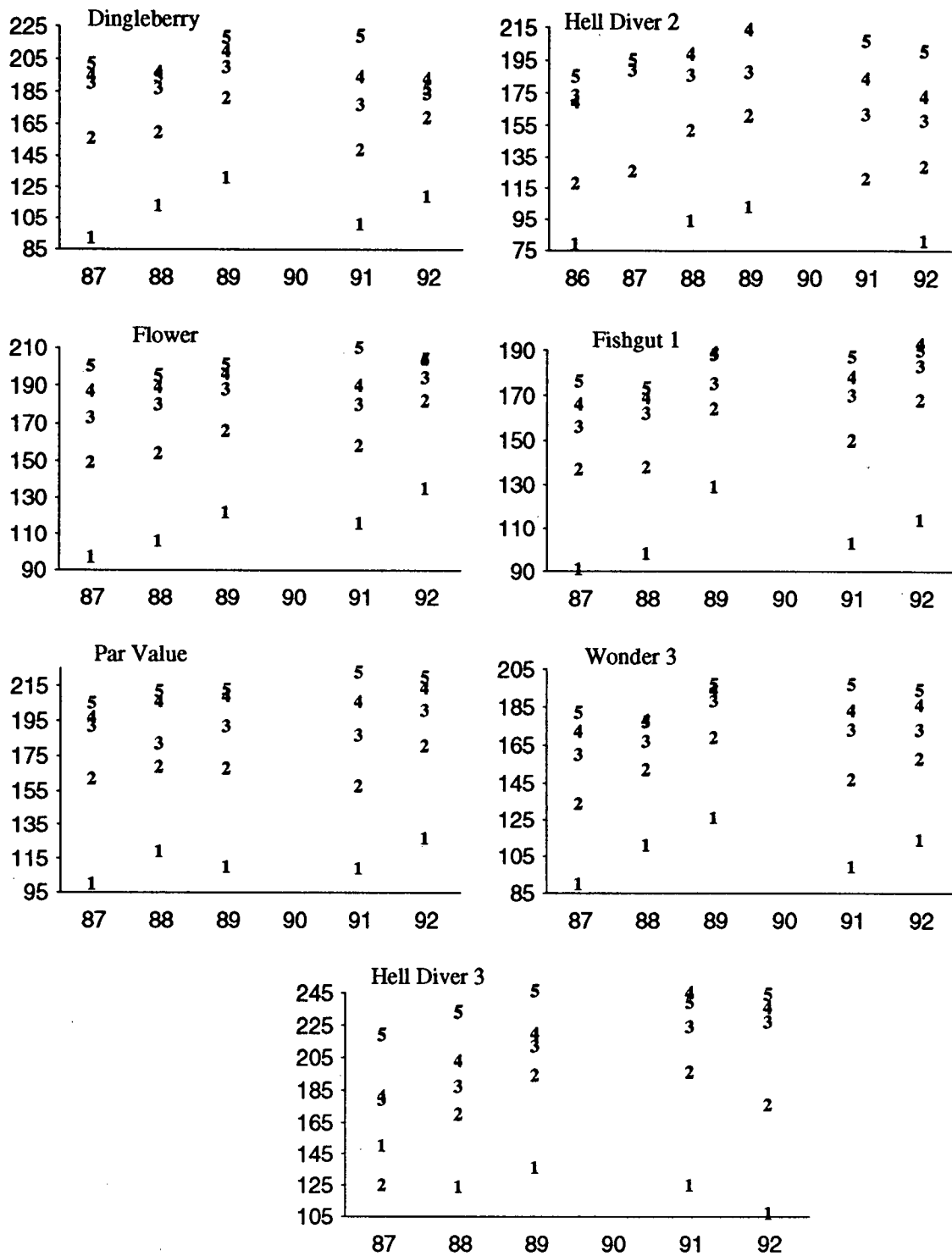


Figure 1.3 . Mean size at age for age 1+ to 5+ brook trout captured in the seven study lakes during depletions from 1986 to 1992. Plot symbol indicates the age group. Across years for age 1+ to 3+ fish, size at age tended to increase from 1987 to 1989, decline in 1991 and increase again in 1992.

Weather, year class strength and survival

The population estimation methods I use in this thesis rely on an independent estimate of natural mortality. Reliable estimates of age specific natural mortality are difficult to obtain. Authors have often assumed age and time invariant natural mortality, lacking definite information to the contrary. Survival at age is often estimated by the catch curve method which involves fitting a function to log-transformed catch at age data, typically combined across years to smooth discontinuities (Ricker 1975). However, catch at age is influenced by year class strength, age-specific vulnerability and ageing error, as well as survival. In this section I briefly consider the following questions concerning weather, year class strength and survival at age. First, are there interlake similarities in year class strength? Do they parallel any obvious patterns in the weather data I have assembled? A striking observation from Hall's study was the ubiquitous convexity of catch curves for 20 distinct lake populations (p. 66, Hall 1991). Here I consider whether similarities in the catch curves are more likely to have arisen from large scale patterns in year class strength due to environmental conditions, or from decreasing survival at age consistent among populations. What would be a highest estimate of adult survival? The depletion data across years might suggest plausible survival values, but the analyses in Chapter 3 require a starting point and for reasons explained there, a highest plausible estimate is needed. Finally, if there is evidence of recruitment-weather correlation, would year class strength during manipulation years likely have been enhanced or retarded by environmental conditions during those years? Given that treatments were not staggered, this information should be weighed when considering the numerical response to adult removals.

Mountain lake salmonid year class strength can be highly variable (Donald and Alger 1989; Hall 1991) and is likely influenced by weather (Lindstrom et al. 1970; Donald and Alger 1989). Droughts and cool wet periods of several years' duration are probably typical for the Sierra Nevada. Brook trout spawn in the fall so overwinter drying and freezing of stream and nearshore gravels can be catastrophic for eggs and fry (Cooper et. al. 1988) and might be implicated in the formation of some

weak year classes (Cooper et al. 1988). But conditions leading to freezing are complex and may occur on a time scale of days to weeks and thus be undetected in monthly or seasonal totals. Generally, year to year variability in winter conditions is presumed buffered by ice and snow cover (Johnson 1983). For this reason, and because studies have demonstrated a link between summer warmth and mountain lake salmonid growth (Jensen 1977) and recruitment (Lindstrom et al. 1970; Donald and Alger 1989), I examine spring and summer conditions as factors affecting year class strength in the study lakes.

Spring and summer lake temperatures are probably influenced both by seasonal atmospheric conditions and by meltwater from the previous winter's snowpack (T. Jenkins, pers. comm.). I created two time series from the data available. I used the East Piute Pass data for May 1 as an index of spring snowpack water content (data obtained from California Cooperative Snow Surveys, Sacramento, CA). This is a biased indicator since snowpack on May 1 is zero in some years, but as a rough index it should be sufficient. I subtracted the Bishop cooling-degree days from heating-degree days (65°F base) totalled for the months May to September as an index of summer atmospheric warming for the east slope of the central Sierra Nevada (data obtained from National Climate Center, Reno, NV). Brook trout spawn in October and November in the Sierra Nevada (Cooper et al. 1988). Hatching occurs from January to April and emergence about two months later, depending on temperature (Cooper et al. 1988). During the age 0+ year, they experience winter conditions as eggs and sac fry, followed by spring and summer conditions as fry and fingerlings. I have labelled cohorts by the year in which fry emergence occurred. For instance, fry from eggs spawned in the fall of 1989 emerge in early-to-mid 1990 and are referred to as the 1990 year class. To look for patterns in year class strength across lakes, I pooled the catch at age data for all lakes sampled in the 1986 survey. The 1986 data is taken from more than 50 lakes and no single lake or group of lakes dominate the age distribution as for other years. Because it is not clear at what age full gillnet vulnerability occurs for unexploited populations, I plotted the residuals from the catch curve, using a linear fit to log-transformed pooled data and including all ages in the catch.

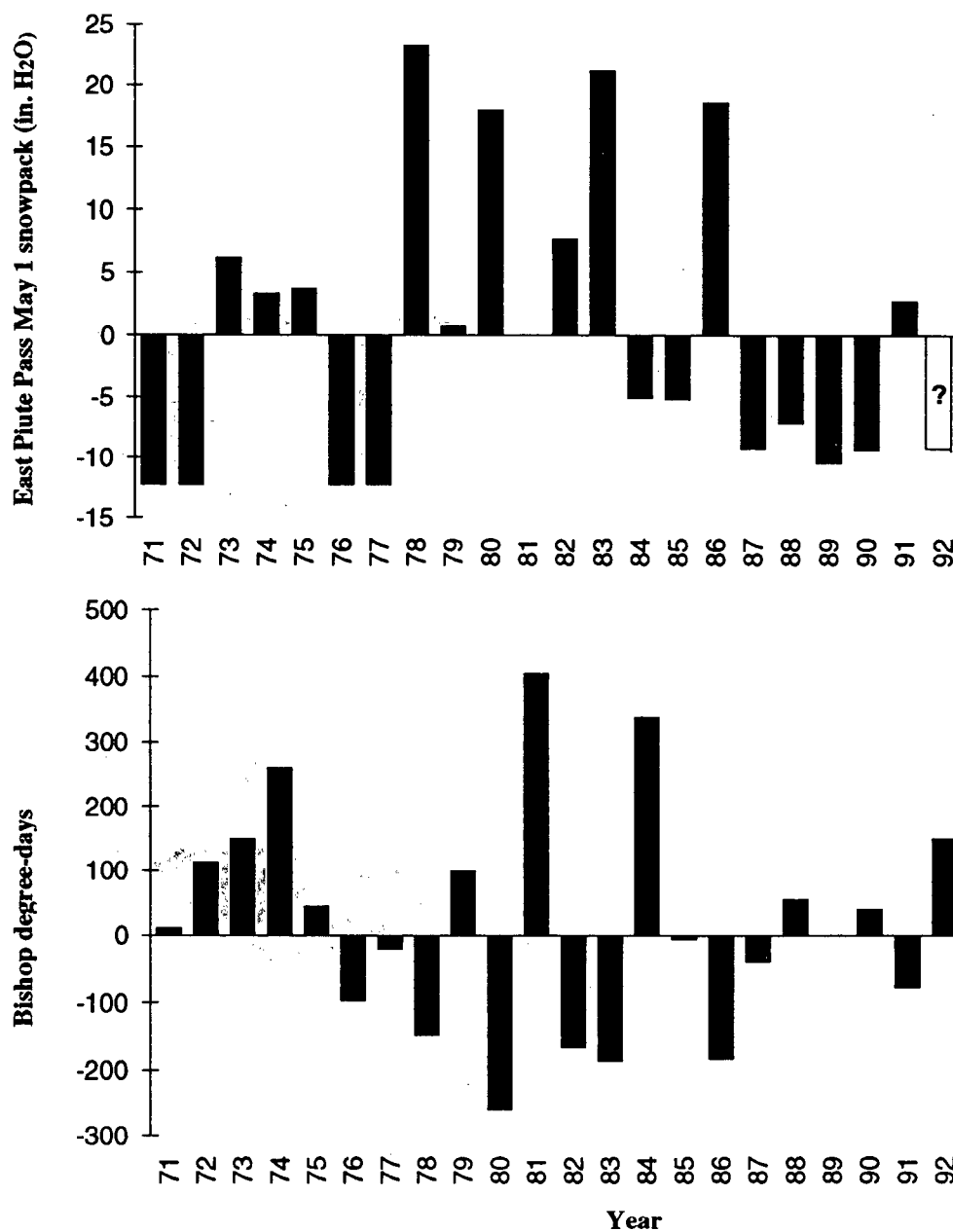


Figure 1.4. East Piute Pass snowpack measured in inches of water equivalent on May 1, and Bishop California total degree-days May through September (65 F base temperature) plotted for 1971 through 1992. Values are deviations from the median for the period 1971 to 92. High snowfall years (1978, 80, 82, 83, 86) tended to have colder than average following summers. Average to dry years with average to warm summers were 1977, 79, 81, 84, 85 and the drought years 1987-90. The May 1 1992 snowpack was unmeasured; estimate based on April 1 1992 measurement and precipitation during April 1992.

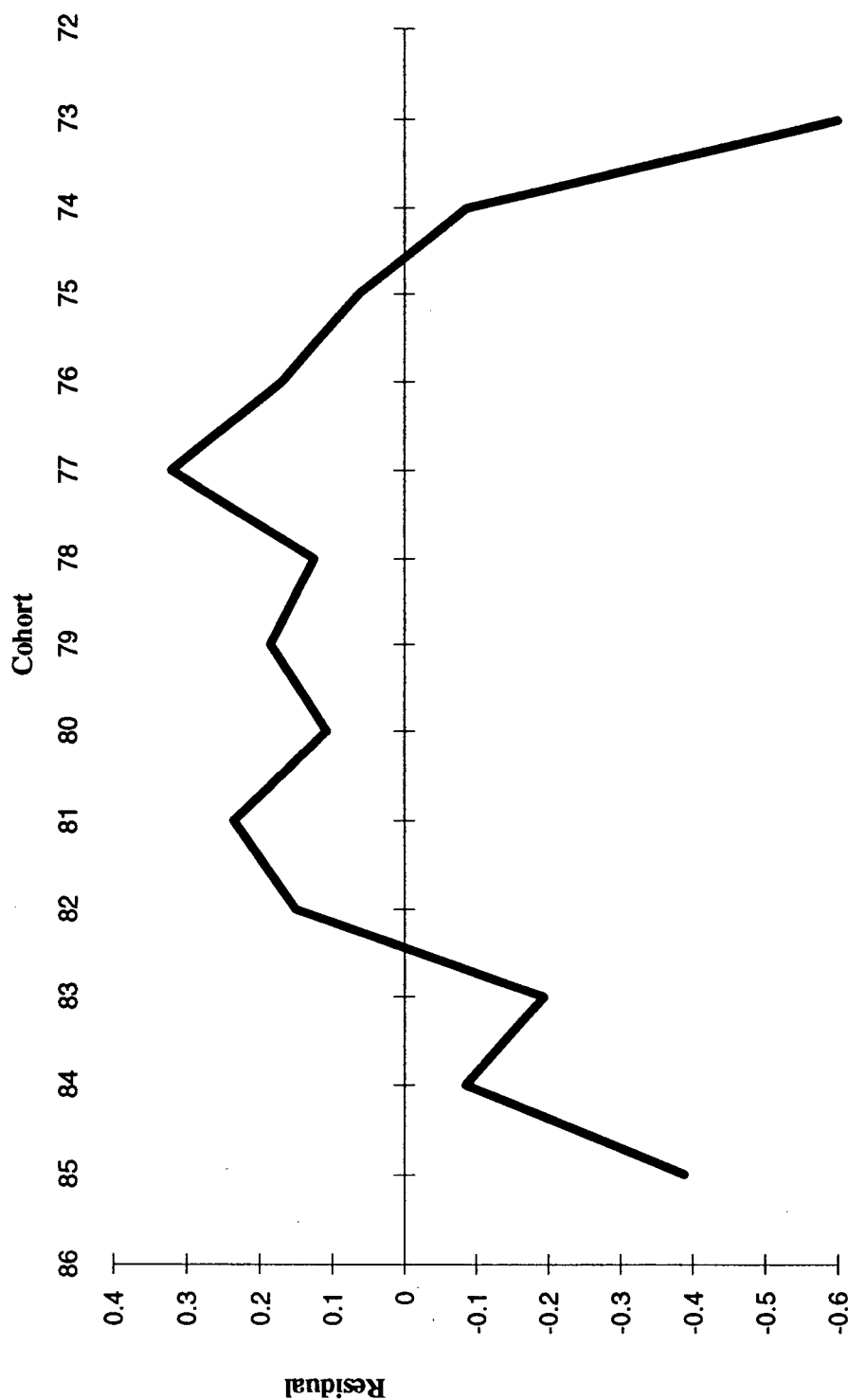


Figure 1.5. Residuals from catch curve fitted to 1986 catch data. The data pools catch from all lakes sampled in the year ($n=51$). Strong year classes are apparent in 1977, 1979 and 1981. Weaker year classes include 1978, 1980, 1982 and 1983. Ageing error likely blurs the residuals considerably, and low vulnerability affects the abundance of 1984 and later cohorts.

The snowpack and temperature data confirm the tendency for runs of dry-warm and cool-wet years during the 1970's and 1980's (Figure 1.4). Cool-wet runs include 1973-75 and 1980-83, with 1981 an outlier year. Warm-dry runs were 1976-77 and 1984-90 with 1986 an outlier year. Residuals for the pooled 1986 catch curve do show strong and weak year classes across the group (Figure 1.5). The overall pattern to the residuals is shaped by apparent lower vulnerability or lower year class strength at the left, which in turn causes the center residuals to be positive. Given the uncertainty about vulnerability and the shape of the survival-age relationship, the strength of a year class should be judged relative to its near neighbors. Clearly 1977, 1979, 1981 and 1984 represent stronger than average cohorts. These years either had low snowpack or high following summer temperatures, or both. Weaker cohorts appear to be 1978, 1980 and 1983. All were high snowpack years, with cold following summers.

To some extent, weather does apparently synchronize year class strength across Sierra Nevada brook trout lakes, with summer lake warmth leading to strong cohorts. Considerable smoothing of the distribution by ageing error has probably diminished the apparent year to year variability of year class strength. As well, for most lakes summer temperatures may lead to stronger than average cohorts, but for some lakes other constraints are probably more important. For instance, the recruitment series for Gem Lake 2 is dissimilar to the general pattern (Figure 1.6). The watershed of Gem 2 is very small and the lake does not have an inlet or outlet stream. Brook trout reproduction was apparently successful there in the winters of 1980, 1983 and 1986. Total precipitation for those winters was far above average, although each was followed by a cool summer. Perhaps only wet years allow eggs and fry to survive the winter in tarn-type lakes.

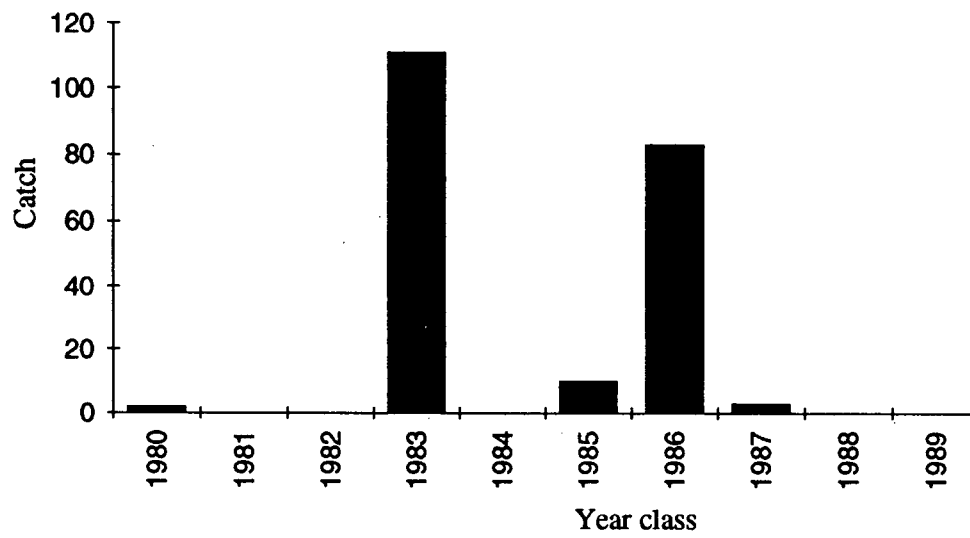


Figure 1.6. Gillnet catch by cohort for Gem Lake #2, 1987 through 1991. Catches for 1985 and 1987 cohorts may represent ageing error. The years 1980, 1983 and 1986 all had high snowfall winters followed by cool summers.

Do the data suggest that the convexity of catch curves may be due to a weather-recruitment correlation? Probably not, since convexity would be created primarily by several adjacent strong years in the center of the distribution (1978 to 82) and several adjacent weak years at the far right (1973 to 75), which is not indicated by the weather data. It appears more likely that age specific survival generally does decrease with age, as reported for long-lived arctic lake *Salvelinus* populations (Power 1978), although to what extent is not clear. Regarding a first estimate of adult survival, the Bunny Lake study suggested an annual survival of about .85 for a single cohort of brook trout stocked into a previously fishless alpine lake (Reimers 1979). The few abundance estimates in the years after stocking indicate a fairly constant rate of decline in numbers (Reimers 1979). Reproduction is believed to be a dominant agent of natural mortality for mature iteroparous salmonids. The change in sex ratios with age for the brook trout collected from the study lakes is evidence for the importance of reproduction as a mortality factor. More older fish are females than males, and the disparity tends to increase with age. For iteroparous salmonids, it is believed that males spend longer at spawning locations and experience more aggression-related stress and injury (E. Parkinson, pers. comm.). The lack of reproductive opportunities for Bunny Lake brook trout (Reimers 1979) probably prolonged their lifespan but whether it impacted the shape of the age-survival relation is not clear.

The drought of 1987 - 1991 created weather conditions similar to those which led to stronger-than-average recruitments in some pre-study years. These years, during which the manipulations were made, were all low snowfall years followed by average to warm summers. These same conditions appear to have been associated with strong year classes in the majority of lakes in the late 1970's and early 1980's.

Synopsis of the chapters

Chapter 2. Ageing error

The recent literature has emphasized the potential for ageing error to mask the patterns which might otherwise emerge from age-structured population estimation methods. Reader error is believed to result in smoothing of age distributions, as more members of dominant cohorts are misclassified into smaller neighboring cohorts than vice versa. The magnitude and rate of occurrence of errors is likely to increase with fish age. In Chapter 2, I use multiple independent ageings of 1124 brook trout otoliths to examine the error process. I follow the methods of Richards et al. (1992) in selecting a model which parameterizes the classification matrix of error probabilities. Repeatability estimates decrease from nearly 100 % at age 1, to 58% at age 15.

I use simulation to demonstrate the bias and variance in age distributions which are created by ageing error of the type estimated for my data. Ageing error correction reduces the sum of absolute mean deviations in the proportions to 17% and 11% of observed mean deviations for two different age distributions typical of study depletion data. I also examine the probable bias and variance of population estimates using the Walters-Collie estimator of Chapter 4, with uncorrected and corrected simulated data. Bias ranges from -2.7 to 6.7 % for estimates using corrected data, while its range is -10.2 to 85.3% for estimates using uncorrected data. However, standard errors for corrected estimates are up to 25% greater than comparable estimates using uncorrected data.

I use the model likelihood and numerical methods to make the most likely corrected estimate of age distributions observed for depletion data for this study. Percent of ages reassigned due to ageing error correction range from 0.9 to 9.9%. Depletions before 1989 tend to display greater percent reassignment due to higher abundance of older fish.

Chapter 3. Depletion estimation at period level resolution

Removals from the eight study lakes were made as individual depletion experiments each year from 1987 through 1992, with no removals in 1990. In Chapter 3, I examine the depletion data with regard to the within-series information it may contain about population size. My original goal was to apply a powerful age-structured depletion estimator which links and simultaneously analyzes removal series for all recruited cohorts across all years' data (Walters and Collie 1988). If the model describes the series well, the high number of observations (one for each cohort for each removal period) reduces the variance of the population estimates. As well, the analysis might suggest which mortality values are most plausible.

Hall (1991) made depletion estimates using age aggregated catch data and found evidence that catchability (q) for the first removal period was higher than for the subsequent periods. If uncorrected this would lead to biased low population estimates, so I first examine the cohort-specific series for evidence of higher initial period q . I use Schnute's (1983) variable q removal estimator which provides statistical criteria for choosing the appropriate number of q 's. Most of the series show diel variation in catch per effort and most begin with a night removal period. I develop a model with distinct day and night q 's to detect and account for this structure before evaluating for distinct initial q . I make depletion estimates for removal series where total catch was at least 20 individuals, using 1989 and later data obtained with consistent effort as required by Schnute's method. The analysis suggests that first removal period q 's are not generally atypical.

I evaluate the bias of the Schnute estimates of population size (\hat{N}) for 1989 and 1991 cohort series by comparing them with minimum known alive (MKA) estimates. In most cases the Schnute \hat{N} 's are less than MKA estimates. Since the Walters-Collie (WC) estimator is essentially a linkage of each year's cohort-specific Leslie removal estimates, bias in the Leslie estimates will lead to bias and inflated variance for the WC estimates. I compare simple Leslie \hat{q} 's to WC \hat{q} 's, to demonstrate that the Leslie estimates are biased and this leads to bias in the WC estimates. Discounting the first two removal

periods does not alleviate the bias, confirming that initial high q is not the main source of bias. For the data from this study the available models fail to describe the within-year structure of the removal series, which leads to biased population estimates. Essentially, the removal series and available models provide estimates which consistently underpredict the number of fish remaining in the lake. This leads to bias and inflated variance of the WC estimates. As well, this means that the estimates cannot provide reliable information about natural mortality.

Chapter 4. Population and catchability estimates at depletion level resolution

Because the models tested in Chapter 3 failed to describe the observed catch series, in Chapter 4 I use the catch data at a different level of time resolution to estimate population size. The WC method can also fit catch at age data with each cohort's catch for a single year's depletion series compressed into one observation. This application of the WC method is parallel to likelihood-based methods of catch at age analysis but does not require any structure to recruitments, can fit series with catch of zero at some times, and uses simple linear regression. As long as the fraction of each cohort vulnerable is relatively consistent from year to year, recruitment of the invulnerable fraction to the vulnerable population is negligible during the depletion, and the vulnerable fraction is not fully depleted, catch per effort aggregated across removal periods can still be a reliable index of abundance even when within-depletion catch data provide biased estimates.

I make WC estimates of year class strength, and adult population abundance for the eight study lakes across the years of the depletions. Ageing error correction provides little change in the estimated strength of cohorts produced during the mid- to late 1980's. Because of uncertainty about natural mortality, estimates of year class strength for earlier cohorts are not reliable regardless of ageing error correction, and cannot provide additional information about whether strong cohorts in the late 1980's were an unusual event likely caused by removals. I use uncorrected data for the analyses presented in this chapter.

Estimates show an inverse relationship between year class strength and adult population size, for cohorts from 1984 to 1990. Age 1+ prerecruit \hat{q} also appears negatively related to adult population density for most lake populations, but the results do not suggest whether this is a direct effect of adult density, or an indirect effect mediated through the effect of density on length at age. I present year and cohort-specific adult \hat{q} 's mainly to demonstrate variability and lack of evidence for density dependence in adult \hat{q} . I use period level Leslie estimates of the vulnerable population to show that the vulnerable proportion of each cohort, and of the adult population in general, appears insensitive to population density.

The WC method estimates a time- and age-invariant "global" q for each lake population. A question of secondary interest in this chapter concerns the sources of between-lake variation in q . Current hypotheses hold that catchability variation may be explained by differences in the rate or probability of fish encountering the capture gear, which presumably is a function of swimming speed and the density of fishing effort (Rudstam et al. 1984; Borgstrom and Plahte 1992). The WC \hat{q} 's are not comparable because of between-lake differences in effort density and fish size, so I develop a modification of the WC fitting to adjust for these factors' presumed impact upon encounter probability. This model includes cohort mean length and lake area, and estimates a dimensionless "relative activity" parameter, \hat{k} , rather than catchability. Key assumptions of such a model are that spatial pattern of movement and proportion of time active do not vary with length, and that effort density is not so high as to create gear competition. I compare between-lake variation in \hat{k} using three different assumptions about depth zones ("effective area") used by brook trout. Variation in \hat{k} is reduced relative to variation in \hat{q} , when effective area is either total lake area or area above the 9 m depth contour. This analysis suggests that brook trout may use all benthic areas of the lake, or all but the deepest benthic areas, and that variation in encounter probability explains some of the variation in \hat{q} . Hell Diver 2 does not fit this pattern, and one parsimonious explanation is that high effort density led to gear competition there. Without independent observations of brook trout movement and use of different areas of the lakes, such models will not be convincing.

Chapter 2. Ageing error estimation

INTRODUCTION

Ageing error is known to have potentially important impacts on the reconstruction of population abundance and estimation of recruitment time series using age structured models. Ageing error is expected to result in smoothing of age distributions, as more fish are misclassified from abundant cohorts into less abundant cohorts than vice versa. Sensitivity analysis using simulated population data has demonstrated the biases created by smoothing of age data in sequential population analysis (Fournier and Archibald 1982; Rivard 1989; Bradford 1991). Recent sequential population analysis models for commercial fishery data (Fournier and Archibald 1982; Methot 1986; Kimura 1990) can explicitly include ageing error as a component of the estimation if the error pattern can be independently estimated. The true age of fish sampled from wild populations is virtually never known. However, multiple independent ageings of samples can be used to examine the observation error pattern. Methods have been developed which use multiple ageings to estimate the classification matrix which describes the error process, and reverse the smoothing of age proportions (Hoenig and Heisey 1989; Richards et al. 1992).

For this study, brook trout removed from 1986 to 1989 were otolith-aged by D. L. Hall. I otolith-aged all fish removed in 1991 and 1992. Hall validated the ageing method by oxytetracycline marking (Hall 1991). Such validation experiments are important to verify the appearance and annular nature of patterns in the matrix of the age structure. However, validation is not a substitute for statistical analysis of patterns in ageing error. Validation studies are usually conducted under experimental conditions which do not mimic the typical methods for processing large numbers of otoliths efficiently. Generally, validation uses a small sample of structures which are handled very carefully. As well, the fish are usually recaptured one to two years after marking. The structures are examined with the expectation of one or two checks distal to the oxytetracycline mark, at the edge of the otolith where increments are most easy to discern. Other factors make ageing error more likely when large age

structure samples are being processed. Increments may be more difficult to identify as annuli towards the center of otoliths of older fish. Discrepancies in counting or in identifying increments as annuli are more likely when large numbers of structures are processed under time constraints. Whatever the process by which error occurs, it is a dominant component of most catch-at-age data. Agreement between two independent readings of the same structure has been reported as 41, 44, 64 and 79 % for Pacific ocean perch, sablefish, walleye pollock, and Pacific hake respectively (Kimura and Lyons 1991). Exact agreement between marked, known age fish and an independent otolith ageing was 45 % for 5- to 11-yr-old rainbow trout stocked into montane and alpine lakes (Donald and Alger 1986).

Methods to estimate and correct for error cannot eliminate fish-source error: failure to generate annuli or generation of multiple increments within a single year, under certain internal or external environmental conditions. Such occasional conditions may not be detected in short-term, small sample validation experiments. Only long term validation (*sensu* Pikitch and Demory 1988) can establish the accuracy of the ageing method. However, Richards' et al. (1992) method should still be useful to parametrize the error process and to eliminate as much of the smoothing due to reader error, as is possible by statistical means. I examined the importance of ageing error as a component of this study, with the following questions and ideas in mind.

(1) What is the best description of the error for the ageing which was done for this study?

How much variation is displayed by independent readings of the same otolith? Which of the available models best describes the error displayed by the multiple-age data? Estimation of the matrix of age-specific error probabilities will allow me to address the questions below.

(2) What are the best estimates of the true catch-at-age?

Given the error probabilities, what is the best estimate of the true age structure of the removals carried out during the study? How much were the estimates of catch-at-age changed by the analysis?

(3) How accurate and precise are the estimates?

What are the variances of the catch-at-age estimates? Applied to simulated data using the error probabilities estimated from my data, how effective is the "desmoothing" process?

(4) Given the likely error, what potential effects will it have on the population estimation methods I have chosen?

I examine questions (1) through (4) in this chapter, predominately through the ageing error models of Richards et al. (1992). I use their models to analyze multiply aged otoliths, to select the model and parameters which best describe the error process for my data. I then use the model and parameters to correct the proportions-at-age and catch-at-age for removal data from 1986 to 1992. I also use Monte Carlo simulation to demonstrate the effectiveness of the methods and to suggest the residual error after correction. I use the estimated error matrix and Monte Carlo methods to examine how uncorrected and corrected error might impact population estimation.

METHODS

Background and general methods

Although many authors have noted the potential effects of ageing error on age structured population estimates, few methods have been proposed for quantifying ageing error and reversing its smoothing effect on catch-at-age data. To date, the only thorough treatment has been that of Richards et al. (1992). They present a complete and consistent statistical framework for modelling ageing error. Their methods provide for estimating the classification matrix which describes the error generation process, as well as reversing the process to estimate either the true ages, or proportions at age for a sample of fish. The estimation of the classification matrix and the age structure can be made simultaneously or independently. Their models are formulated using maximum likelihood and are easily modified for other specific analyses.

In discussing the theory and computational methods of ageing error analysis I follow the notation of Richards et al. (1992). I attempt only to present sufficient detail to clarify the general methods and assumptions. Further computational detail can be found in their work.

Let \mathbf{P} represent a vector of proportions, or probabilities that a fish from the population has true age b . Then the vector \mathbf{P} has an element p_b for each true age, and the elements of \mathbf{P} must sum to one. \mathbf{P} is acted upon by an error-generating process which results in a vector of observed proportions, represented as \mathbf{P}^* . The expected value of the error-generating process can be represented as a classification matrix. This classification matrix, designated \mathbf{Q} , is a square matrix, each element $q(a|b)$ of which gives the probability of observing the structure as age a given that its true age is b . Thus:

$$\begin{bmatrix} p_1 \\ \vdots \\ p_n \end{bmatrix} \begin{bmatrix} q(1|1) & \vdots & \vdots \\ \vdots & \vdots & \vdots \\ \vdots & \vdots & q(n|n) \end{bmatrix} = \begin{bmatrix} p_1^* \\ \vdots \\ p_n^* \end{bmatrix} \quad (2.1)$$

can be expressed as $\mathbf{P}^* = \mathbf{Q}\mathbf{P}$. If \mathbf{Q} can be estimated, then the error process can be reversed to estimate \mathbf{P} so that $\hat{\mathbf{P}} = \mathbf{Q}^{-1}\mathbf{P}^*$. Under certain restricted conditions, the estimation of $\hat{\mathbf{P}}$ has an analytical solution. When the inverse classification matrix \mathbf{Q}^{-1} exists and is non-singular and when no elements of \mathbf{P}^* are near zero, the solution is direct. However, when the sample is small for some ages, these constraints may not be met and numerical methods must be used.

With true ages rescaled to range from 1 to A , the form of the classification matrix could be described by any set of up to A^2 parameters. Richards et al. present two parsimonious representations, which they designate as "normal" and "exponential" models. Each involves a vector of two to four parameters:

σ_1 , σ_A , and possibly α , β , or both. Together the parameters constitute Φ , the parameter vector which determines Q for the two models as follows:

$$\sigma(b) = \sigma_1 + (\sigma_A - \sigma_1) \frac{1 - e^{-\alpha(b-1)}}{1 - e^{-\alpha(A-1)}}; \quad \alpha \neq 0 \quad (2.2)$$

$$\sigma(b) = \sigma_1 + (\sigma_A - \sigma_1) \frac{b-1}{A-1}; \quad \alpha = 0 \quad (2.3)$$

Then for the normal model, a matrix $X(\Phi)$ is determined by (2.4).

$$x_{ab}(\Phi) = \frac{1}{\sqrt{2\pi}\sigma(b)} e^{-\frac{1}{2} \left[\frac{a-b}{\sigma(b)} \right]^2} \quad (2.4)$$

Finally, the column totals are rescaled to sum to one by (2.5).

$$q(a|b, \Phi) = \frac{x_{ab}(\Phi)}{\sum_{a=1}^A x_{ab}(\Phi)} \quad (2.5)$$

For the exponential model, the matrix $X(\Phi)$ is calculated not by (2.4) but by (2.6)

$$x_{ab}(\Phi) = \sigma(b)^{|a-b|^\beta} \quad (2.6)$$

followed again by (2.5) to rescale the column elements, with σ_1 and σ_A constrained to values between zero and one. Probably the most important assumption made by these models for Q is the modality assumption: for each true age b the distribution of observed ages has its mode at b . In other words, for any true age b , the most likely observed age must also be b , even if observing b is less likely than the total probability of observing "not b ". The vector Φ parameterizes the shape of the general error probability distribution and the rate at which error increases with age. The models may also be

reduced by the constraints $\alpha = 0$ and $\beta = 1$, which makes an additional three special cases of the two basic models. For a particular set of multiply aged samples, selection of the most appropriate model among these can be accomplished informally using the Akaike Information Criteria :

$$AIC = l(\hat{\theta}) + 2N \quad (2.7).$$

N equals the number of parameters so that the term $2N$ acts as a penalty for additional parameters (Akaike 1974). The inference function $l(\Theta)$ quantifies the fit of the model to the data. Generally the models are fit by minimizing the inference function

$$l(\Theta) = -2 \log L(\Theta) \quad (2.8)$$

where $L(\Theta)$ is the likelihood for the specific estimation problem being addressed. Estimates of the variances of the parameters can be made if the asymptotic variance-covariance matrix can be determined. One approach would be analytical calculation of the variance-covariance matrix. However, in the maximum likelihood case, the asymptotic variance-covariance matrix is the inverse of the Hessian, which can be estimated directly through numerical derivatives using quadratic approximation (Richards et al. 1992; Mittertreiner and Schnute 1985). One disadvantage is that this method requires highly precise location of the function minimum. This can be difficult when proportions at age are estimated, since the inference function is relatively insensitive to small changes in the proportions (Richards et al. 1992).

Estimation of Q and \hat{P}

The methods of Richards et al. allow for simultaneous estimation of the parameters in Φ as well as either the vector \hat{B} of estimated true ages for the fish in the sample, or proportions-at-age \hat{P} . If A^* is a matrix of observed ageings for a total of I fish each aged J times, with observed ages rescaled to range from 1 to A , then the likelihood for estimating Φ and \hat{B} is expressed as:

$$L(A^*|B, Q) = \prod_{i=1}^I \prod_{j=1}^J q(a_{ij}|b, \Phi) \quad (2.8).$$

My approach was to estimate a general $Q(\Phi)$ using a large number of multiple ageings from different lakes and years. Since this did not constitute a distinct sample, I estimated $Q(\Phi)$ using likelihood (2.8), treating $\hat{\mathbf{B}}$ as a vector of nuisance parameters. To create the matrix of multiple ageings \mathbf{A}^* for the estimation, I selected the first fifty otoliths each from the seven study lakes in 1991 and 1992, which had already been aged by my usual techniques. I covered the labels on these samples and shuffled them before reageing them. In order to increase sample size for ages 5+ and older, I independently aged two additional times all of the otoliths which had been initially aged as 5+ or older in the 1991 and 1992 collections, with the exception of Fishgut 1 and Wonder 3 1991 samples. After removing unreadable samples, this gave a total of 1129 multiply aged brook trout, of which 680 were aged twice and 449 were aged three times. I excluded young-of-year from ageing error analysis.

After obtaining the model and parameters to best describe $Q(\Phi)$ for the multiply aged sample, I used the estimate of $Q(\Phi)$ to correct the age frequencies \mathbf{P}^* obtained by tabulating the singly-aged observed catch-at-age \mathbf{A}^* for each depletion. I tabulated \mathbf{P}^* and made estimates of $\hat{\mathbf{P}}$ by depletion rather than by removal period because period level data would give small samples, and was found uninformative about population size elsewhere in this thesis. For otoliths aged three times, I used the middle ageing when tabulating observed age frequencies \mathbf{P}^* ; for those aged twice I used the first ageing.

The likelihood for estimation of $\hat{\mathbf{P}}$ is expressed as:

$$L(\mathbf{A}^*|\mathbf{P}, \mathbf{Q}) = \prod_{i=1}^I \sum_{b=1}^A \left(p_b \prod_{j=1}^J q(a_{ij}|b, \Phi) \right) \quad (2.9)$$

Conceptually, the likelihood of the data given the model is the product of the likelihoods for individual fish. In turn, the likelihood for each fish is the sum, over all possible true ages admitted, of the probability of observing the ageings which occurred. That probability is the product of the probability of observing a fish of true age b , multiplied by the probabilities of observing the ageings a_1 to a_j given the true age b . Direct calculation of $\hat{\mathbf{P}} = \mathbf{Q}^{-1}\mathbf{P}^*$ was not expected to be reliable because some elements

of P^* were zero or near zero. Instead, use of the likelihood (2.9) and numerical methods was always necessary. Once \hat{P} had been obtained for a depletion, true catch at age was estimated as $\hat{N} = N\hat{P}$, where N is the total catch disregarding age 0's.

I programmed the inference functions in BASIC and minimized the fitting criteria with a direct search routine. I used the AMOEBA implementation (Spratt 1991) of the simplex method (Nelder and Mead 1956) from multiple starting points and driven by a restarting algorithm, to find the minimum. The simplex method is computationally expensive and known to have problems with local minima. However, proper tuning and a suitable restarting algorithm to drive the search seem to produce reliable minima.

For each depletion I calculated the total percentage of ages reassigned after error correction as

$$50 * \sum_{a=1}^A |\hat{P}_a - P_a^*| \quad (2.10)$$

Simulations

Performance of ageing error correction

Richards et al. exercised their models with age data from a walleye pollock population for which true ages were unknown. The performance of their models could be expected to depend on sample size, age-dependence of the error process and smoothness of the age distribution. I wanted to know how much error might typically remain after their correction processes have been applied to my data. The most effective way to approach such questions is with Monte Carlo methods (Hilborn and Walters 1991). I used simulation to generate data to explore the performance of their model under different conditions. I generated two population age distributions similar to those observed for Sierra brook trout populations. Such distributions are often highly "uneven", with apparent strong and weak year classes persisting across several years' catch data (Hall 1991). Distribution A was typical of age

distributions early in the study, when fish of age 5 and older were a dominant component of the catch. Distribution B was more typical of age distributions after several years of depletions, when the catch was dominated by fish age 4 and younger. I made 500 runs for each population age distribution. For each run, I created a stochastic catch with each individual having the same capture probability, effectively a multinomial sample with mean total catch of 625. I subjected the catches to stochastic ageing error, using the error probabilities estimated from brook trout multiple ageings. I then corrected each observed data set by minimizing the inference function for the likelihood (2.9). I calculated the mean and variance for the observed and corrected proportions-at-age. To quantify bias, for each age I calculated the deviation of the mean observed proportion at age and the mean corrected proportion-at-age, from the true proportion-at-age. I summed the absolute value of the deviations as an overall index of the mean bias of the observed and corrected proportions.

Ageing error and population estimation

In order to examine the impact on population estimation of uncorrected stochastic ageing error, and ageing error with error correction using Richards' methods, I used a 22 yr time series of age 1 recruitments and the catch equation:

$$N_{t+1} = (N_t - C_t) * S$$

to generate simulated population dynamics. I subjected the population to seven years' stochastic removals. Full recruitment was at age 2 with capture probability $q = .462$ and partial recruitment at age 1 with $q = .042$. Annual natural mortality was fixed at .3. I subjected each year's catch to stochastic ageing error using the probabilities estimated for this study. I estimated the corrected age proportions for each year's catch by maximizing the likelihood (2.9), and analyzed the uncorrected and corrected catch data for each run using the WC method to estimate recruitment for cohorts 8 to 20 only. I made two identical sets of 100 runs, except the second set used $q = 0$ in the fifth year to parallel the removals for this study.

RESULTS

Estimates of Q and \hat{P}

Of the five models I evaluated, the exponential model with $\alpha = 0$ and the full exponential model provided the best fit and were equally likely given the data from 1129 multiply-aged brook trout (Table 2.1). In such cases, the Akaike criterion selects the model with fewer parameters, hence the selection of the exponential model with $\alpha = 0$. Richards' et al. exponential distribution is more peaked than the normal density distribution (Richards et al. 1992). Selection of the exponential model implies lower sensitivity to outlier observations and generally less blurring of age distributions due to error.

Correspondingly, correction produces less adjustment of proportions.

Repeatability estimates range from nearly 100 % at age 1, to 58% at age 15 (Table 2.2). Repeatability increases at age 16 to 67% as an artifact of the estimation procedure which truncates the distributions at the highest observed age (Richards et al. 1992). This is a strongly diagonal matrix, relative to those which have been used in studies simulating the effect of ageing error on population estimation (e.g. Bradford 1991).

Table 2.1. Parameter estimates for Φ based on the normal and exponential models, applied to multiply-aged brook trout from 1991 and 1992 removals.

Model	$\hat{\sigma}_1$	$\hat{\sigma}_A$	$\hat{\alpha}$	$\hat{\beta}$	$l(\hat{\theta})$	AIC
Exponential	0.0000027	0.43664	-0.04983	1	2932.8	5196.8
Exponential	0.0000022	0.31957	-0.017009	0.84076	2917.9	5183.9
Exponential	0.0000074	0.29259	0	0.82779	2917.9	5181.9
Normal	0.2687200	1.16962	0	-	3115.3	5377.3
Normal	0.2964660	1.45443	-0.070961	-	3109.3	5373.3

Table 2.2. Ageing error classification matrix for 1129 multiply aged brook trout, estimated by procedures explained in the text. Each entry is the probability for that true age (column), of obtaining the observed age (row). Column totals may not sum to one, due to rounding.

	true age															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
observed age	1	.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2	.96	.04	.01	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	.02	.92	.05	.01	0	0	0	0	0	0	0	0	0	0
	4	0	0	.04	.88	.07	.01	0	0	0	0	0	0	0	0	0
	5	0	0	0	.05	.85	.08	.02	.01	0	0	0	0	0	0	0
	6	0	0	0	.01	.07	.81	.09	.02	0	0	0	0	0	0	0
	7	0	0	0	0	.01	.08	.77	.10	.03	.01	0	0	0	0	0
	8	0	0	0	0	0	.01	.09	.74	.11	.03	.01	0	0	0	0
	9	0	0	0	0	0	0	.02	.10	.71	.12	.04	.01	.01	0	0
	10	0	0	0	0	0	0	0	.02	.11	.68	.13	.04	.02	0.01	0
	11	0	0	0	0	0	0	0	.01	.03	.12	.64	.13	.04	.02	.01
	12	0	0	0	0	0	0	0	0	.01	.03	.13	.62	.14	.05	.02
	13	0	0	0	0	0	0	0	0	0	.01	.04	.13	.59	.15	.06
	14	0	0	0	0	0	0	0	0	0	0	.01	.04	.14	.58	.16
	15	0	0	0	0	0	0	0	0	0	0	0	.01	.04	.15	.58
	16	0	0	0	0	0	0	0	0	0	0	0	.02	.05	.16	.67

Table 2.3. Percent of ages reassigned due to ageing error correction for depletions from 1986 to 1992. Each year has two columns; column 'a' lists first depletions in a year, column 'b' second depletions.

	1986a	1986b	1987a	1987b	1988a	1988b	1989a	1991a	1991b	1992
Hell Diver 2	9.0	1.7	7.4	-	4.6	-	0.9	4.9	-	2.9
Dingleberry	-	-	3.0	-	2.7	4.0	1.4	3.1	2.7	1.5
Flower	-	-	2.5	-	2.5	-	1.7	3	-	2.8
Fishgut 1	-	-	4.1	-	3.4	-	2.9	2.5	-	2.2
Par Value	-	-	8.9	-	3.6	2.6	3.4	2.2	-	2.3
Wonder 3	-	-	4.4	5.3	3.5	-	2.2	2.4	-	2.1
Hell Diver 3	-	-	9.9	-	4.8	-	4.5	1.4	-	1.9

Estimates of corrected age proportions and standard errors for age 1+ to age 16+ catch aggregated by depletion are presented in Appendix A. Percent of ages reassigned due to ageing error correction range from 0.9 to 9.9% (Table 2.3). The percent of ages reassigned tends to decrease over the course of the

study (Table 2.3). Post-1988 age distributions tended to be dominated by fish of age 3+ and younger, and were generally more even distributions. Distributions which are already smooth are less prone to further smoothing by error, so estimated corrections for these distributions are correspondingly low. As well distributions dominated by young age groups will have experienced less smoothing since error is low for the youngest ages.

Simulations

Performance of ageing error correction: age distributions

Simulated catch-at-age data with stochastic ageing error of the form estimated for brook trout in this study, led to observed distributions which exhibit the smoothing typical of ageing error effects (Table 2.4). Age classes which are less abundant relative to their near neighbors tend to pick up more observations than they lose, while the opposite is true for the age classes which are more abundant than their near neighbors. The result was positive bias for relatively lower p^* 's and negative bias for relatively higher p^* 's (Table 2.4). Observed proportion bias was more severe for the more uneven distribution A than for the smooth distribution B. Correction relieved much of the smoothing for ages less than 10 and reduced the sum of absolute mean deviations in the proportions to 17% and 11% of observed mean deviations for A and B respectively (Table 2.4). Bias was still present in the corrected proportions for zero and near zero true proportions, but was generally quite reduced relative to uncorrected proportions (Table 2.4).

Variance was less for the corrected than the observed proportions at the lowest ages, but became higher as ageing error increased and proportions decreased with age (Table 2.4). The increase in variance was primarily due to the lower proportions and higher error rates with increased age, which for some runs produce false modes. The correction method cannot distinguish false modes. Such modes were subsequently exaggerated by the correction method, which resulted in increased variance.

Table 2.4. Simulation of ageing error correction. Values shown are means of 500 runs. For each run, a sample of 625 was drawn from a population with true proportion-at-age b p_b , and subjected to stochastic ageing error, using error probabilities estimated from brook trout samples. Estimates were made from each sample according to methods described in the text. Symbols are: \hat{p}_b estimated age b proportion; p_b^* observed age b proportion. Variances are indicated $V(\)$. Proportions are times 10^2 , variances are times 10^3 . Total = total of absolute deviations. Distribution A is representative of age distributions obtained by pre-1989 removals. Distribution B is typical of 1989 and later removals.

age	p_b	$p_b^* - p_b$	$\hat{p}_b - p_b$	$V(p_b)$	$V(p_b^*)$	$V(\hat{p}_b)$
Distribution A						
1	12.8	0.14	-0.04	0.179	0.208	0.191
2	14.4	-0.21	0.01	0.197	0.209	0.189
3	5.6	-0.05	-0.01	0.085	0.088	0.096
4	0.8	0.34	-0.04	0.013	0.014	0.017
5	2.4	0.87	-0.04	0.037	0.045	0.055
6	19.2	-2.09	-0.05	0.248	0.294	0.316
7	1.6	1.98	0.03	0.025	0.050	0.073
8	12.8	-1.14	-0.08	0.179	0.163	0.226
9	7.2	1.32	0.29	0.107	0.114	0.191
10	17.6	-2.92	-0.15	0.232	0.246	0.402
11	4.8	0.50	-0.14	0.073	0.085	0.150
12	0.0	0.96	0.23	0.000	0.014	0.012
13	0.8	0.01	-0.13	0.013	0.011	0.019
14	0.0	0.15	0.06	0.000	0.002	0.001
15	0.0	0.05	0.03	0.000	0.001	0.000
16	0.0	0.02	0.02	0.000	0.000	0.000
Total		12.75	1.35			
Distribution B						
1	11.04	0.41	0.08	0.157	0.161	0.155
2	22.40	0.39	-0.03	0.278	0.409	0.343
3	42.24	-1.48	0.08	0.390	0.732	0.478
4	13.44	0.07	-0.09	0.186	0.211	0.205
5	4.80	0.11	0.01	0.073	0.074	0.091
6	0.80	0.36	0.01	0.013	0.017	0.022
7	2.72	-0.29	-0.04	0.042	0.033	0.048
8	1.12	0.00	-0.02	0.018	0.017	0.025
9	0.32	0.06	-0.02	0.005	0.005	0.007
10	0.00	0.08	0.06	0.000	0.001	0.001
11	0.16	0.02	-0.01	0.003	0.002	0.003
12	0.48	-0.09	-0.04	0.008	0.006	0.010
13	0.32	-0.03	-0.03	0.005	0.004	0.006
14	0.16	-0.01	-0.02	0.003	0.002	0.003
15	0.00	0.04	0.03	0.000	0.001	0.001
16	0.00	0.01	0.01	0.000	0.000	0.000
Total		3.45	.58			

Table 2.5. Results for 2 sets of 100 simulations of catch, ageing error and correction, and population estimation using the WC estimator after seven years of sampling. Population simulation, ageing error correction and estimation methods are described in the text. The two sets used identical methods except that set 1 used no sampling effort in year 5, while set 2 used equal effort in all seven years.

seven years

Cohort	Age, yr	7	N	set 1				set 2							
				\hat{N}	$SE(\hat{N})$	bias	\hat{N}^*	$SE(\hat{N}^*)$	bias	\hat{N}^*	$SE(\hat{N}^*)$	bias			
1	14		75	80	41.2	6.7	139	34.5	85.3	80	45.5	6.7	139	38.4	85.3
2	13		500	492	56.2	-1.6	449	46.3	-10.2	495	56.4	-1.0	450	47.6	-10.0
3	12		150	146	32.0	-2.7	214	27.0	42.7	154	38.0	2.7	220	32.3	46.7
4	11		900	904	48.1	0.4	832	42.9	-7.6	894	51.0	-0.7	819	45.4	-9.0
5	10		350	352	24.5	0.6	359	22.4	2.6	348	25.1	-0.6	353	22.8	0.9
6	9		75	75	8.8	0.0	94	8.4	25.3	75	10.4	0.0	93	9.7	24.0
7	8		450	449	19.5	-0.2	445	19.0	-1.1	450	27.6	0.0	444	26.8	-1.3
8	7		750	751	22.0	0.1	736	20.7	-1.9	748	22.8	-0.3	730	21.8	-2.7
9	6		50	51	7.7	2.0	65	7.5	30.0	50	6.6	0.0	64	6.7	28.0
10	5		400	398	21.3	-0.5	397	20.8	-0.8	395	21.9	-1.3	393	21.4	-1.8
11	4		1000	999	42.5	-0.1	959	39.7	-4.1	996	44.2	-0.4	971	42.1	-2.9
12	3		200	201	15.6	0.5	217	15.4	8.5	201	16.2	0.5	214	16.1	7.0
13	2		750	746	40.0	-0.5	734	39.1	-2.1	746	43.4	-0.5	729	42.1	-2.8

Ageing error and population estimation

Again, the uncorrected population estimates showed the expected pattern of smoothing of year class strength, while the corrected estimates had much lower bias (Table 2.5). Bias ranged from -2.7 to 6.7 % for corrected data, while its range was -10.2 to 85.3% for uncorrected observed estimates. Bias was highest for small cohorts. There was a variance increase due to correction, however. Estimated SE's are 1-20% higher for the estimates made from corrected data than from observed uncorrected data, with the greater increase in SE's occurring for older cohorts again due to occasional false modes.

DISCUSSION

Comparable estimates of ageing error matrices are virtually absent from the literature. Aside from Richards et al. exercising their methods on a small sample of multiply-aged pollock, not a single application of their models has been reported in the literature. Occasionally authors report on repeatability but rarely give results with enough detail to assess the age-dependence of error. For instance, Kristofferson and Klemmetson (1991) studied age determination methods for arctic charr (*S. alpinus*) but with regard to repeatability they reported only that "within-method agreement was *reasonably good*", showing "agreement *within +/-1 year* for 84.1 % of the otoliths" (my italics). Simulation studies (Fournier and Archibald 1982; Rivard 1989; Bradford 1991) have generally used error matrices reflecting the authors' subjective notions about error rates and their dependence on age. The effect ("seriousness") of error and its correctibility can only be judged in the context of the analysis for which the ageing data is intended. In this chapter, I did not simulate fitting of stock - recruitment relationships or recruitment - environmental variable correlations. However, my analysis of multiply aged samples has given me an objective basis for making such simulations with both uncorrected and corrected catch at age data.

My simulations have assumed that the parameters comprising Φ are estimated without error. I did not make formal simulations of the likely error in estimation of Φ and its dependence on sample size, nor the

likely error in $\hat{\mathbf{P}}$ which results. I have implicitly assumed that the multiply aged sample was large enough to estimate Φ with negligible error. By doing so, I have underestimated the variance of proportion and population estimates by an unknown amount. Trial simulations showed that estimates of the vector $\hat{\mathbf{B}}$ were quite insensitive to the values of the parameters in Φ ; however, $\hat{\mathbf{P}}$ is probably more sensitive.

Some lake populations tend to produce otoliths with very clear increments, while others are much less apparent as increments. One way to examine whether this apparent difference in the ease of ageing otoliths for different populations impacts the ageing error process, would be to examine the estimates and variances of the parameters in Φ describing \mathbf{Q} , the classification matrix, for each lake's reageing data treated separately. Independent analysis of each lake's data might seem an attractive approach. Large sample sizes for individual lakes would likely be necessary to give sufficient statistical power to detect differences in the ageing-error process between lakes. Again, simulation of the error in estimation of Φ could suggest sample size needed for such an analysis.

The ageing procedures used for this study were constrained for time and financial efficiency and were not optimal for ageing error analysis and correction. The proper design for ensuring a relatively consistent error rate would be randomly mixed otoliths from different lakes and years with blind labelling. As well, the multiple observations should be obtained by blind mixing of repeat samples with the singly-aged samples, so that extra care is not given to multiply-aged samples. Neither of these procedures was followed in this study. Multiply-aged samples were blind but were handled as a distinct batch. Batch processing of multiply-aged otoliths probably led to lower estimated error rates since the time spent per otolith was higher for these samples. As well, for singly-aged samples we aged otoliths from each lake for each year as a batch. This was done in order to speed processing, reduce tedium, and allow immediate preparation of the second otolith from a pair when the first was unreadable. Batch handling of singly-aged samples may tend to reduce error rates below those estimated by blind multiple ageings, and might even exaggerate differences in year class strength. For instance, an otolith reader who sees many samples of age 6 may begin to read samples that are age 5 or 7, as age 6 also. It would be possible to analyze the study

age distributions to determine whether they are consistently less smooth than would be predicted, based on estimated error rates from this study. I did not attempt such an analysis.

In addition, reader effects may occur where ageings are conducted by multiple readers (Richards et al. 1992). For this study, all ages for the 1986 -1989 depletions were read by one reader, while those from 1991 and 1992 were read by a second. Richards et. al. (1992) develop models for analysis of reader effects. I did not have multiple ageings from the first reader. Consequently I did not analyze the data for such effects.

Chapter 3. Depletion estimation at period-level resolution

INTRODUCTION

Removals from the study lakes were made each year as depletion series of 3 to 11 consecutive half-day periods' duration. The removal method of population estimation rests on the assumption that an observable index of abundance declines in direct proportion to the decline in numbers, as members of the population are removed. To estimate population size, the study removal data could be used at either of two levels of time resolution. If the decline in catch per effort across capture periods during single depletions is informative with respect to population size using a simple Leslie (1939) removal estimator, then an extended model which links removal estimates across years and cohorts could estimate abundance with low variance by simultaneously using all the information present in all the series. However, if the removal series within each year do not provide reliable information about population size because of bias or high variance, use of the data at period level resolution will only degrade population and recruitment time series estimates. The alternative in this event is to use the data across years and cohorts at depletion level resolution, so that each removal series is compressed into a single relative abundance and catch data point. This chapter examines whether the removal data are informative at period level resolution.

In order to extract detailed information with regard to patterns in recruitment and catchability over time, I use age structured methods. Walters and Collie (1989) provide a multi-year multi-cohort depletion estimator for commercial catch at age and survey data. This model is statistically less efficient than catch-at-age methods introduced by Fournier, Deriso, Schnute and others in the 1980's (Walters and Collie 1989). However, it has a number of desirable properties, including:

- (1) ease of solution, by simple linear regression
- (2) does not require assumptions about a recruitment relationship with stock or time
- (3) occurrence of zero catch for some cohorts at some times is not problematic, as for log-likelihood based methods.

The estimator is easily adapted to simultaneously use all removal data for a closed population composed of cohorts which are subject to multi-period removals within each of several years. Essentially, the assumptions are negligible natural mortality during the removal period, population closed to migration, and constant and homogeneous catchability. Survival is assumed known as with virtual population analysis (Walters and Collie 1989). If the assumptions are met this model can link the cohort-specific removal data across years and cohorts to estimate recruitment and abundance with low variance for each recruited cohort present in the catch.

Many studies have found that removal data give estimates which are biased low (Bohlin and Sundstrom 1977; Cowx 1983; Peterson and Cederholm 1984; Kelso and Shuter 1989; Hall 1991; Hilborn and Walters 1992). Because the Walters-Collie (WC) model is essentially a statistical linkage of year and cohort specific Leslie estimates, bias in the Leslie estimates implies bias and inflated variance of the WC parameter estimates. Hall (1991) used Schnute's (1983) maximum likelihood removal estimator for 1989 data aggregated by age and concluded that for some lakes the initial capture period had higher catchability than the rest of the series. Distinct first period catchability has been used to model concavity of the cpe - cumulative removal relationship which would lead to biased low estimates if not corrected (Schnute 1983; Hilborn and Walters 1992).

In this chapter my primary objective is to establish whether the available estimators, and depletion data at period level resolution, can be used to obtain unbiased estimates of population size. I first use Schnute removal models to examine the series for evidence of diel variation in catchability and higher first period catchability. I show the potential bias of the Schnute estimates by comparison with minimum known alive population estimates. Similarly, I demonstrate the bias of the WC estimates by comparing the catchability to single-year single-cohort Leslie catchabilities. I examine the performance of age-aggregated estimates. Finally, I use patterns in catchability as evidence about brook trout behavior in the study lakes.

METHODS

Following a summary of field methods, data treatment, and terminology, in this section I present my approach to population and catchability estimation using the removal method. I use two estimators : Schnute's (1983) maximum likelihood estimator, and the Walters-Collie (1989) method, which is an extension of Leslie's (1934) regression technique. For each, I explain my use of the estimator to evaluate for distinct initial point catchability, and for estimate bias. Last, I detail my use of Schnute estimates to assess the size dependence of catchability and the performance of age-aggregated estimates.

Field methods

To ensure consistency of the data, I followed Hall's (1991) methods to the extent possible. I fished the same Lundgrens (Sweden) light green, nylon, weighted gillnets of length 36 m, height 1.5 m, on bottom. The nets were composed of twelve randomly ordered panels of bar mesh size 4, 6.25, 8, 10, 12.5, 16.5, 18.5, 22, 25, 30, 33 and 38 mm, and were randomly chosen from a pool of ten such nets. Nets were anchored at and set perpendicular to shore, but we also made sets offshore oriented at random or downwind. The removals began in 1987 with the exception of Hell Diver #2 which began in 1986. At least one depletion was made per lake each year through 1992, with no removals in 1990. Each depletion was structured as a continuous series of three to eleven removal periods over a 1.5 to 5.5 day period. The 1986 through 1988 data display greater variability in effort from period to period; effort often increased during a depletion. By 1989 and later we fished a fixed number of nets (4 to 6, depending on the size of the lake) throughout a particular depletion and maintained consistent set and haul times from day to day through the depletion. In 1989 the day sets and night sets were each 12 hours, while in 1991 and 1992 night periods were longer than day periods.

Treatment of the data

I used one net fished for one hour as the standard unit of effort, and pooled data from all nets fished during a removal period to provide a single estimate of catch-per-unit-effort (cpe). Some of the 1987 and 1988 removals had two short consecutive removal periods during the day, which I combined into one full day period. Occasionally, logistics made the final set of a depletion longer than 20 hours. I have treated these catches as removals but not as relative abundance data. In some years we made two depletions in some lakes. I have used the first depletion as relative abundance data and the second as removals only. An exception is the double removal for Dingleberry in 1991; the original removal was terminated with a series of 4 periods. I used the second series of 9 periods commencing 10 days later to make population estimates.

For a few removal periods during 1989, some or all fish were not sampled for age. For these periods, I have estimated catch-at-age based on the age proportions in the sampled catch for the period. If no fish were sampled for age during a period, I estimated the age proportions as the average proportions of the sampled catch of the previous and subsequent period.

Fish were occasionally removed by other capture methods. The Leslie method allows the removal process and the estimation of relative abundance to occur independently (Hilborn and Walters 1992). I accurately accounted for all such removals in the estimation procedure. For these analyses I have considered age 2+ and older fish to be fully recruited to the gear (Hall 1991), except for Hell Diver #2 where full recruitment to the gear has been at age 3+. Prerecruit cohorts are age 1+ in all lakes except Hell Diver #2, where prerecruit cohorts are 2+, and 1+ in 1989.

Population and catchability estimation

Terminology and assumptions

When I use the terms "depletion series" and "removal series" I refer to data for a single cohort from a single multi-period depletion unless stated otherwise. I also evaluate estimates which group all recruited cohorts and refer to these as age aggregated. The WC method estimates a global catchability across cohorts and years. I refer to Leslie removal estimates made for single cohorts in single depletion experiments as local estimates. The methods assume independence of catches between recruited cohorts which is not strictly true due to ageing error. The low error rates demonstrated elsewhere in this thesis render this point minor. I evaluate models for removal estimates with multiple catchabilities. The motive is detection and elimination of initial points of high catchability. I refer to the estimated catchability, after initial distinct points have been separated, as the terminal catchability. In cases where diel variation in catchability is indicated, there are both day and night terminal catchabilities.

Estimation

I required methods for two tasks for this chapter: to evaluate removal series for evidence of higher initial period catchability, and to evaluate potential bias of estimates of population abundance. The most developed single-series removal estimator is Schnute's (1983) maximum likelihood method. It allows time variation in catchability but requires constant effort, a criteria not met by 1986-88 removals for this study. As well it would necessitate a new procedure for simultaneously analyzing multiple series across years and cohorts. However, Schnute's method offers a statistically rigorous way of evaluating and fitting series with multiple catchabilities, so I use his method for the first task.

The central problem in evaluating the bias of the removal estimates is that population size is unknown. Additional information about population size is present in depletions from subsequent years, for cohorts which appear in several years' catch. I use two distinct approaches to evaluation of potential bias of depletion estimates. First, I use the Schnute estimates of population size which were made to evaluate for distinct initial q . Minimal information about the likely population size during a depletion

can be obtained by summing the catch for the cohort for the years including and subsequent to the depletion series. For a closed population, this minimum known alive (MKA) estimate provides a low bound for population size during a depletion (Kelso and Shuter 1989). Such an estimate is itself biased since it neglects natural mortality subsequent to the depletion and fish still alive after the final year's catch. For this reason Schnute estimates which do not exceed MKA estimates can be considered to display severe bias.

Second, I use Leslie estimates and the WC method. The WC fitting integrates information about population size across years within a cohort, and about q across cohorts. Essentially the method reconciles information about population size from the decline in cpe during the depletion series, with information about population size from subsequent years depletion series, weighted by natural mortality. In order for the WC estimates to be unbiased, the individual depletions must provide unbiased information about population size. The global \hat{q} from the WC fitting should be similar, on average, to the individual Leslie \hat{q} 's. If the WC global \hat{q} differs systematically from the local \hat{q} 's then the information about population size within the series is not in agreement with survival-weighted information about population size from earlier and later years' catch.

Schnute removal estimates

Models

Hall (1991) used three types of Schnute estimates: a single catchability model, and models with one and two initial distinct catchabilities. However, most of the study removal series display strong diel variation in cpe. Most depletion experiments for the study, and all depletions from 1989 to 1992, began with a night removal period. The analysis should account for diel catchability variation before evaluating for distinct initial period catchability. Schnute (1983) alluded to a model with distinct capture probabilities for alternating gear types. I developed a simple night-day model and a night-day model with distinct first period catchability, based on Schnute's (1983) methods for developing multiple catchability removal models. As well, I programmed the three models used by Hall (1991). I used

Schnute's (1983) approximate statistical criterion for model selection among the five choices which are listed in Table 3.2. The criterion requires that the negative log-likelihood be improved by at least 1.92 units, ($.5 * \chi^2$ with 1 *df*; $\alpha = .05$) before rejecting a model for one with an additional parameter. At each step, I evaluated the class of models with an additional q according to the criterion. Once the appropriate number of q 's was determined I selected the best-fitting model for that class to provide the estimate of N and q 's.

Table 3.1. Notation.

Symbol	Meaning
$y_{i,j}$	Catch per unit effort for a cohort in the j^{th} removal period of the i^{th} year's depletion
$K_{i,j}$	Removals during all periods before the j^{th} removal period of the i^{th} year's depletion
$C_{i,j}$	Catch during the j^{th} removal period of the i^{th} year's depletion
N_0	Number of fish which were present before any experimental removals occurred
S_i	Natural survival rate from year i to year $i + 1$, assumed independent of i
q	Catchability, or proportion of the population removed by one unit of effort
n_i	Number of removal periods in year i
T_i	Sum of all removals in year i

Table 3.2. Five Schnute removal models which were fit to depletion series.

Model	Symbol	Catchabilities
Single q	i1	1
Single terminal q with one distinct initial q	i2	2
Single terminal q with two distinct initial q 's	i3	3
Independent day q and night q	dn	2
Independent day q and night q with one initial q	dn3	3

Initial point catchability

I made Schnute population estimates for depletion series with catch ≥ 20 , from 1989, 1991 and 1992. If the best-fit model was not one with an distinct initial q , I estimated catchability for the first period as:

$$\hat{q}_1 = C_1 / \hat{N} \quad (3.1)$$

Some series had no catch for one or two periods. Since the estimates use log-likelihood, values of zero catch are inadmissible. I used 0.001 instead of zero for these estimates. Simulations showed that the estimate was insensitive to the size of the surrogate value, near zero.

Estimate bias

To evaluate potential bias of Schnute estimates, I included estimates for which there was at least one subsequent year's catch, so that comparable MKA estimates would include at least two years' data. Schnute's method offers no clear criterion for eliminating poorly determined estimates. For this analysis I arbitrarily chose to discard, as poorly determined, estimates for which the ratio of the value of the upper confidence limit to the value of the estimate was greater than five, based on the distribution of values of this ratio. This ratio was always less than 5 or greater than 100.

Walters-Collie depletion estimator

The Walters-Collie age-structured depletion model requires an independent estimate of natural mortality along with data from at least two years' removals. The dependence of natural mortality on age can assume any form. The method assumes a single time- and age-invariant q and estimates the number of fish in each cohort at the time the cohort recruited to the fishery, along with the global q (Walters and Collie 1989). The estimator is derived as follows (symbols defined in Table 3.1):

$$y_{1,1} = q(N_0 - K_{1,1}) = qN_0 - qK_{1,1} \quad (3.2)$$

$$y_{1,2} = q(N_0 - K_{1,2}) = qN_0 - qK_{1,2} \quad (3.3)$$

and generally for the first year:

$$y_{1,n} = qN_0 - qK_{1,n} \quad (3.4).$$

Then for the second year:

$$y_{2,1} = q(S_1(N_0 - T_1) - K_{2,1}) = qN_0S_1 - q(T_1S_1 - K_{2,1}) \quad (3.5)$$

$$y_{2,2} = q(S_1(N_0 - T_1) - K_{2,2}) = qN_0S_1 - q(T_1S_1 - K_{2,2}) \quad (3.6)$$

and generally for all following years and periods:

$$y_{m,n} = qN_0 \left(\prod_{a=1}^{m-1} S_a \right) - q \left(K_{m,n} + \sum_{b=1}^{m-1} T_b \left(\prod_{c=1}^{b-1} S_c \right) \right) \quad (3.7).$$

The estimates of qN_0 and q are made by least-squares linear regression as for the classic Leslie (1939) method. The quantities within square brackets are the x_i 's in the multiple regression. I used the "corrected" cumulative removals (K), which includes the cumulative removals made before a removal period plus half the catch taken during the period (Braaten 1969; Ricker 1975). Confidence intervals for the recruitment parameters can be estimated as for standard least-squares multiple regression. I fit the estimator using the first depletion in each year, treating any subsequent depletions as removals but not catch. Negligible natural mortality was assumed in the elapsed time between multiple depletions in the same year. To demonstrate the influence of the initial removal periods I also fit the model with the first two relative abundance points omitted. This parallels Cross and Scott's (1975) ad hoc modification of the Leslie estimator to allow initial distinct \hat{q} 's. I omitted two initial points (both a night and a day point) to allow for diel differences in q .

Survival

WC estimate bias can also be created by incorrect survival parameterization. For this analysis, I used age-invariant annual survival $s=.85$. This is likely at the high end of the range of possible survival values for Sierra brook trout (Hall 1991; Reimers 1979). Use of the highest potential survival reflects my expectation that Leslie estimates and WC estimates are biased low (Hall 1991). If Leslie \hat{q} 's are systematically greater than WC global \hat{q} 's using the highest potential survival, then both estimates are definitively biased low.

Leslie estimates

I made Leslie estimates of q for all series with catch ≥ 20 from 1986 to 1992, to compare to the global \hat{q} for each lake from the WC fittings. The Leslie method uses the regression of cpe on corrected cumulative removals. The estimate generally displays only slight bias due to its errors-in-covariates structure, although the variance may be considerably underestimated (Crittenden and Thomas 1989). I compared the global \hat{q} from the WC model with 0 and 2 initial points omitted to the local Leslie \hat{q} 's made with 0 and 2 initial points omitted. When two points were omitted, I compared only series from Dingleberry, Flower, Fishgut 1, Par Value and Wonder 3 lakes since series for the Hell Diver lakes were usually less than 5 periods.

Catchability variation

To examine how q varied among cohorts and between years, I included recruited and prerecruit cohorts and used \hat{q} from the best-fit Schnute model for each cohort. I used the terminal \hat{q} for series without significant diel variation, and the terminal night \hat{q} for those with diel variation, as the most representative \hat{q} for each series.

In order to examine how diel variation in q varied among cohorts, I included recruited and prerecruit removal series which used both day and night sets, for which catch in every period was greater than zero and total catch greater than forty. I used only series from Dingleberry, Flower, Fishgut 1, Par

Value and Wonder 3 lakes, since series for the Hell Diver Lakes were generally short (5 periods or less) and thus with poorly determined night-day q differences. I calculated the ratio $q_{\text{night}}:q_{\text{day}}$. To correct for differences in effort, I divided by the ratio of mean night period duration to mean day period duration.

Age-aggregated removal estimates

I also evaluated the potential bias of age-aggregated removal estimates. I used Schnute's method for the fully recruited age-aggregated 1989 and 1991 data. I used the models and selection criteria already described and compared the estimates to age-aggregated MKA estimates.

RESULTS

Schnute estimates

Day and night catchability

Fifty-four of 60 depletions of fully recruited cohorts for 1989 to 1992 used both day and night removal periods. Use of distinct day and night q 's provided a significant improvement in fit for 45 of the 54 series (83%) (Table 3.3). For those day-night series with catch in every removal period, 35 of 38 (92%) were best fit by a model with distinct day and night catchabilities.

First period catchabilities

Twelve of the 60 series were best fit by the single catchability model and 39 by the simple day-night catchability model (Table 3.3). Nine of 60 (15%) were best fit by models with a distinct initial catchability. Of these nine, five showed higher first period catchability while four showed lower first period catchability. Estimated first period catchability was higher than the corresponding night or terminal catchability for 32 of 60 series (53%) and lower for 28 of 30 (Figure 3.1). This is not significantly different from the expected occurrence of 30 of 60 higher first point catchabilities, if first point catchability is a random variable with mean equal to the comparable terminal q ($p = .69$,

Table 3.3. Schnute estimates of population size for cohorts with catch ≥ 20 from 1989, 1991 and 1992. YC = year class, Model = model selected, F = Schnute fitting criterion, \hat{N} = population estimate, LCI / UCI = lower / upper 95% confidence intervals, MKA = minimum known alive estimate, \hat{q} 's = estimated catchabilities. Model abbreviations are: i = single q; i2 = distinct first period q; i3 = two distinct initial q's; dn = day and night q's; idn = day and night q's with distinct initial period q. Estimation methods are explained in the text. Asterisk indicates that one period had catch of zero. Order of estimated q's: initial period q's if any, followed by single terminal q or terminal night and day q's.

Lake	Year	YC	Model	F	\hat{N}	LCI	UCI	MKA	\hat{q} 's
Hell Diver #2	89	86	dn	2.20	52	51	55	63.2	0.6923 0.3500
Hell Diver #2	91	88	i2	4.87	4097	180.4	1173497	195	0.0156 0.0043
Hell Diver #2	92	88	dn	2.48	65	60.7	76.7	61.3	0.5305 0.2126
Hell Diver #2	92	89	dn	2.76	129	110.2	186.2	102	0.3659 0.0843
Dingleberry	89	82	idn*	0.89	21	20.1	23.1	24.3	0.1611 0.6109 0.2712
Dingleberry	89	84	i*	4.32	32	30.5	33.5	30.1	0.4631
Dingleberry	89	85	dn	6.35	88	82.7	98.7	87.6	0.3302 0.1849
Dingleberry	89	86	dn	8.77	142	119.5	208.5	128	0.1784 0.1058
Dingleberry	89	87	dn	7.63	100	83.5	155.5	101	0.1873 0.1127
Dingleberry	91	88	idn	4.83	616	351.4	835000	623	0.1136 0.0559 0.0356
Dingleberry	91	89	dn	6.27	622	539.6	778.6	903	0.1510 0.0747
Dingleberry	92	88	dn	2.70	86	78.4	105.4	78	0.3632 0.1469
Dingleberry	92	89	dn	5.54	222	196.3	277.3	177	0.2575 0.1221
Dingleberry	92	90	dn	6.60	203	179.3	255.3	163	0.2661 0.1161
Flower	89	82	i	1.94	40	32.4	104.4	44.2	0.2800
Flower	89	83	i	1.82	29	25.2	56.2	35.1	0.3423
Flower	89	84	i	2.42	53	45.3	86.3	66.4	0.3112
Flower	89	85	i	2.90	61	51.6	93.6	79.1	0.3092
Flower	89	86	i	2.37	92	78.8	130.8	122	0.2936
Flower	89	87	i	5.30	394	333	533	372	0.2047
Flower	91	86	i*	4.34	26	25.3	32.3	41.1	0.3176
Flower	91	87	dn*	11.35	75	66.6	96.6	101	0.2652 0.1336
Flower	91	88	dn	6.78	578	534.2	647.2	669	0.2134 0.1012
Flower	91	89	idn	5.16	524	456.6	679.6	613	0.2120 0.1579 0.0987
Flower	92	87	dn*	4.15	38	35	52.8	35	0.3696 0.1848
Flower	92	88	dn	7.28	261	226	340	198	0.2405 0.0905
Flower	92	89	dn	5.39	362	283.8	615.8	218	0.1713 0.0527
Flower	92	90	dn*	5.12	92	70.6	227.6	65	0.2455 0.0317

Table 3.3 concluded.

Lake	Year	YC	Model	F	N	LCI	UCI	MKA	\hat{q} 's
Fishgut #1	89	82	i	7.11	331	23.1	1807000	37.1	0.0124
Fishgut #1	89	84	dn	2.87	49	45.3	62.3	67.3	0.5081
Fishgut #1	89	85	dn*	2.78	33	32.1	38.1	53.2	0.6456
Fishgut #1	89	87	dn	3.60	89	81.7	105.7	106	0.4604
Fishgut #1	91	88	dn	4.08	121	108.6	147.6	147	0.3172
Fishgut #1	91	89	dn	6.84	202	182.4	242.4	258	0.2674
Fishgut #1	92	88	dn	2.86	58	43.9	341.9	42.2	0.2876
Fishgut #1	92	89	idn	2.62	112	93.1	211.1	88.5	0.1785
Fishgut #1	92	90	i	5.63	67	61.3	84	61.3	0.3225
Par Value	89	77	dn*	6.56	35	29.2	92.2	36.9	0.1931
Par Value	89	81	dn*	5.67	38	29.5	134.5	39	0.1926
Par Value	89	86	i3*	5.25	32	30.4	49.4	45	0.3396
Par Value	89	87	idn	9.94	457	387.2	648.2	445	0.1947
Par Value	91	87	dn	9.73	115	94.4	194.4	122	0.1762
Par Value	91	88	dn	6.09	359	328.8	409.8	401	0.2469
Par Value	91	89	dn	5.48	267	225.1	372.1	262	0.1777
Par Value	92	87	dn*	6.00	61	42.3	100060	36	0.1926
Par Value	92	88	dn	3.46	224	135.9	255025	104	0.1302
Par Value	92	89	dn	5.11	104	79.7	253.7	72	0.2325
Par Value	92	90	dn	4.76	360	286.7	581.7	223	0.1849
Wonder #3	89	81	i*	8.26	41	26.2	356000	35.1	0.1030
Wonder #3	89	85	i3*	3.02	28	27.3	36.3	50.1	0.3538
Wonder #3	89	87	i*	4.44	60	57.8	66.8	102	0.3030
Wonder #3	91	87	dn*	7.24	59	30.7	808000	44	0.0915
Wonder #3	91	88	dn	6.01	168	154	197	218	0.2560
Wonder #3	91	89	dn	7.15	299	267.3	360.3	341	0.2126
Wonder #3	92	88	dn	3.69	107	77.7	497.7	72.2	0.2236
Wonder #3	92	89	idn	4.37	119	106.4	161.4	104	0.2597
Wonder #3	92	90	dn	2.92	106	94.5	133.5	92.3	0.3731
Hell Diver #3	89	87	dn*	0.41	22	21	26	33.3	0.8800
Hell Diver #3	91	89	dn	5.60	60	50.9	99.9	59.4	0.2903
Hell Diver #3	92	90	dn*	1.61	23	22	34.5	22	0.7118
									0.2471

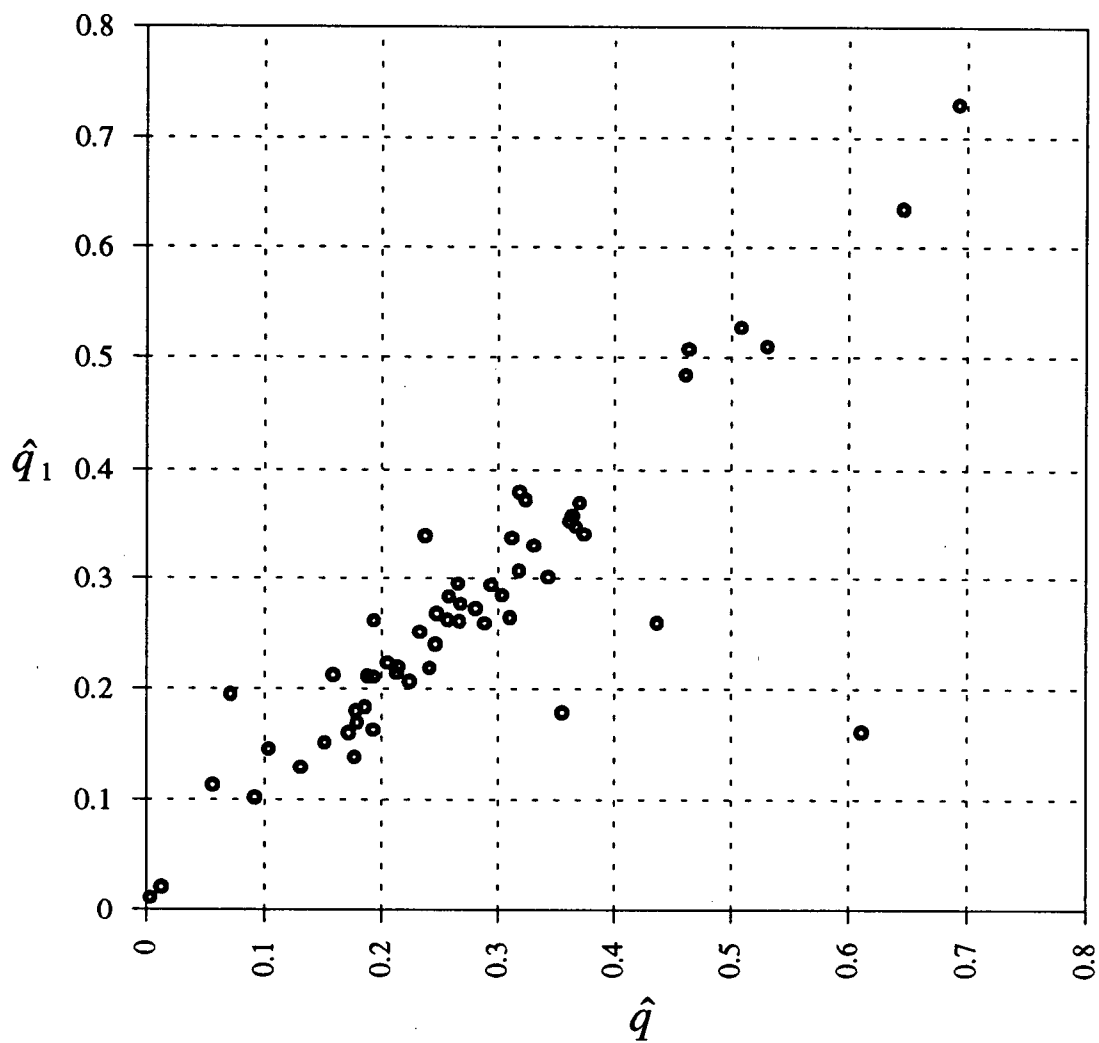


Figure 3.1. Terminal \hat{q} versus initial period \hat{q}_1 for 60 cohort-specific Schnute estimates from 1989 to 1992. Estimates are for fully-recruited cohorts with total catch >19. Estimation methods are described in the text. Initial period \hat{q} 's do not differ systematically from \hat{q} 's for the remainder of the series.

binomial test). The estimates do not support the hypothesis that first period catchability is generally higher than comparable catchabilities later in the series, for data from 1989 through 1992.

Schnute estimate bias

Five of 40 estimates for recruited cohorts from 1989 and 1991 were eliminated as poorly determined. Of the remaining 35 estimates, only seven were equal to or greater than the corresponding MKA estimate, and only one exceeded the MKA estimate by more than 10% (Figure 3.2). Schnute estimates were on average 84% of corresponding MKA estimates. Of 14 prerecruit series from 1989 and 1991, eight estimates were poorly determined. Of the remaining 6, the MKA estimate exceeded the Schnute estimate in all cases; on average the Schnute estimates were 70% of the corresponding MKA estimate (Fig 3.2).

Walters-Collie estimates

Walters-Collie and Leslie estimate bias

If the Leslie and WC estimates are unbiased, then the Leslie \hat{q} 's should be distributed approximately evenly about the WC global \hat{q} . Of 120 Leslie estimates, 108 (90%) showed \hat{q} greater than the comparable WC global \hat{q} (Figure 3.3a). Similarly, 87 of 99 (88%) of Leslie \hat{q} 's made with the first two points omitted, were greater than the comparable WC global \hat{q} with two points omitted (Figure 3.3b).

Catchability variation

Catchability related to size

For most lakes in most years, \hat{q} is higher for recruited fish than for pre-recruits (Figure 3.4). There appears to be a general pattern of positive correlation between \hat{q} and size, although this may be blurred by inter-year variation in \hat{q} (Figure 3.4).

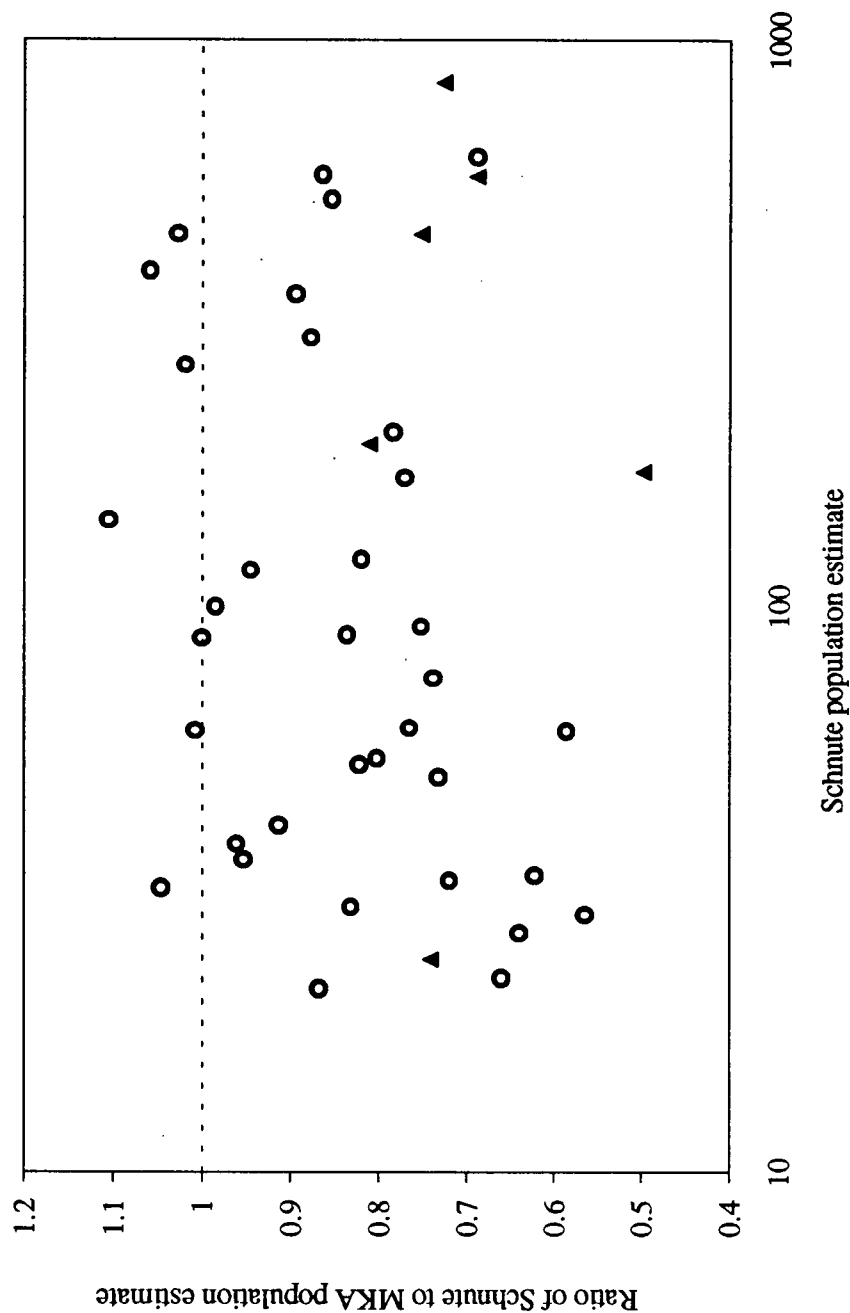


Figure 3.2. Ratio of Schnute estimate to MKA estimate plotted versus Schnute estimate. Open circles represent recruited cohorts while darkened triangles are prerecruit cohorts. Estimation methods are explained in the text. Data are from 1989 and 1991 depletions. Schnute estimates are generally less than the corresponding MKA estimate, hence the ratio of the estimates is less than one.

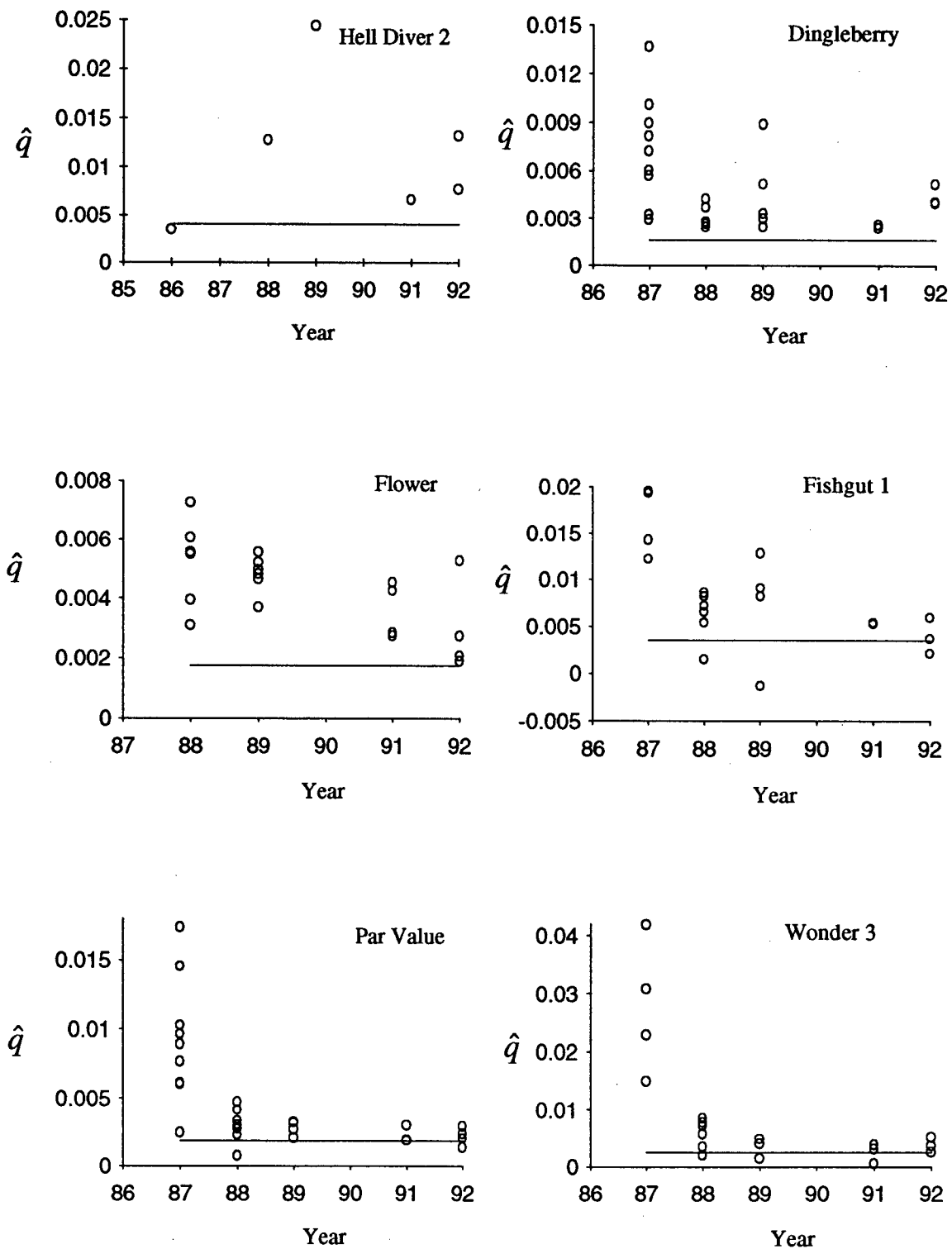


Figure 3.3a. Leslie estimates of q for recruited cohorts with catch > 19, plotted by year for six study lakes. The solid line shows the WC estimate of q , using survival = .85. No initial points were eliminated from the fittings.

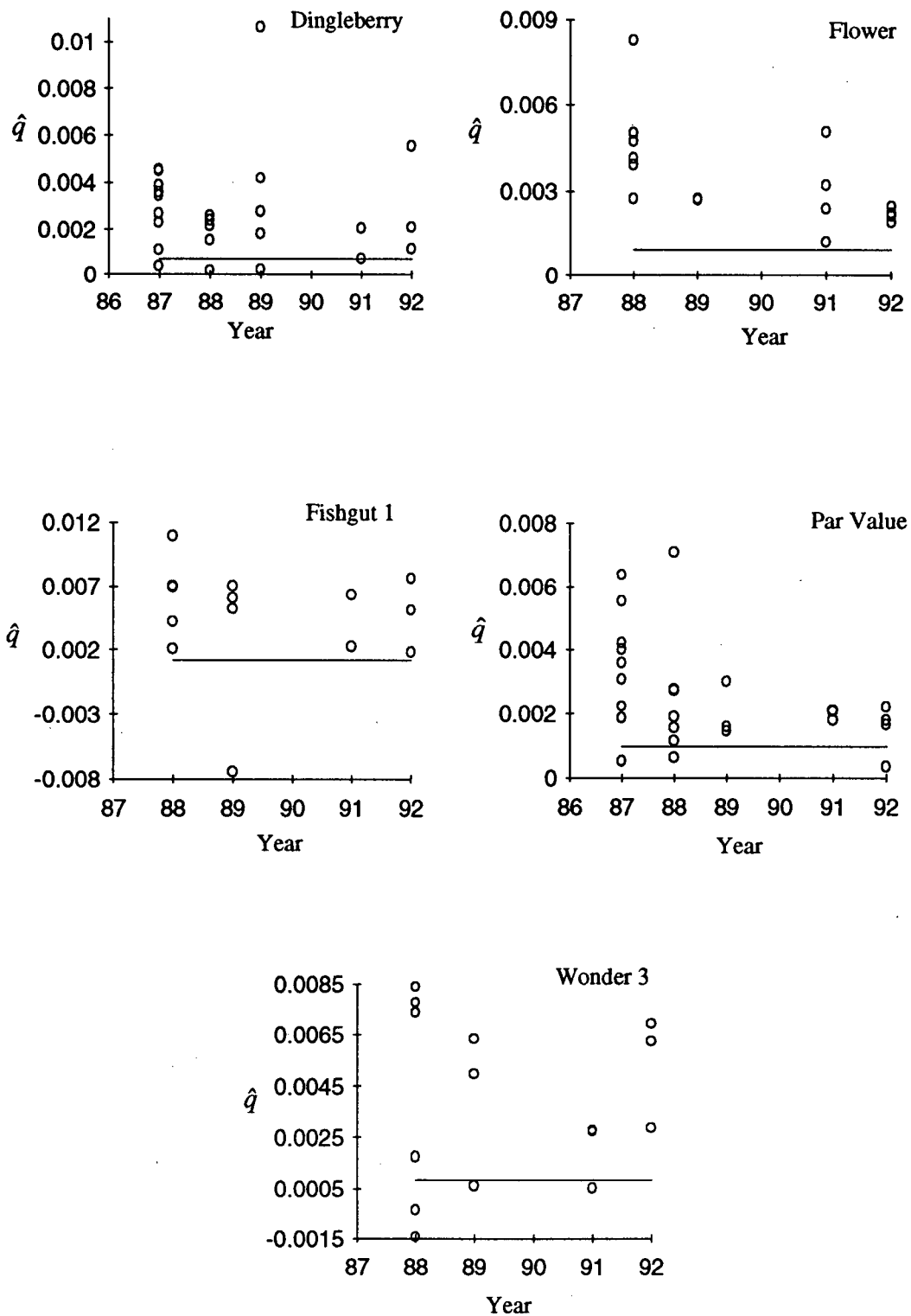


Figure 3.3b. Leslie estimates of q for depletions for five lakes from 1986 to 1992. Includes all fully recruited cohorts with total catch > 19. Solid line shows WC estimate of global q . Initial two points omitted for all estimates.

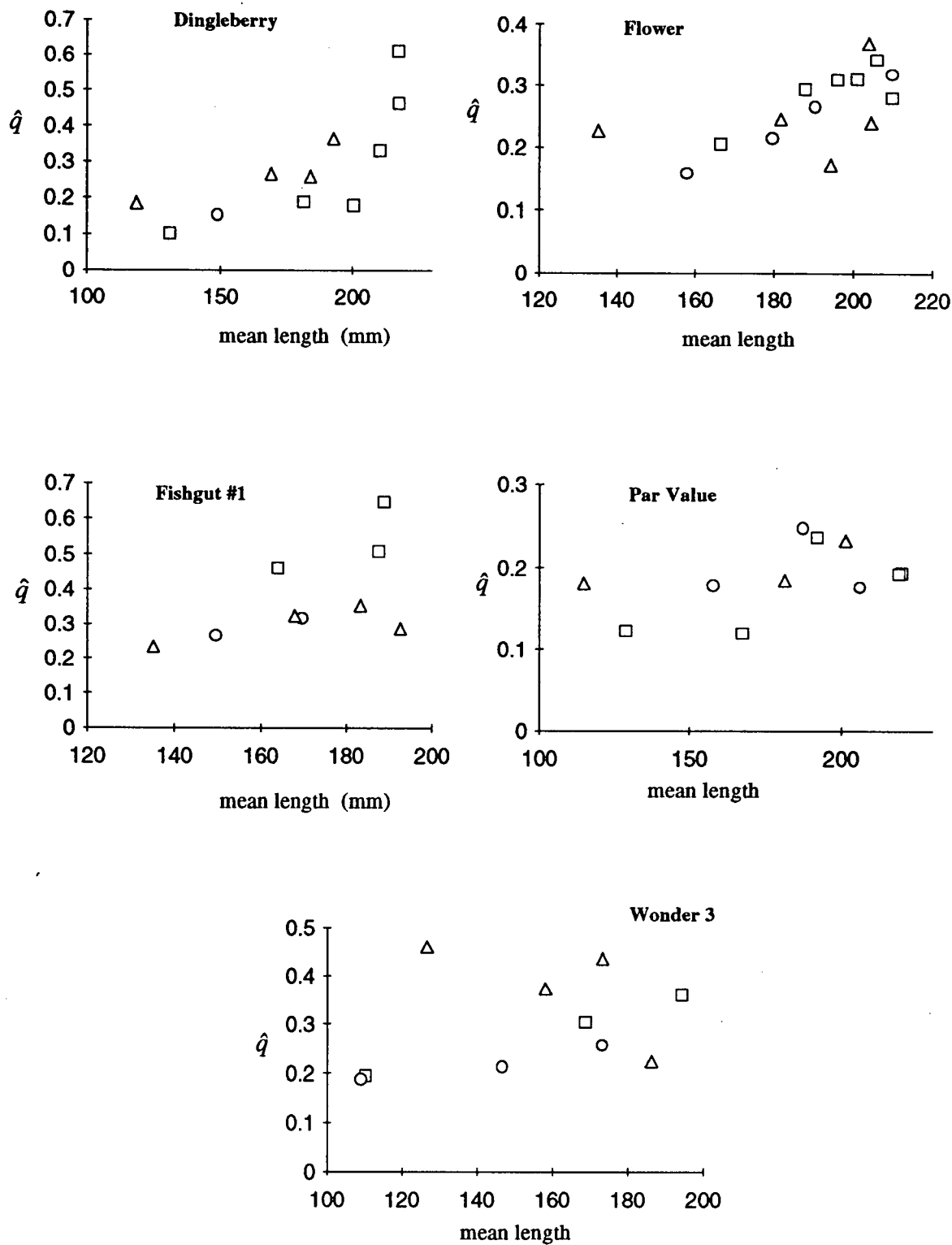


Figure 3.4. Mean fork length versus Schnute estimates of q for five study lakes from 1989 to 1992. Estimation methods are explained in the text. For most lakes in most years, q increases with length. Plot symbols: squares are 1989 estimates, circles are 1991 estimates, triangles are 1992 estimates.

Diel variation in catchability related to size

The effort-adjusted ratio of \hat{q}_{night} to \hat{q}_{day} was lower for prerecruits than for recruited cohorts (Figure 3.5). The general pattern is that of greater \hat{q}_{night} relative to \hat{q}_{day} with increasing age/size.

Age-aggregated estimates

Schnute estimates

For the seven study lakes, twenty of 21 removal experiments from 1989 to 1992 used both day and night capture periods. Of the 20, 17 were best fit by a model with day-night structure (Table 3.4). Six of the 21 (29%) showed significantly different \hat{q}_1 . For five of the six, \hat{q}_1 was higher than the corresponding terminal \hat{q} .

Of fourteen age-aggregated estimates from 1989 and 1991, one was eliminated as poorly determined. Only 3 of the remaining 13 (23%) were equal to or greater than the corresponding MKA estimate and only one exceeded the MKA estimate by more than 10% (Table 3.4). Schnute estimates averaged 92% of corresponding MKA estimates.

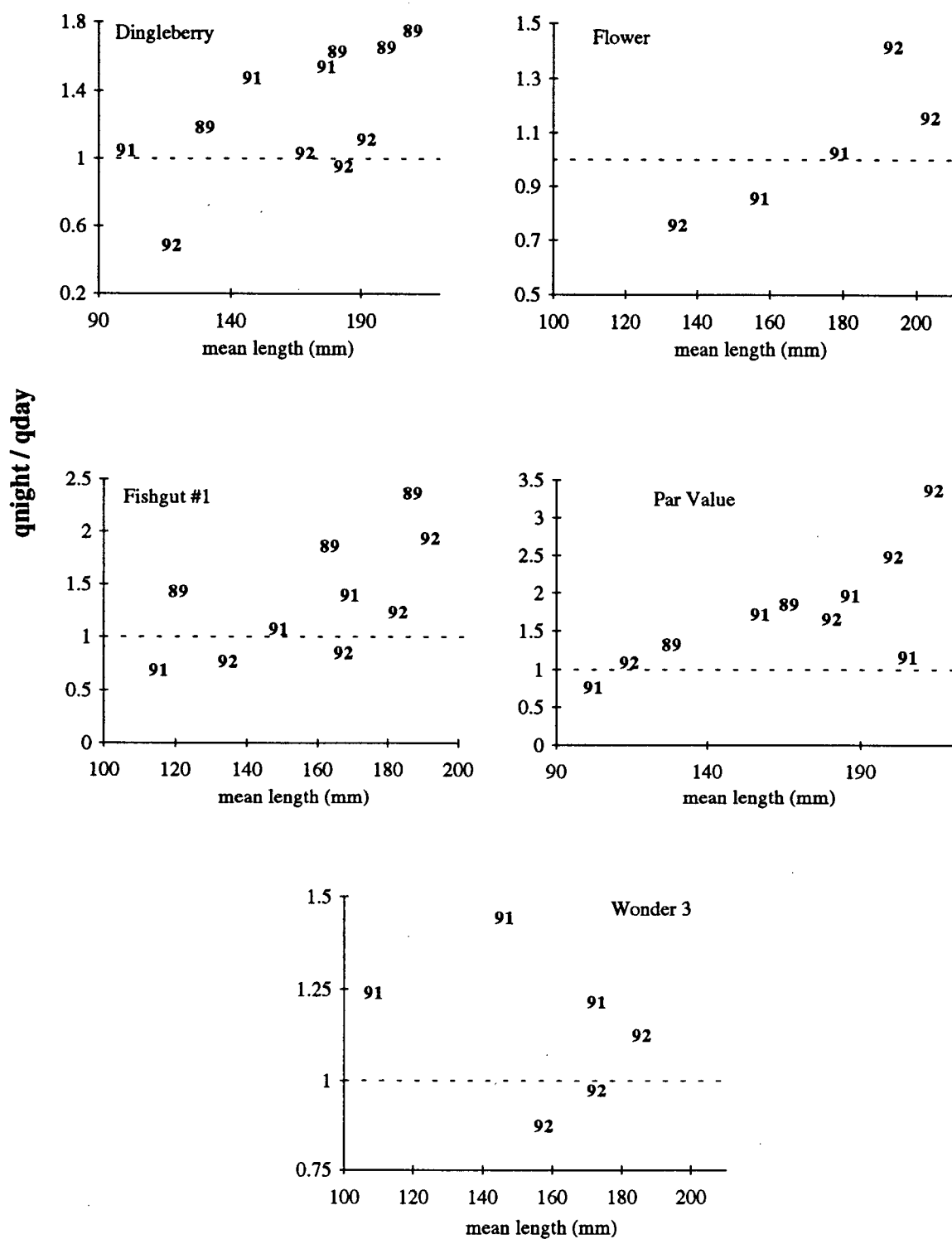


Figure 3.5. The effort-adjusted ratio of q_{night} to q_{day} , plotted versus fork length for prerecruit and recruited cohorts with catch ≥ 40 . Plot symbol indicates the year of the estimate. In most years, the ratio tends to increase with length.

Table 3.4. Schnute estimates of population size for age aggregated removals from 1989, 1991 and 1992. YC = year class, Model = model selected, F = Schnute fitting criterion, N = population estimate, LCI / UCI = lower / upper 95% confidence intervals, MKA = minimum known alive estimate, q's = estimated catchabilities. Model abbreviations are: i = single q; i2 = distinct first period q; i3= two distinct initial q's; dn = day and night q's; idn = day and night q's with distinct initial period q. Estimation methods are explained in the text. Order of estimated q's: initial period q's if any, followed by single terminal q or terminal night then day q's. Estimates include only fully-recruited ages.

Lake	Year	Model	F	N	LCI	UCI	MKA	q's
Hell Diver #2	89	dn	3.48	80	78	86	94	0.6467 0.2062
Hell Diver #2	91	i2	5.08	800	202	1284230	221	0.0279 0.0900
Hell Diver #2	92	dn	3.11	203	185	240	173	0.4218 0.1178
Dingleberry	89	dn	15.05	418	394	455	440	0.2454 0.1498
Dingleberry	91	idn	5.58	1183	968	1753	958	0.1428 0.1100 0.0596
Dingleberry	92	dn	7.74	536	496	600	435	0.2736 0.1218
Flower	89	i	5.06	681	626	767	703	0.2617
Flower	91	dn	11.53	1212	1147	1302	1485	0.2151 0.1121
Flower	92	dn	8.58	789	701	940	550	0.2137 0.0742
Fishgut #1	89	i3	3.91	313	255	4317	328	0.3870 0.1096 0.2230
Fishgut #1	91	idn	11.16	526	427	903	522	0.2226 0.1607 0.0952
Fishgut #1	92	dn	4.02	313	273	400	236	0.2819 0.1250
Par Value	89	idn	9.99	732	627	979	693	0.1917 0.1176 0.0602
Par Value	91	dn	7.34	798	736	893	853	0.2073 0.0760
Par Value	92	dn	5.34	779	645	1079	459	0.1756 0.0379
Wonder #3	89	i	7.56	221	205	250	308	0.2066
Wonder #3	91	dn	5.94	593	542	675	670	0.2028 0.0881
Wonder #3	92	idn	2.97	354	325	418	301	0.2964 0.3912 0.1657
Hell Diver #3	89	dn	1.75	50	45	73	66	0.6564 0.1126
Hell Diver #3	91	dn	3.77	93	79	139	101	0.2729 0.0451
Hell Diver #3	92	dn	1.59	51	47	66	48	0.6607 0.2264

DISCUSSION

In a study of the use of the removal method for estimation of small lake fish populations, Kelso and Shuter (1989) used gillnets to capture brook trout, rainbow trout (*O. mykiss*) and lake trout (*S. namaycush*) released accidentally into an 11.7 ha lake. Over three years, they made 50 day-long sets of 210m of gillnet. They could not account for natural mortality but the populations were otherwise closed during the study. Although during the depletion, a constant q model and then a declining q model fit the data well, both were underestimating the true number of fish present. Their study highlights two observations for removal experiments on salmonids in small lakes: catches frequently follow a pattern for which available models fit poorly, and even when models do fit the data well, population numbers are underestimated.

One mechanism which has been implicated in the underestimation of population size by removal estimates is atypical initial period q . Concavity of the cpe-K relationship is often hypothesized as due to early catch of some individuals with high capture probability (Schnute 1983; Hilborn and Walters 1992). Analysis of depletion series collected during this study suggest that initial period q was not atypical, for the 1989-92 series which I modelled using Schnute's (1983) methods. Nevertheless, the pattern of decline in cpe within removal series was not informative about population size, at least in the manner suggested by available models. Comparison of MKA with Schnute estimates, and of Leslie \hat{q} 's with WC global \hat{q} 's, showed that the removal estimators consistently underestimated population size. Omitting the first two points of the Leslie and WC fitting confirmed that this bias was not mainly due to atypical q for initial points. The removal estimates in each year generally give the appearance that almost all of the cohort has been caught. The next year's catch there nearly always shows that this was not the case. This bias translates into bias of the WC estimate. The information present in the pattern of decline of cpe only serves to degrade the WC estimates as well as inflating the variances. Bias of the WC estimates would be more serious with lower (and probably more realistic) estimates of survival. This finding is not surprising in light of results with the early part of this data set (Hall 1991),

and experience with subsequent depletions in the same year. Generally cpe for a cohort rebounds considerably from the end of the first depletion after an unfished period of ten days or more (Hall 1991). It appears there is a substantial portion of the population that is essentially invulnerable during any single multi-period depletion like those used in this study.

Age aggregated Schnute \hat{N} 's also showed negative bias relative to MKA estimates. Bias of age-aggregated estimates was not apparently as severe as for cohort-specific Schnute estimates. As well, there was greater suggestion of distinct initial point catchability. These two observations may be related. Aggregating data for cohorts with different \hat{q} 's will tend to produce a concave, curvilinear relation between cpe and K. This could increase the likelihood of assigning distinct (higher) initial \hat{q} 's, leaving a lower terminal \hat{q} and thus a higher population estimate.

The removal method has been criticized in several recent studies using both passive and active gear (Kelso and Shuter 1989; Riley and Fausch 1992; Miller and Mohn 1993). The assumptions of the removal method (constant and homogeneous capture probability, or in the case of Schnute's method, simply homogeneous capture probability) have never been shown to hold for any animal population. Minor violations of the assumptions may not cause serious bias, but the method itself does not allow the assessment of how seriously its assumptions are being violated. Nonlinearity of the cpe-K relation implies violation of the assumptions. Statistical detection and correction of nonlinearity may improve the fit, but goodness-of-fit does not indicate an accurate or unbiased estimate (Kelso and Shuter 1989; Miller and Mohn 1993), despite assertions by some primary investigators (DeLury 1947; Seber 1982). Variance in catch per effort is often high, which means that it is difficult to detect nonlinearity in the later depletion points. Cone et al. (1988) found violation of nearly all of the assumptions of mark-recapture estimation, including capture probability heterogeneity, for brook trout in an Adirondack pond which they drained to allow complete enumeration.

Explanations for the downward bias of the estimates should account for the apparent variation of q with time. For abundant cohorts, cpe generally increases from the last period of a depletion to the first period of the following year's depletion. For a closed population, this implies that q has increased in the interim. One possible explanation concerns the spatial pattern of netting: study gillnets did not fish pelagic areas of the lakes. Although we have seldom observed fish in the pelagia, it is conceivable that a portion of the population is essentially pelagic and uncatchable, but may later occupy benthic-littoral areas when fish there are removed. A second explanation is that a portion of the population has low capture probability which increases after part of the population is removed. Low q might be due to low basic activity, different spatial pattern of activity, different feeding style, or a behavioral hierarchy, any of which might change in response to the removal of other fish. Hall (1991) suggested that net shyness may change with time, increasing during a depletion but then forgotten in the interim between depletions. The first two explanations imply that capture probability varies not only with time but among individuals, a situation which invalidates the use of any of the available estimators. Gillnet removal data alone cannot be used to distinguish among these hypotheses, although trials with pelagic nets could suggest whether the first hypothesis has merit.

Estimate bias may not interfere with interpretation of patterns in \hat{q} . If bias is relatively constant or even a linear function of another variable, \hat{q} 's can still be compared among cohorts and between years. My analyses do not distinguish between age and size as variables influencing catchability. Size increases with age, across the cohorts which are sufficiently abundant to allow confident estimation of q with these models. The variance of length-at-age is low enough that grouping and analyzing by length rather than age would still effectively be an age-based analysis, although the largest size class would also include data for older less abundant cohorts.

A positive relationship between size and \hat{q} has been reported previously (Borgstrom 1992; Crecco and Savoy 1985). For most lakes in most years of this study, the data are suggestive of such a relationship. Diel variation in cpe is another common feature of lake gillnet fisheries. For this study, most series with

both day and night removal periods were best fit by models with distinct night and day \hat{q} 's. The results suggest effort-corrected night \hat{q} is usually greater than day \hat{q} and that diel differences in \hat{q} increase with size or age. Several hypotheses might account for this difference. One possible explanation is that nets may be easier to see and avoid during the day. Visual acuity improves with size, which might exaggerate this difference. A second possibility is that diel differences in basic activity level may vary with size. Third, the spatial pattern of activity may be diel and may vary with size. Larger fish may tend to occupy day-time habitats where they are less vulnerable to our gillnets, while smaller fish may not use such habitats. Or foraging style may change dependent on size, with a resulting effect on the spatial pattern of activity. cursory examination of adult stomachs often reveals freshwater clams (*Pisidium sp.*) as a dominant component of the gut contents. Daytime benthic foraging may result in lower encounter rate than other foraging modes. My design does not allow me to distinguish between the hypotheses I have suggested.

Current models of gillnet catchability decompose q into encounter rate and retention probability. Retention probability is partially a function of the size, shape and swimming velocity of the fish and the configuration of the capture gear (Hamley 1975). Assuming identical behavior, the relation between body size and swimming speed would govern variation in encounter rate (Rudstam et al. 1984; Borgstrom and Plahte 1992). Such simple physical explanations for catchability variation are favoured because fish size and shape are easy to measure, and the length - routine swimming speed relation has been quantified in laboratory studies. Other size-based variation in behavior and its impact upon q is much more difficult to quantify (Borgstrom and Plahte 1992). More complex models have been used to try to isolate encounter probability variation. Borgstrom and Plahte (1992) developed a model of gillnet retention probability based on fish girth and mesh size, implying wedging as the dominant retention mechanism. They applied the model to catch data for a stunted brown trout (*Salmo trutta*) population, and used seining and gillnetting to make mark - recapture estimates of population size. They found that encounter probability appeared to decrease with length. Borgstrom and Plahte (1992) suggested that large brown trout might adopt a piscivorous ambush foraging mode which would lower

their probability of encountering nets. Again, gillnet data can suggest such patterns, but without direct observation of fish behavior in the field, residual variation in q cannot be attributed to swimming speed, spatial pattern of movement, visual acuity, wariness or any other single factor. Further development with regard to population estimation will likely rest upon improved understanding of fish behavior, through observation techniques such as metabolic radio tagging and video monitoring.

Chapter 4. Population and catchability estimates at depletion-level resolution

INTRODUCTION

Previously reviewed studies suggested numerical or catchability responses of juvenile lake salmonids to removals of adult conspecifics (Lindstrom et al. 1970; Fagerstrom 1972; Healey 1978, 1980; Johnson 1976, 1983, 1994; Langeland 1986; Donald and Alger 1989; Hall 1991; Borgstrom 1992). The primary goal of this chapter is to examine the relationships between year class strength, prerecruit gillnet catchability and adult population density during experimental manipulation of adult brook trout density in the study lakes. Estimates of population size before and during the removals are necessary to interpret the response to experimental exploitation. Depletion data at period level resolution gave downward biased estimates of population size in Chapter 3. In this chapter I make population estimates which do not use the period level structure of the data, but instead compress each cohort's catch in a depletion into a single catch-effort observation. Bias in the period level estimates does not necessarily lead to bias in estimates made with depletion level resolution. If the fraction of each cohort vulnerable is relatively consistent from year to year, the invulnerable fraction does not recruit substantially to the vulnerable population during the depletion, and if the vulnerable fraction is not fully depleted, catch-age analysis at depletion level resolution can provide reliable estimates of year class strength, population size and catchability.

Of secondary interest in this chapter are patterns in adult brook trout gillnet catchability (q). Gillnets are often used for fish surveys, as well as experimental and commercial exploitation. Because of the difficulty in obtaining direct observations of fish behavior in lakes, recent work has attempted to use gillnet data to deduce how behavior may change with body size and population density (Borgstrom et al. 1992). This chapter's population estimates and the catch data can be used to estimate year and cohort-specific \hat{q} 's. Analysis of within-lake adult \hat{q} 's for size and density dependence might seem a tempting focus. However, such \hat{q} 's are likely to be quite variable due to ageing error, errors in survival parameterization, changes in survival due to the removals, variation in q due to sampling date

and small sample size, as well as possible size and density-dependence. Essentially, the pattern of removals and year class strength during the study combined with errors of the type mentioned, are virtually certain to blur any within-lake across-year patterns in adult \hat{q} . I report within-lake adult \hat{q} 's in this chapter to demonstrate the variability and lack of pattern across years.

Among lake patterns in \hat{q} may also carry information about fish behavior (Hall 1991; Borgstrom 1992). The Walters-Collie (WC) method estimates a single global \hat{q} for each lake adult population. This parameter is less sensitive to the previously mentioned error sources because it is estimated across years and cohorts; the parameter may be biased by such errors but the bias should be relatively consistent between lakes if the populations were treated and responded similarly. Current models decompose q into encounter and retention probability (Rudstam et al. 1984; Borgstrom and Plahte 1992). The WC \hat{q} 's are not directly comparable because of between-population differences in lake area and fish size which presumably effect the fish-gear encounter rate. Size at age varied between lakes, and the magnitude of the size response to removals also varied. In this chapter, I develop an encounter rate model based on fish size, lake area and effort density, to attempt to explain variation in \hat{q} between lakes.

Finally, period level estimates of adult population size, such as those made in Chapter 3, can be interpreted as estimates of the adult population which was vulnerable to gillnetting during the depletion. Of interest is how that population, as a fraction of the true population, might vary with density. I use estimates made with depletion level resolution as estimates of the true population, to examine how the apparent vulnerable fraction changed from year to year during the removals.

METHODS

The objectives of this chapter require methods for population and catchability estimation, using the catch data at depletion level resolution. I first review the field methodology used for gillnet depletions, and establish the terminology which I use during the remainder of the chapter. Next I introduce methods to estimate year class strength and population density for the years prior to and during the experimental removals. I use two estimators: the Walters-Collic (WC) multiple regression technique, and an alternative non-linear estimation method which uses logarithmically transformed catch data. I describe the method used for survival parameterization, required by the estimation procedures used in this chapter. I detail estimation of the fraction of the population vulnerable to gillnetting, using period level estimates of the adult population. Finally, I develop the methods for catchability estimation, including a model based on fish-gear encounter probability which allows between-lake comparisons of relative activity.

General methodology

Field methods

I described the depletion methodology in Chapters 1 and 3 so I reiterate only briefly here. We fished Lundgrens (Sweden) light green, nylon, weighted gillnets of length 36 m and height 1.5 m, on bottom. The nets were composed of twelve randomly ordered panels of bar mesh size 4 to 38 mm, and were chosen from a pool of ten such nets. Nets were anchored at and set perpendicular to shore, but we also made sets offshore oriented at random or downwind; we usually fished 4 to 6 nets throughout a depletion. The removals began in 1986-87 with at least one depletion per lake each year through 1992, but no depletions in 1990. Nets were hauled, cleared of fish and reset in different locations twice every 24 hrs, for a total fishing time of 36 to 132 hrs per depletion.

Terminology and treatment of the data

I used one net fished for one hour as the standard unit of effort, and pool data from all sets to provide a single estimate of catch-per-unit-effort (cpe) for each cohort for the entire depletion. In some years for some lakes, two depletions were made, separated by 7 to 30 days. Except for Dingleberry Lake in

1991, I used the first depletion as relative abundance data for estimation and the second as removals only. The data were collected, and analyzed in Chapter 3, at period-level resolution. Accordingly, I refer to estimates which do not use the period-level structure of the data, as "depletion-level" estimates.

The term "recruitment" remains loosely defined in the fisheries literature and I avoid its use to the extent possible. I use "recruit" as a verb, meaning to join as a full member. For this study, "recruitment" might be used in reference to two important stages: the time or age when year class strength is considered determined, and that when catchability can be considered full adult catchability for the purposes of an estimation scheme. Instead, I use the term "year class strength" to refer to the number of fish present in a cohort when the cohort's numerical strength is roughly established. In contrast, I refer to the catchability of cohorts when discussing their vulnerability to sampling. I use the term "prerecruit" to refer to cohorts in the year before they are recruited to the gear, and "new recruit" to refer to cohorts in their first year of recruitment to the gear. Neither time of year class strength determination nor catchability is believed primarily determined by age, but rather by size for most fishes. However, I generally rely on age-structured rather than size-structured or mixed estimation methods in this thesis, and I provide explanation for my choice of ages for these definitions in the appropriate context below.

Catch-age estimation

Table 4.1. Notation.

Symbol	Meaning
y_i	Catch per unit effort for a cohort in the i^{th} year's depletion
K_i	Removals for a cohort during the i^{th} year, before the start of the i^{th} year's depletion
C_i	Catch for a cohort during the i^{th} year's depletion
N_0	Number of fish in a cohort, present before any experimental removals occurred
S_i	Natural survival rate from year i to year $i + 1$, assumed independent of i
q	Catchability, or proportion of the population removed by one unit of effort
T_i	Sum of all removals for a cohort in year i

WC estimator

I presented the development of the WC estimator for period-level data in Chapter 3, so I reiterate only briefly here (symbols defined in Table 4.1). The general assumption is that cpe is related to abundance and catch as:

$$y_1 = q(N_0 - K_1) = qN_0 - qK_1 \quad (4.1)$$

$$y_2 = q[S_1(N_0 - T_1) - K_2] = qN_0S_1 - q(S_1T_1 + K_2) \quad (4.2)$$

And generally:

$$y_i = qN_0 \left[\prod_{a=1}^{i-1} S_a \right] - q \left[K_i + \sum_{b=1}^{i-1} \left(T_b \prod_{c=b+1}^{i-1} S_c \right) \right] \quad (4.3)$$

The estimates of q and qN_0 are made using least-squares linear regression. I programmed the multiple regression in BASIC, performing the matrix inversion by the partitioned matrix method

(Searle 1967). I validated my algorithm by comparing its parameter output for a reduced problem to the manually calculated regression parameters. The quantities in square brackets are the x_j 's in the multiple regression. Confidence intervals for the parameters are generated as for standard least squares linear regression.

Two important points should be made concerning my use of the WC estimator for depletion-level data. First, although analyses in Chapter 3 revealed that the data at period level resolution gave downward biased estimates, under certain conditions cpe aggregated across removal periods is still a reliable index of abundance. The analyses in Chapter 3 suggested that only part of the population was vulnerable during any particular depletion. As long as the fraction vulnerable at the beginning of the depletion is relatively consistent across years and recruitment from the invulnerable fraction is negligible during a depletion, aggregated cpe can still be a reliable abundance index for population estimation. Second, if q is size- or density-dependent across years and a simple WC estimator is fit to the data, minor estimate bias may result. When co-occurring with other error, size or density dependence in q will be blurred and possibly undetectable. Bias will generally not be so severe as to mask, or falsely create, relationships between adult stock size and year class strength or between adult stock size and juvenile catchability.

I fit the WC estimates across all depletions and used the corrected definition of cumulative catch (Ricker 1975). Period-level data suggest that in most years gillnet catchability approaches full adult catchability by age 2+ (Hall 1991; Chapter 3 of this thesis), while age 1+ catchability is highly variable. Accordingly, the estimation used cohorts aged 2+ and older for all populations except Hell Diver 2, which are fit to age 3+ and older cohorts since length-at-age is lower there. I also made estimates using catch data which was corrected for ageing error using methods described in Chapter 2.

Log transformation

Other likelihood-based catch at age methods transform catch data using logarithms (Fournier and Archibald 1982; Deriso 1985). Simple linear least squares fitting (as used by the WC method) results in parameter estimates which may be dominated by a few of the largest cohort catches. Log transformation gives greater weight to the catches from cohorts which are less abundant due to low year class strength, age, or previous experimental removals.

To examine the sensitivity of year class strength, population, and catchability estimates to the fitting criterion, I made estimates using a non-linear search method. My algorithm uses a direct search to simultaneously estimate N_0 , the number of fish present in each cohort at the beginning of experimental depletions or at recruitment, and a global q . The algorithm looks forward in time from the first year of removals, so that each cohort's abundance is calculated using the following relation recursively:

$$N_{t+1} = (N_t - T_t) * S_t \quad (4.5)$$

The fitting criterion is the sum of squared deviations between logarithm of predicted and observed catch. I used the AMOEBA implementation (Sprott 1991) of the simplex search method (Nelder and Mead 1959) to find the minimum. Because the catches are log transformed, values of zero are inadmissible. Collie and Sissenwine (1982) and others suggest pooling catches of fish greater than age x into a single "plus group", with x chosen so that the plus group always has catch greater than zero. When age estimates are at least moderately uncertain for older fish, this method is additionally reasonable but requires assuming age-invariant natural mortality for fish of age x and older. I pooled catches older than 6+ into the plus group, except for Hell Diver 3 where the plus group included fish older than 5+ due to the absence of 6+ fish in the 1989 catch. Unlike the catch-age methods of Fournier et al. (1982), Deriso (1985) and others, my approach is not statistically rigorous. Their estimators generally require longer catch-age series and implement a variety of assumptions about stock-recruitment relationships and variance contributions to extract more information from the fitting. My informal method should be sufficient to indicate whether the patterns in year class strength,

population size and catchability which emerge from the WC fitting, are generally robust to the fitting criterion.

Survival

The estimators require an independent estimate of age specific survival. Ideally, estimates would be available for each population. The catch data offer the only means of making such estimates, but the data are not necessarily informative about mortality rates since they are also influenced by age specific vulnerability, year class strength variation, and ageing error. Smoothing of discontinuities by combining multiple years' catch is possible (Ricker 1975) but must include the same ages for all years data used, and the population must be roughly at equilibrium. For this study, the equilibrium assumption requires that the fit be made across cohorts which existed before the experiments began. Assuming full vulnerability to the gear at age 2+ (Hall 1991), combining data beyond 1989 would necessitate dropping one age for each additional year's catch used. Post-1989 catches contain few older fish, so they would contribute little to defining or smoothing the survival estimates. Given the numerical dominance of the first two years' data, year class strength variation and ageing error could have a major impact on the age-specific survival estimates.

Faced with high uncertainty about population-specific survival estimates, I estimated two general survival parameterizations to use for population estimates. I pooled the 1986 to 1988 catch-at-age data and fit two functions to the logged frequencies for ages 2+ and older. First, I used a linear fit to estimate a single age invariant survival. Second, I used the four parameter equation (Hall 1991)

$$\log_{10} C_a = Y - b \left(\frac{a^m}{k^m + a^m} \right) \quad (4.6)$$

to smooth the same data, and estimated survival at age as

$$S_a = 10^{\log_{10} \hat{C}_{a+1} - \log_{10} \hat{C}_a} \quad (4.7)$$

as described by Hall (1991). Finally, I also used (4.6) and (4.7) to make lake-specific survival estimates using age 2+ and older 1986 to 1989 catches. No information is available about survival for ages before full vulnerability to the sampling gear. To estimate N for cohorts in the year before recruitment to the gear, I assumed that survival during the year before recruitment was the same as estimated for the first year following recruitment.

Population estimation

I used the catch equation:

$$N_{t+1} = (N_t - C_t) * S \quad (4.8)$$

to make population estimates from the year class strength estimates.

Stock and Recruitment

Both the WC method, and my direct search method, estimate time series of the numerical strength of cohorts produced before and during the experimental removals. While such time series offer a general picture of how year class strength varied with time, it is often more useful to examine year class strength with respect to the adult stock from which it resulted. Year class strength is probably established by the 1+ year for most cohorts; many individuals are sexually maturing at that age (Hall 1991), and their length by that time is usually >50% of population L_∞ so it is unlikely that they experience variable natural mortality much higher than older fish. Thus I chose to use estimated numbers before experimental removals in the summer of the 1+ year, as an index of year class strength.

Because the experimental design manipulated adult numbers every year except 1990, adult population varied widely and in different ways for cohorts, during the 18 months between spawning of a cohort and its age 1+ summer. Which estimate should be used to examine the relationship between year class strength and adult population size ("stock")? I chose to use the estimate of adult population size following removals during the summer of the age 0+ year. This is about midway during the 18 months between spawning and the 1+ summer for a cohort, and represents the adult population size

experienced by the cohort during the late summer, fall and winter of the 0+ year. Evidence presented in Chapter 1 suggested that low snowpack and high summer warmth during the 0+ year often led to high year class strength, so this is probably an important time period for year class strength determination. I considered the adult population to include fish aged 2+ and older (3+ in Hell Diver 2). The number of age 1+ fish may influence growth and survival of age 0+ cohorts. I also calculated stock including age 1+ prerecruits but discounting their numbers by .5 to reflect my subjective feeling that they have less impact on 0+ growth and survival.

Vulnerability

Period-level analyses of catch data gave downward biased population estimates, suggesting a fraction of the population is invulnerable to gillnets. To examine how the vulnerable fraction varied with total adult population density, I used the Leslie removal method for adult cohorts with catch ≥ 20 and for age-aggregated adult catch, to estimate the size of the vulnerable population in each lake for each depletion. I used the WC method to estimate the true population, and divide the estimate of the vulnerable population by the estimate of the true population, to estimate the vulnerable fraction. I excluded the Hell Diver lakes from this analysis because depletions there were of short duration so estimates were poorly defined. I also excluded the 1987 Leslie estimates because "effort was adjusted from period to period to attempt to maintain a constant total catch" (Hall 1991) which I felt resulted in unusually severe bias.

Catchability

Simple q

The WC method and my direct search method estimate a single global catchability, \hat{q} . I estimated year-specific cohort-specific catchability \hat{q}_t , using \hat{N}_t 's obtained from the year class strength estimates and the catch equation, as:

$$\hat{q}_t = \frac{C_t/E_t}{\hat{N}_t} \quad (4.9)$$

I made both cohort-specific estimates as well as estimates pooled across cohorts within a year. Like the Leslie estimator, the WC method uses linear regression, so negative population estimates occasionally result from the use of year class strength estimates and forward calculation of population size using (4.8) across several years' catch. When I have pooled population and catch estimates, I have excluded cohorts whose catch estimate exceeds the population estimate for that year.

Encounter rate model

Recent models decompose q into encounter and retention probability (Rudstam et al. 1984; Henderson and Wong 1991; Helser et al. 1991; Borgstrom and Plahte 1992). Encounter probability is thought to reflect the intersection of the volume swept by an animal per unit time and the volume sampled by the gear as a proportion of the total volume used. A general model for q should thus take into account changes in these volumes within a single lake across cohorts and years, and between lakes. Such a model would factor out the differences in encounter probability caused by size-based variation in area swept between lakes and years, and variation in effort and population density. In theory, this would alleviate bias caused by changes in size at age, put all \hat{q} 's on a common scale, and potentially reveal relationships between \hat{q} and density across lakes.

Here I develop a two dimensional representation of the study depletion situation, based on the assumption that variation in gear encounter probability drives most of the variation in catchability between lakes. Consider a fish swimming constantly and randomly with respect to other fish and the gillnets, at an hourly velocity v directly proportional to its body length. Imagine gillnets set along various straight-line paths across the lake bottom, so that each period there are a total of η meter-hours of net available to capture the fish. If the lake has area A , the animal's probability p of encountering a net is then approximated by:

$$p = \frac{k \cdot v \cdot \eta}{A} \quad (4.10) .$$

The dimensionless "relative activity" parameter k combines the proportion of time that the fish is active and the constant of proportionality between body length and swimming speed. The key assumptions

are that the proportion of time active and retention probability are constant for all sizes of fish considered and that spatial pattern of activity is the same across sizes. The observation model is then just

$$C_t = p N_t \quad (4.11) .$$

The models (4.10) and (4.11) can be converted into the basic WC estimator observation model $y_t = qN_t$ where y_t is expressed in units of fish per unit effort, in this case net-hrs. In the WC formulation, q represents the proportion of the population captured by a unit of effort, so q is expressed in units of (effort)⁻¹. To make the encounter probability model compatible with the WC estimator, substitute (4.10) into (4.11) and move effort, η , to the left side of the formulation so that

$$C_t \eta^{-1} = k v A^{-1} N_t \quad (4.12)$$

with the units cancelling in expression (4.11) so that k is dimensionless:

$$\text{fish} \cdot \text{m}^{-1} \cdot \text{hr}^{-1} = k \cdot \text{m} \cdot \text{hr}^{-1} \cdot \text{m}^{-2} \cdot \text{fish} \quad (4.13) .$$

Expression (4.12) is directly compatible with the WC fitting, so that where q appears in expression (4.3), $k v A^{-1}$ is substituted. Computationally, the regression x_i 's are multiplied by the value of $v A^{-1}$ for that cohort in that lake and year, converting all terms to units of m and hr. I assume mean swimming velocity v for each cohort proportional to mean body length of fish captured in gillnets for each cohort in each year. When fit using the encounter probability model, the WC method estimates k and kN_0 .

The model requires an estimate of the "effective area" of the lake used by brook trout. We set bottom-fishing nets in all areas of the lake but shore anchored nets always caught more fish than offshore deep water sets. However, I have no independent data on the use of different depth zones by brook trout, so I cannot assert that brook trout do not use benthic areas in deep water. Low occurrence in sets there might also be due to low catchability. Because I wanted to examine how k varied among lakes, and

area used was uncertain, I estimated k using area above the 3 m and 9m depth contours, symbolized A_{ab3} and A_{ab9} , with corresponding k_{ab3} and k_{ab9} , as well as total surface area (A_{tot} and k_{tot}). The three definitions of effective area reflect three general hypotheses about the use of habitats within the lakes:

- (1) ab3 : brook trout mainly use relatively shallow benthic areas;
- (2) ab9 : brook trout use all but the deepest benthic areas of the lakes;
- (3) tot : brook trout use all benthic areas of the lakes.

Areas above the various depth contours were estimated by weighing polygons cut from photocopies of bathymetric maps prepared by Hall (1991). Using the encounter rate model for the WC fitting, the year class strength estimates are independent of area. The estimate of k is sensitive to effective area, but since

$$k_{abx}/k_{tot} = A_{abx}/A_{tot} \quad (4.14) ,$$

the k_{abx} 's can be estimated directly as $k_{abx} = k_{tot} * A_{abx}/A_{tot}$. One important additional assumption is that competition between nets is negligible. I calculated the mean number of nets fished during depletions for each lake, and the mean density of adults during the period 1987 to 1992, to look for potential relationships between lake-specific \hat{k} and these variables.

I fit the WC estimates across all depletions using the encounter rate model and the corrected definition of cumulative catch (Ricker 1975). The estimates were made across cohorts aged 2+ and older for all lakes except Hell Diver 2 (age 3+). Inclusion of age 2+ cohorts in the encounter rate fitting assumes that residual variation in catchability of age 2+ fish is explained primarily by size, whereas this is probably not the case for age 1+ fish so they are excluded. I estimated year-specific cohort-specific activity, \hat{k}_t , for the encounter rate model as:

$$\hat{k}_t = \frac{C_t/E_t}{\hat{N}_t} * v^{-1} A \quad (4.15).$$

Again, because this is a regression method, negative estimates can result, and I exclude these from any estimates pooled across cohorts within a year.

RESULTS

Population size

Survival

Use of a linear fit to catch at age data gave an age-invariant survival estimate of $s = .82$, while the four parameter model fit to the same catch data resulted in the general and lake-specific age-survival relationships shown in Figure 4.1. Of the lake specific age-varying survival estimates, those for Dingleberry, Flower, Fishgut 1, and Wonder 3 are relatively similar to the general age-varying survival estimate. Those for the Hell Diver lakes and Par Value are quite dissimilar, and those for the Hell Diver lakes appear unlikely since they imply no natural mortality up to age 8+. Lacking a method of resolving uncertainty about survival parameterization, I often present analyses using both the age-invariant value $s = .82$ and the lake-specific age-varying parameterizations, in order to demonstrate whether patterns and conclusions are robust to the survival parameterization. I do not present results using the general age-varying parameterization since it is usually intermediate to the others.

Year class strength

For both survival parameterizations using the WC method, the study populations show increased year class strength from 1988 through 1990, relative to year class strength in the early and mid- 1980's (Figure 4.2). The apparent strength of 1980 and earlier cohorts is more dependent on the survival parameterization; use of age-invariant $s = .82$ produces time series for which the 1988 to 1990 cohorts are still generally the largest observed, while for some lakes the age-varying parameterization implies that equally large cohorts may have been formed in the 1970's (Figure 4.2). Only for Par Value was year class strength in the first year of removals definitely higher than earlier in the 1980's (Figure 4.2).

Estimates made with data corrected for ageing error produced only minor changes in the pattern of year class strength (Figure 4.3). As expected after correction, estimates for locally strong year classes were increased while those for locally weak year classes were decreased. Estimated ageing error was relatively low for young fish, so year class strength estimates for the cohorts produced during the

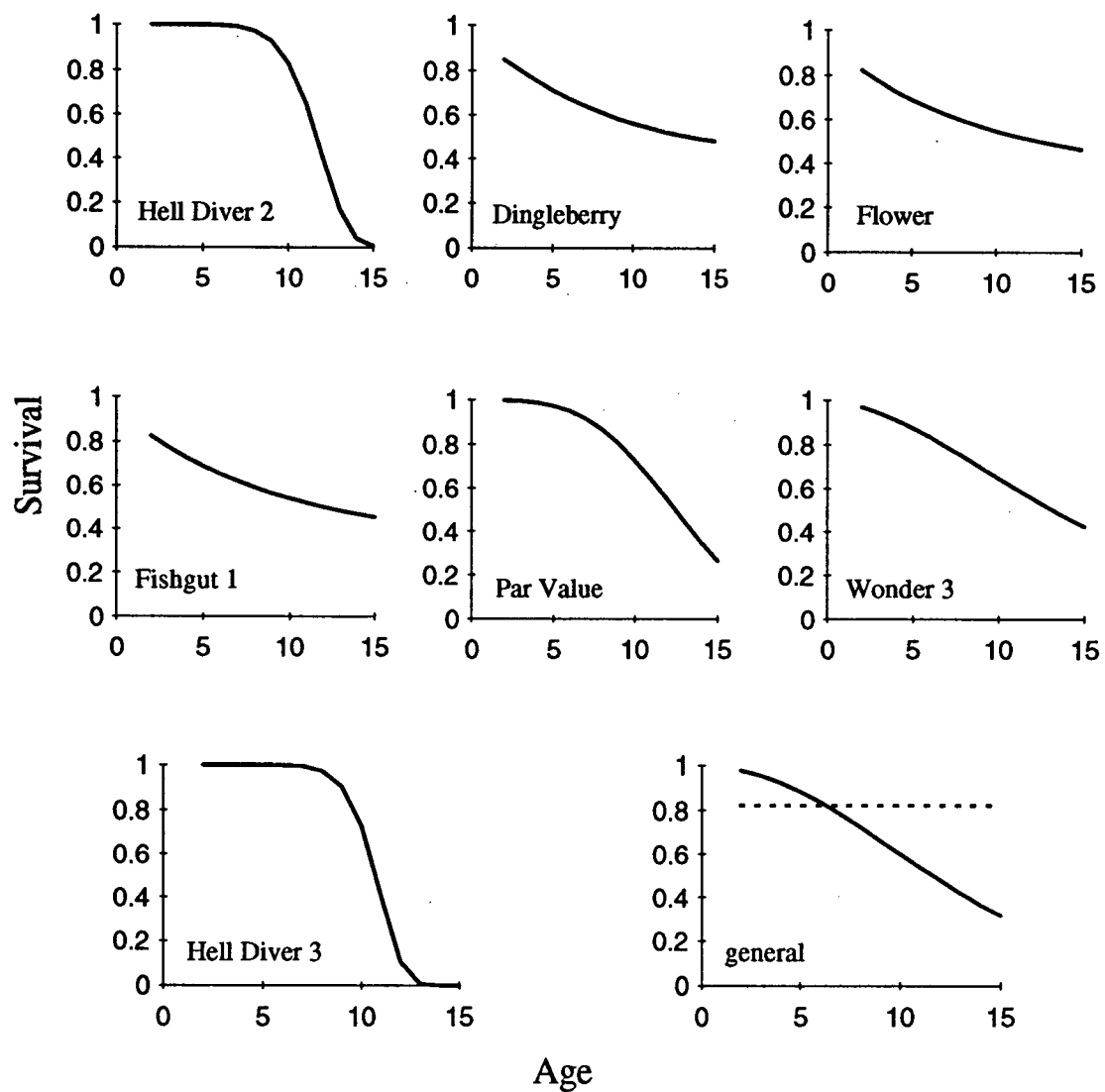


Figure 4.1. Estimated age-specific survival for seven study lakes. Estimation method explained in the text. Also shown is a general age-specific and age-invariant survival estimated from the seven lakes' data combined.

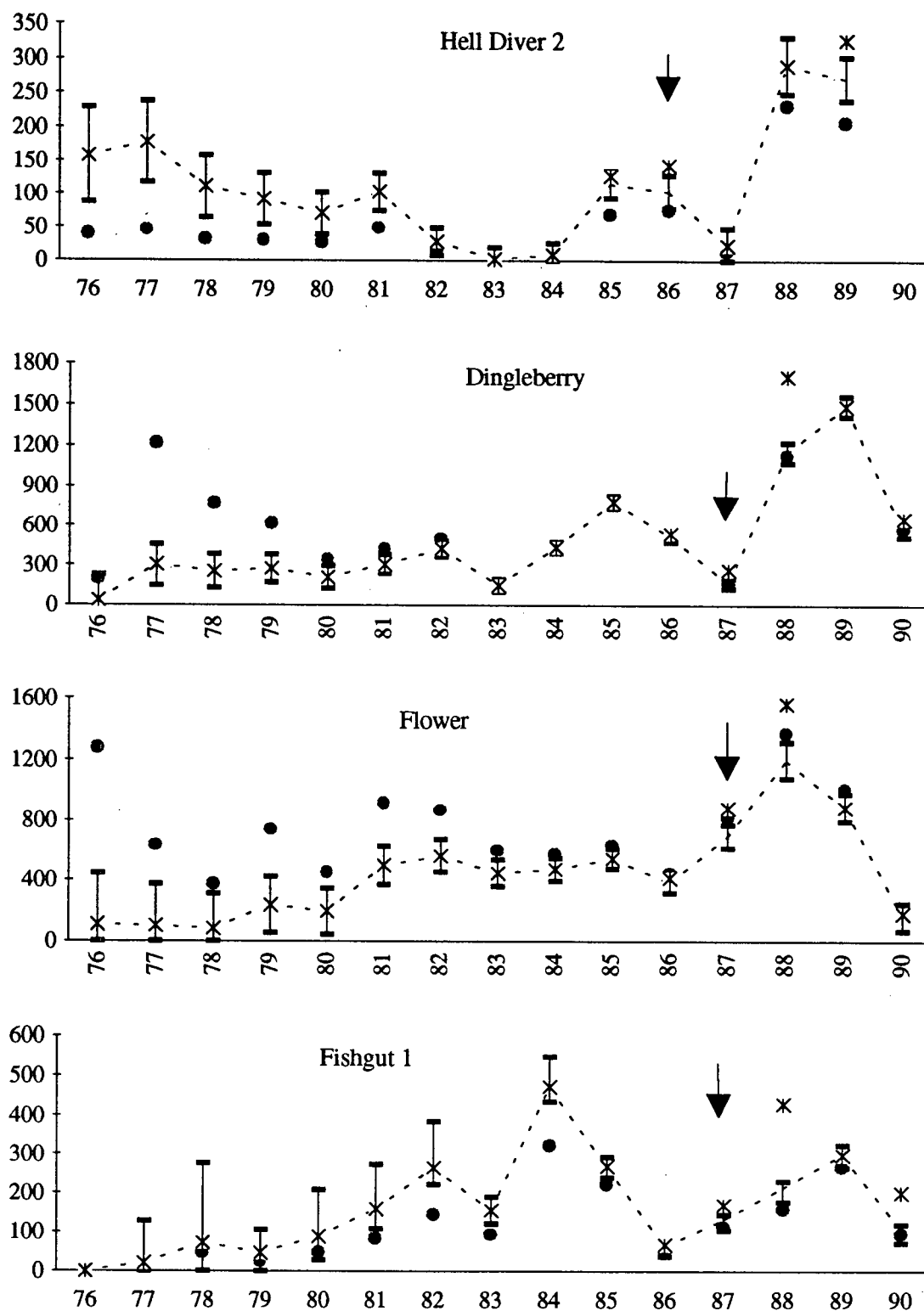


Figure 4.2. Year class strength estimates for seven study lakes, 1976 to 1990 cohorts. The WC estimation method is explained in the text. Estimates made using $s = .82$ lie on the dashed line. Error bars show 95% confidence intervals. Filled circles are estimates using lake-specific age-varying mortality. Recruitment is at age 2, except Hell Diver 2 at age 3. The symbol \times shows catch for the cohort in the year before recruitment, added to the $s = .82$ estimate. The arrow indicates the first year of removals.

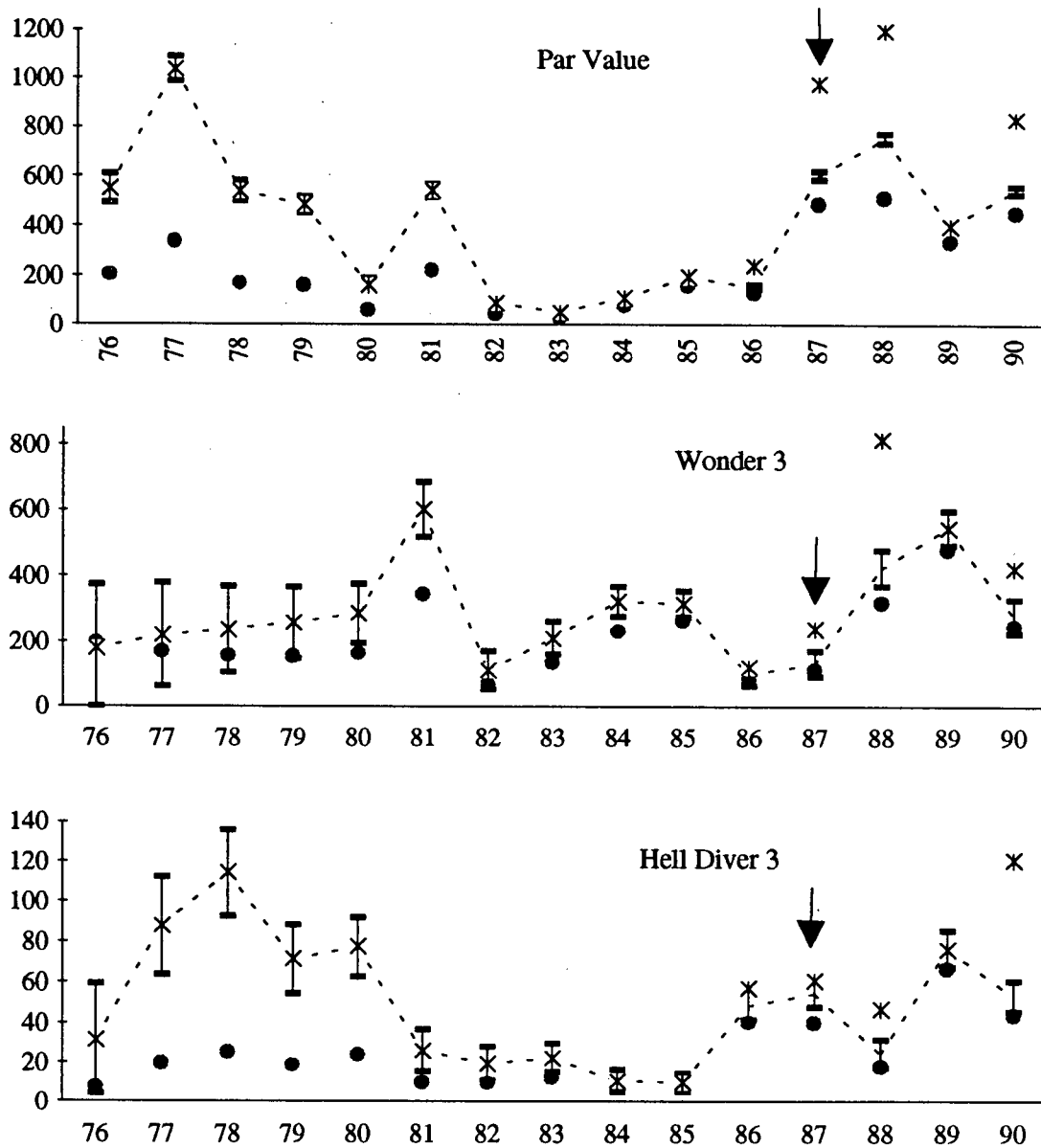


Figure 4.2 concluded.

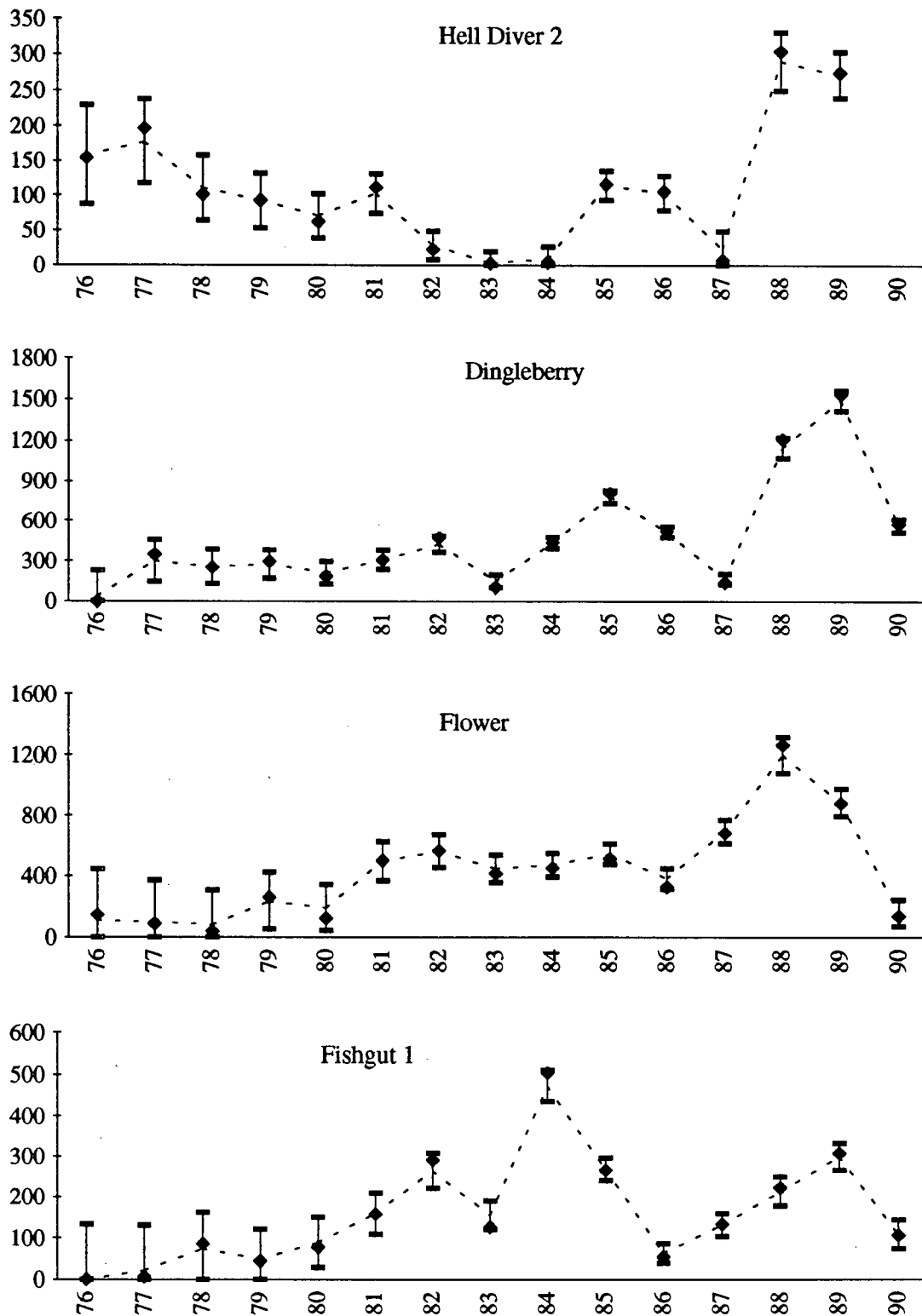


Figure 4.3. Year class strength estimates for seven study lakes, 1976 to 1990 cohorts. The WC estimation method is explained in the text. All estimates were made using age-invariant $s = .82$. Error bars show 95% confidence intervals. Filled diamonds are estimates using ageing-error corrected catch data. Recruitment is at age 2, except Hell Diver 2 at age 3.

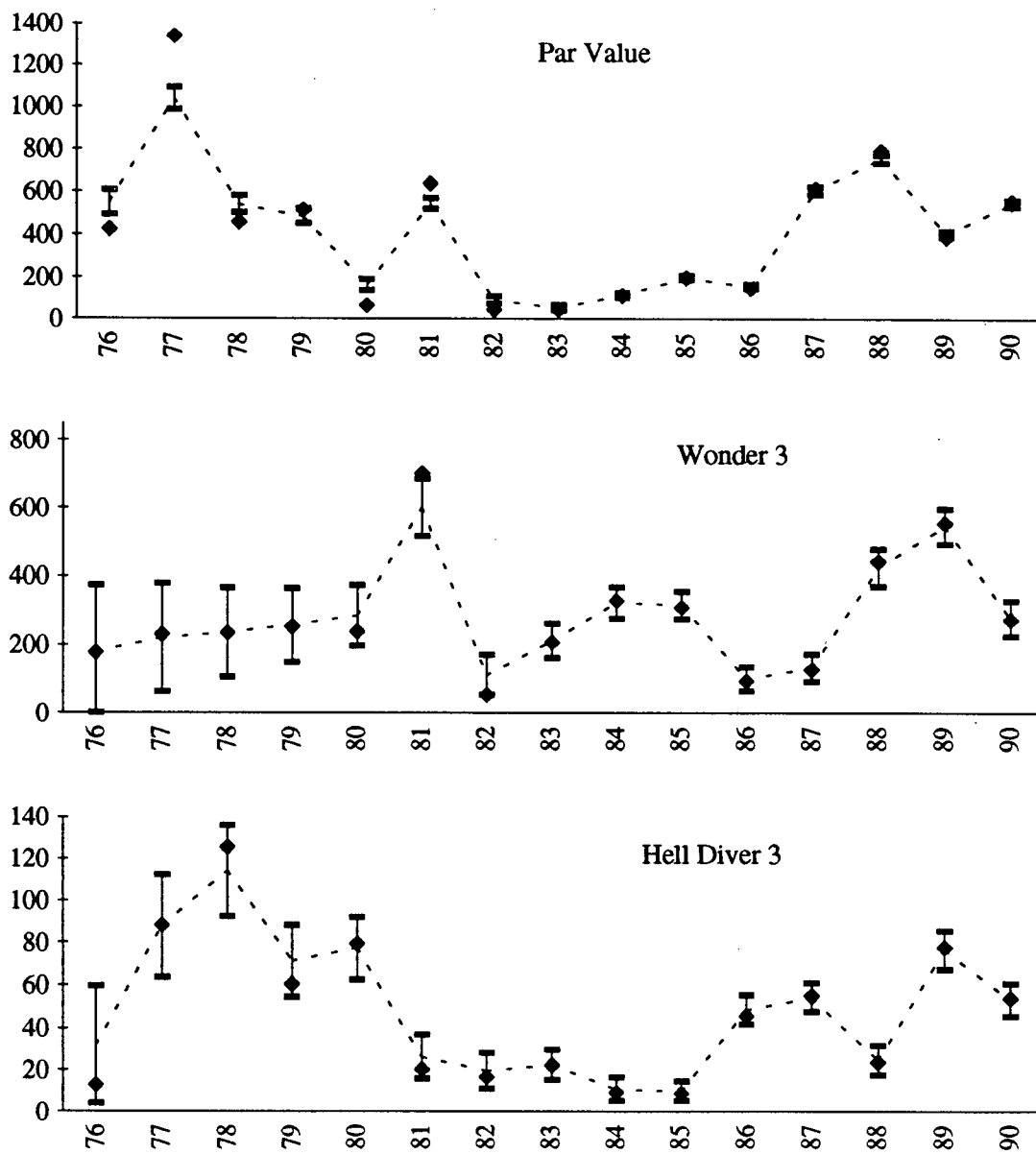


Figure 4.3. concluded.

removals were relatively unaffected (Figure 4.3). Estimates for very strong year classes in the late 1970's and early 1980's, for example Par Value in 1977 and Wonder 3 in 1981, were most sensitive to ageing error correction because of their greater age during the experimental removals.

Stock and recruitment

Adult stock and year class strength appear to be inversely related, over the range of stock sizes created by the experimental removals and the year classes formed during the removals (Figure 4.4a). The pattern is robust to survival parameterization, although lake-specific parameters lead to greater apparent variability for some lakes (Figure 4.4b). Nor did logarithmic transformation of catch data affect the general negative relationship between the number of recruits and adult stock size, when estimates were made using my informal method (Figure 4.5). Inclusion of prerecruit numbers, weighted by .5, apparently reduces the variation in the relation between stock and year class strength for some lakes (Figure 4.6).

Vulnerability

Estimated adult cohort vulnerability did not appear to vary systematically with adult population density (Figure 4.7). Pooled adult vulnerability also was not related to adult density, for the limited estimates available (Figure 4.8).

Catchability

Simple q WC estimator

Estimated adult cohort q was highly variable (Figure 4.9). Length of fish captured in gillnets did not appear to explain much of the variation in cohort q (Figure 4.9). Pooled adult q was less variable. For some lakes (Dingleberry, Par Value) pooled q appeared relatively constant over a wide range of adult densities (Figure 4.10). Others were more variable and show a suggestion of an inverse relationship between density and q , but no dominant relationship between q and adult density is apparent.

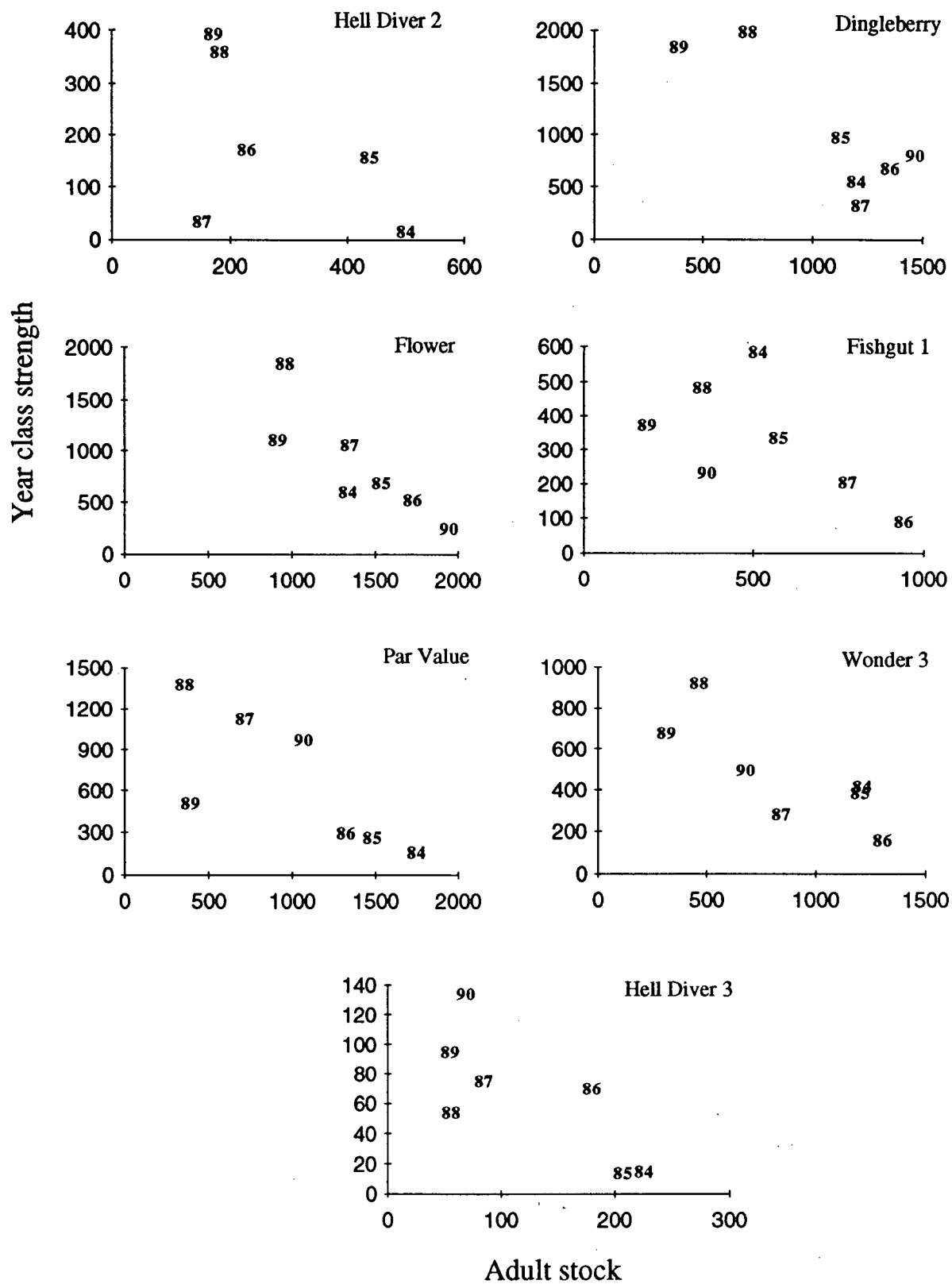


Figure 4.4a. Estimates of age 1+ year class strength plotted versus estimates of adult stock in the fall of the cohort's 0+ year. Adult stock includes age 2+ and older fish. For Hell Diver 2 adult stock was considered age 3+ and older, and year class strength determined at age 2+. Estimates were made with the WC estimator and age-invariant $s = .82$; methods explained in the text.

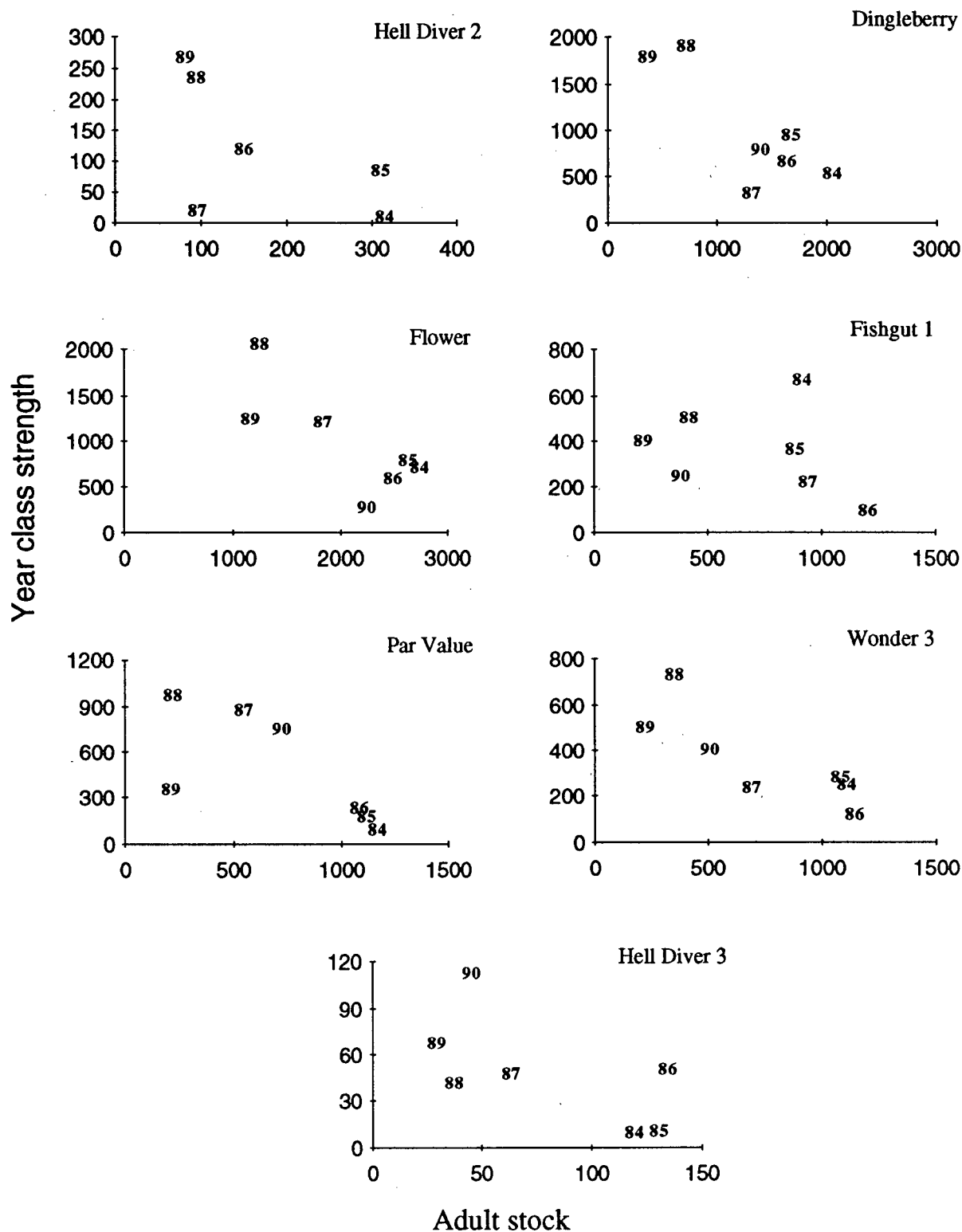


Figure 4.4b. Estimates of year class strength during the summer of the 0+ year, plotted versus adult stock for seven study lakes. Estimates made using the WC method with lake-specific survival parameters. For Hell Diver 2, adult stock includes age 3+ and older cohorts and year class strength is at age 2+. Plot symbol indicates the cohort's calendar year of emergence. Year class strength appears negatively correlated with adult stock over the observed range.

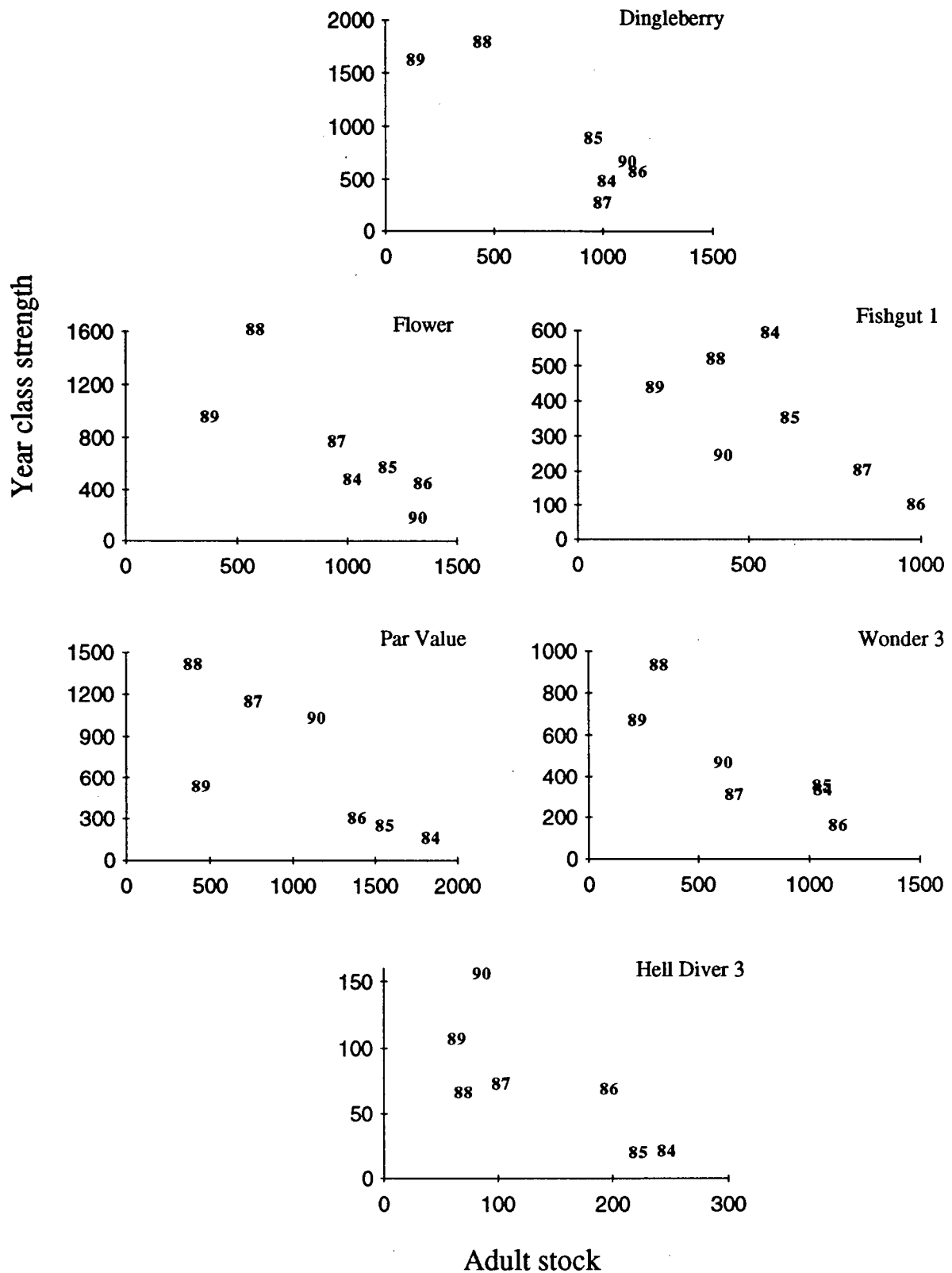


Figure 4.5. Estimates of age 1+ recruitment plotted versus estimates of adult stock after removals in the cohorts 0+ year. Adult stock includes age 2+ and older cohorts. Plot symbol indicates the cohort's year of emergence. No estimates were made for Hell Diver 2. Estimates made using log-transformed catch data and a direct search method explained in the text.

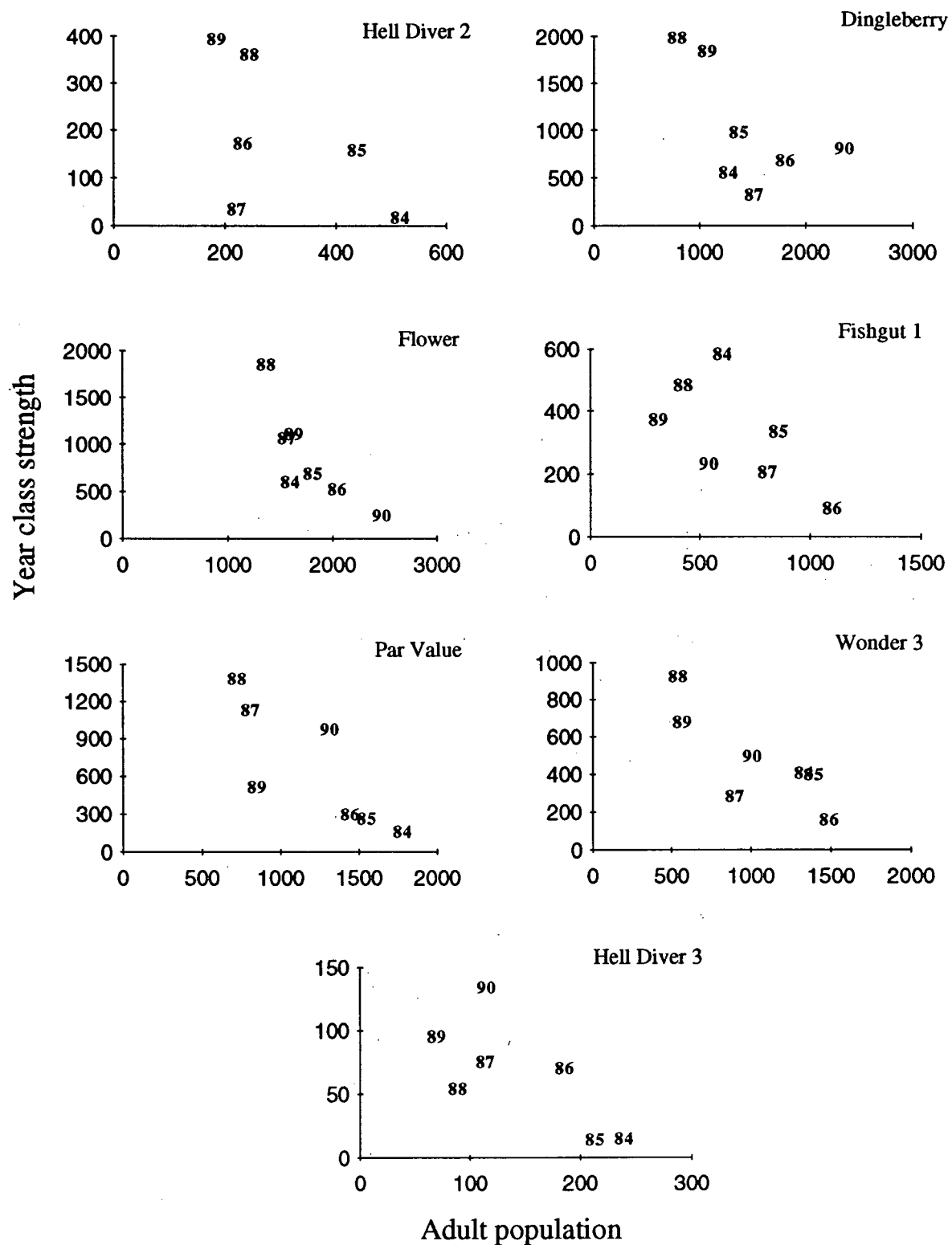


Figure 4.6. Estimates of year class strength during the summer of the 0+ year, plotted versus adult stock for seven study lakes. Adult stock includes half of precruit numbers. Estimates made using the WC method and age-invariant $s = .82$. Plot symbol indicates cohort year of emergence. Hell Diver 2 year class strength was considered established at age 2+ and adult stock was age 3+ and older.

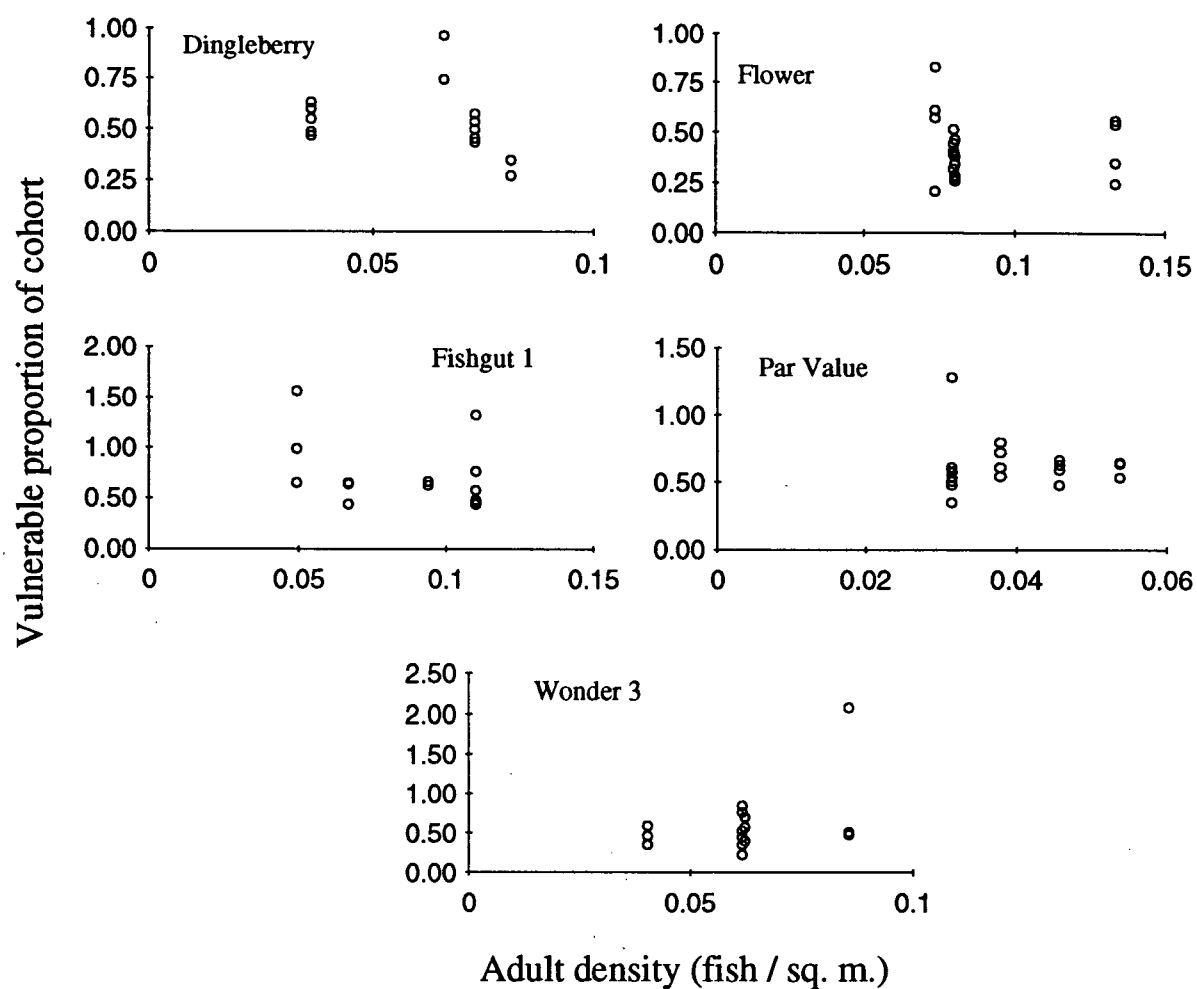


Figure 4.7. Estimated proportion of cohort vulnerable, plotted versus estimated adult density for five study lakes, 1988 to 1992. Population estimates were made using the WC estimator with $s = .82$ and depletion-level data. For each cohort, the vulnerable population was estimated by the Leslie method using period level depletion data, for adult cohorts with catch > 19 . There is little evidence of density-dependence in vulnerability.

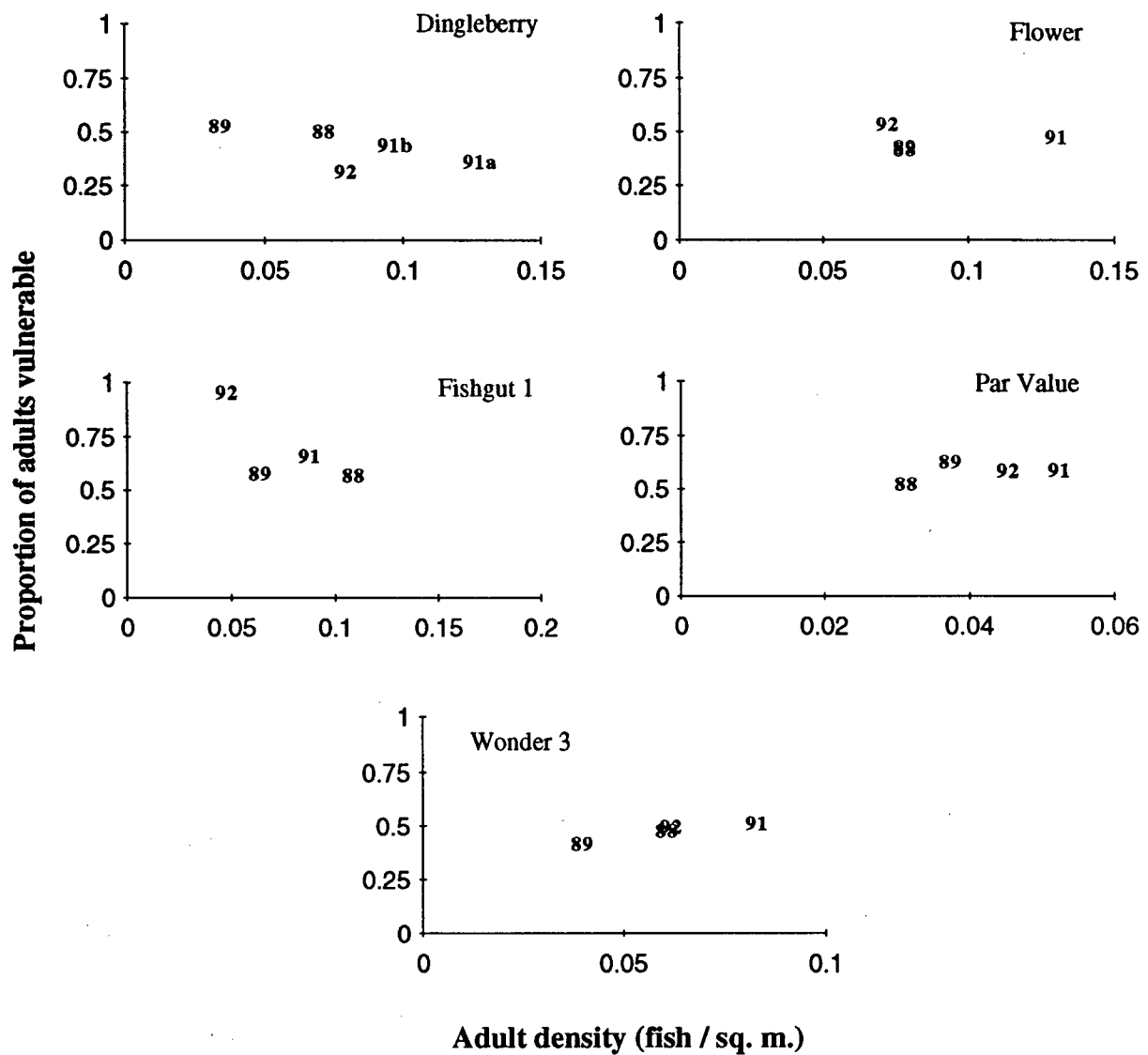


Figure 4.8. Estimated proportion of adults vulnerable, plotted versus estimated adult density for five study lakes, 1988 to 1992. Population estimates were made using the WC estimator with $s = .82$ and depletion-level data. Vulnerable population was estimated by the Leslie method using period level depletion data. With the possible exception of Fishgut 1, there is little evidence of density-dependence in vulnerability.

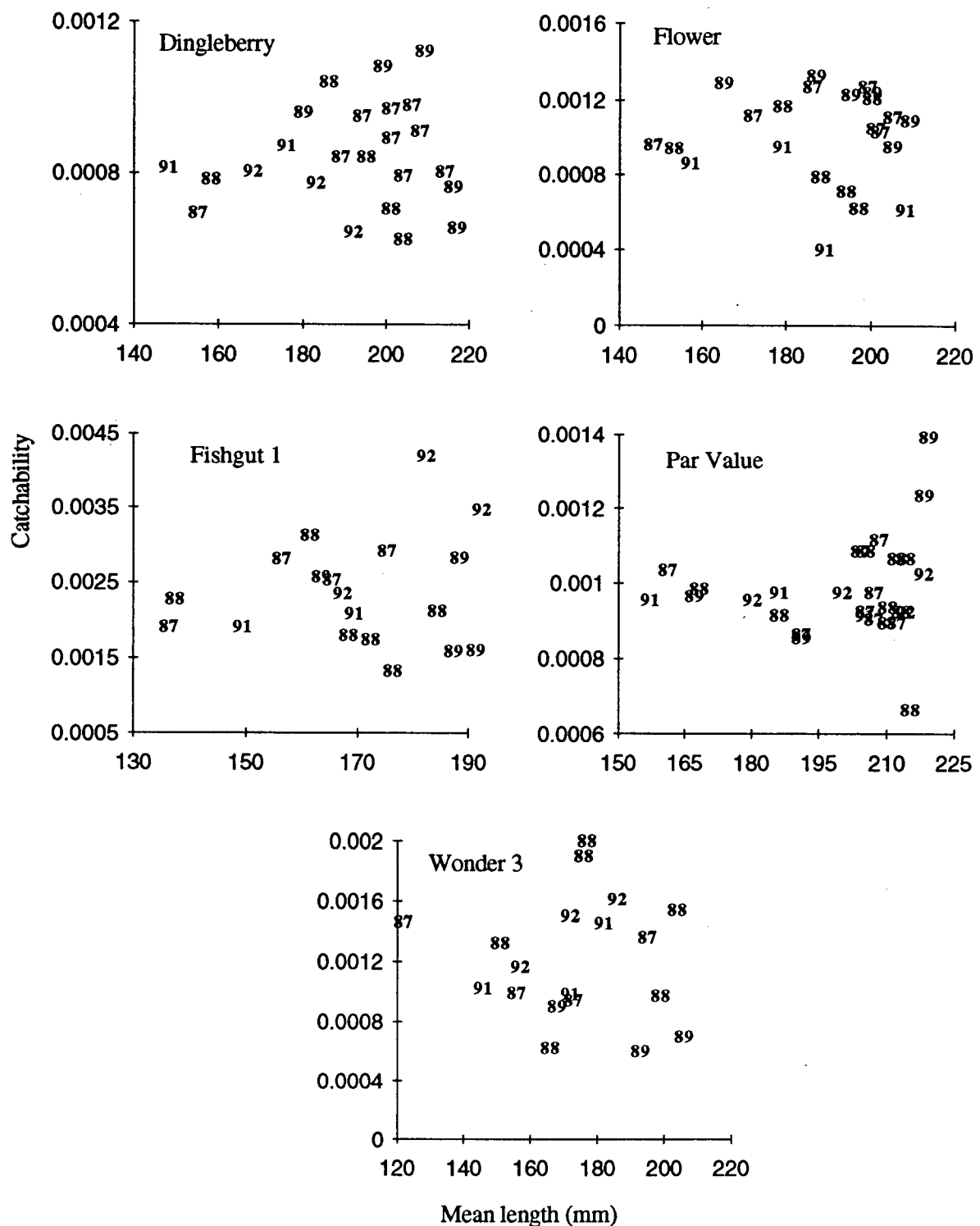


Figure 4.9. Estimates of catchability, plotted versus mean length, for cohorts age 2+ and older with catch > 19, for five study lakes 1987 through 1992. Estimates made using the WC method with $s = .82$. Plot symbol gives the year of the estimate. Estimated catchability is highly variable, and length does not appear to explain much of the variation.

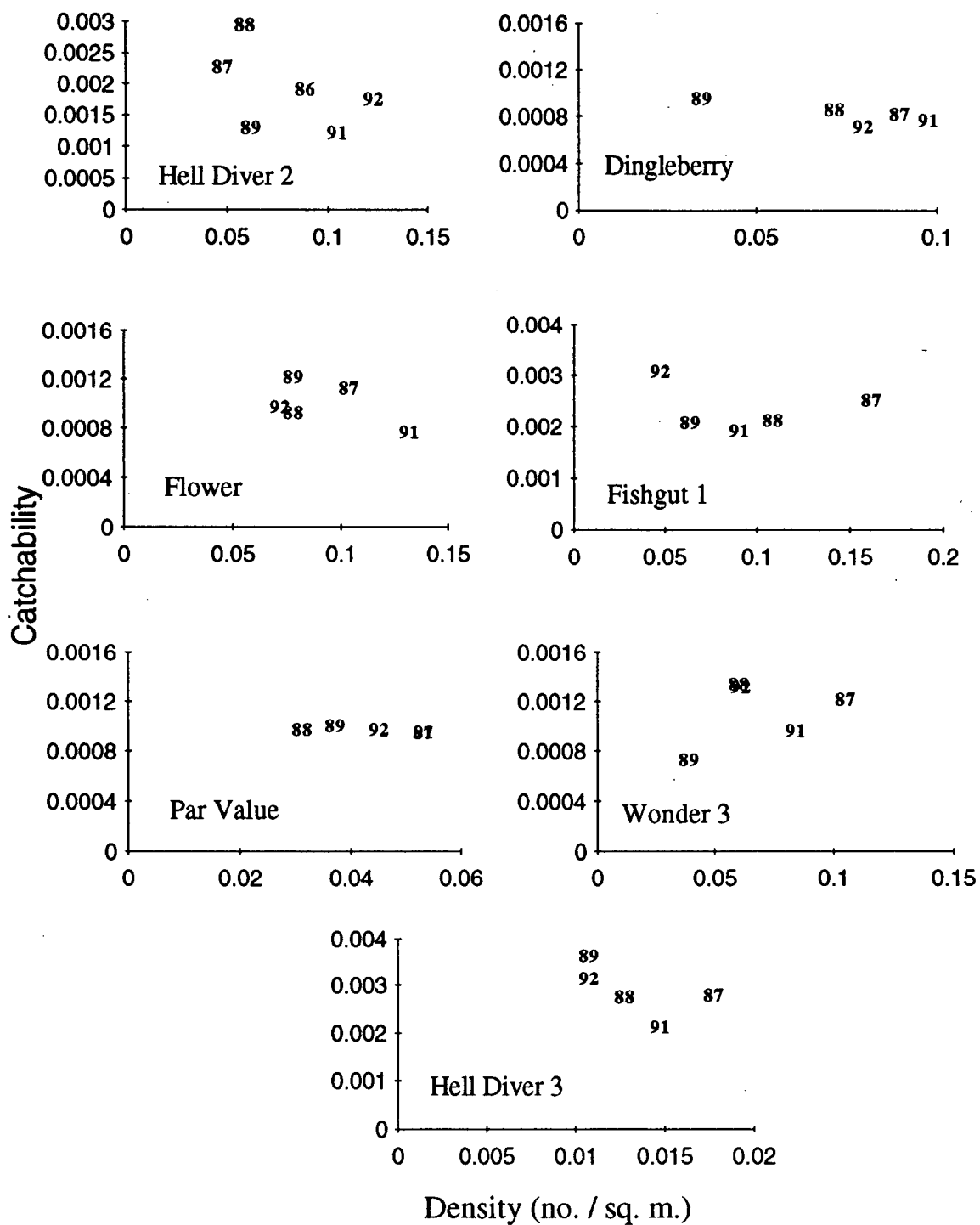


Figure 4. 10. Pooled yearly estimates of adult catchability plotted versus estimated adult density for seven study lakes, 1987 to 1992. Estimates made using the WC estimator and age-invariant $s = .82$, with the plot symbol indicating the year of the estimate. For most of the lakes, there is no apparent strong relationship between adult catchability and adult density.

Table 4.2. Estimates of activity, \hat{k} , for three area parameterizations of the WC encounter rate model for seven study lakes. All values are multiplied by 100. Ab3 = area above the 3 m depth contour, Ab9 = area above the 9 m depth contour; Total = total lake area. Also shown is \hat{q} from the simple WC estimator.

Lake	Ab3	Ab9	Total	simple \hat{q}
Hell Diver 2	0.0172	0.0350	0.0350	0.1900
Dingleberry	0.0727	0.0889	0.0889	0.1135
Flower	0.0988	0.0988	0.0988	0.1002
Fishgut 1	0.0621	0.0795	0.0795	0.2328
Par Value	0.0219	0.0666	0.1055	0.0954
Wonder 3	0.0298	0.0776	0.0776	0.1146
Hell Diver 3	0.0244	0.0720	0.1098	0.2912

Encounter rate WC estimator

With the exception of Hell Diver 2, \hat{k} is much less variable among lakes than q , when effective area is assumed to be either total lake area or area above the 9m contour. (Table 4.2). The \hat{k} 's for Par Value and Hell Diver 3 were lower than the other lake \hat{k} 's when area assumed was Ab9, but higher at total area. Maximum depths for Par Value and Hell Diver 3 are 18 and 13m respectively. Probably an intermediate area parameterization, such as area above the 11m depth contour, would bring their \hat{k} 's within the range displayed by the other four similar lakes. Regardless, the estimates do not support the hypothesis that adult brook trout use only littoral benthic areas, but instead suggest that they use all, or almost all, of the lake benthic areas. The estimate of k for the low density population of Hell Diver 3 is not dissimilar to those of the other lakes. (Figure 4.11). The estimated k for Hell Diver 2 is quite different from the other lakes (Table 4.2). Although mean population density for Hell Diver 2 was apparently similar to the other lakes, effort density was much higher there (Figure 4.11).

Prerecruit and new recruit catchability

With the exception of Par Value, prerecruit q tended to vary inversely with adult population density (Figure 4.12a). Prerecruit q was positively related to mean prerecruit length (Figure 4.12b). New recruit catchability did not vary in any systematic way from pooled adult q (Figure 4.13).

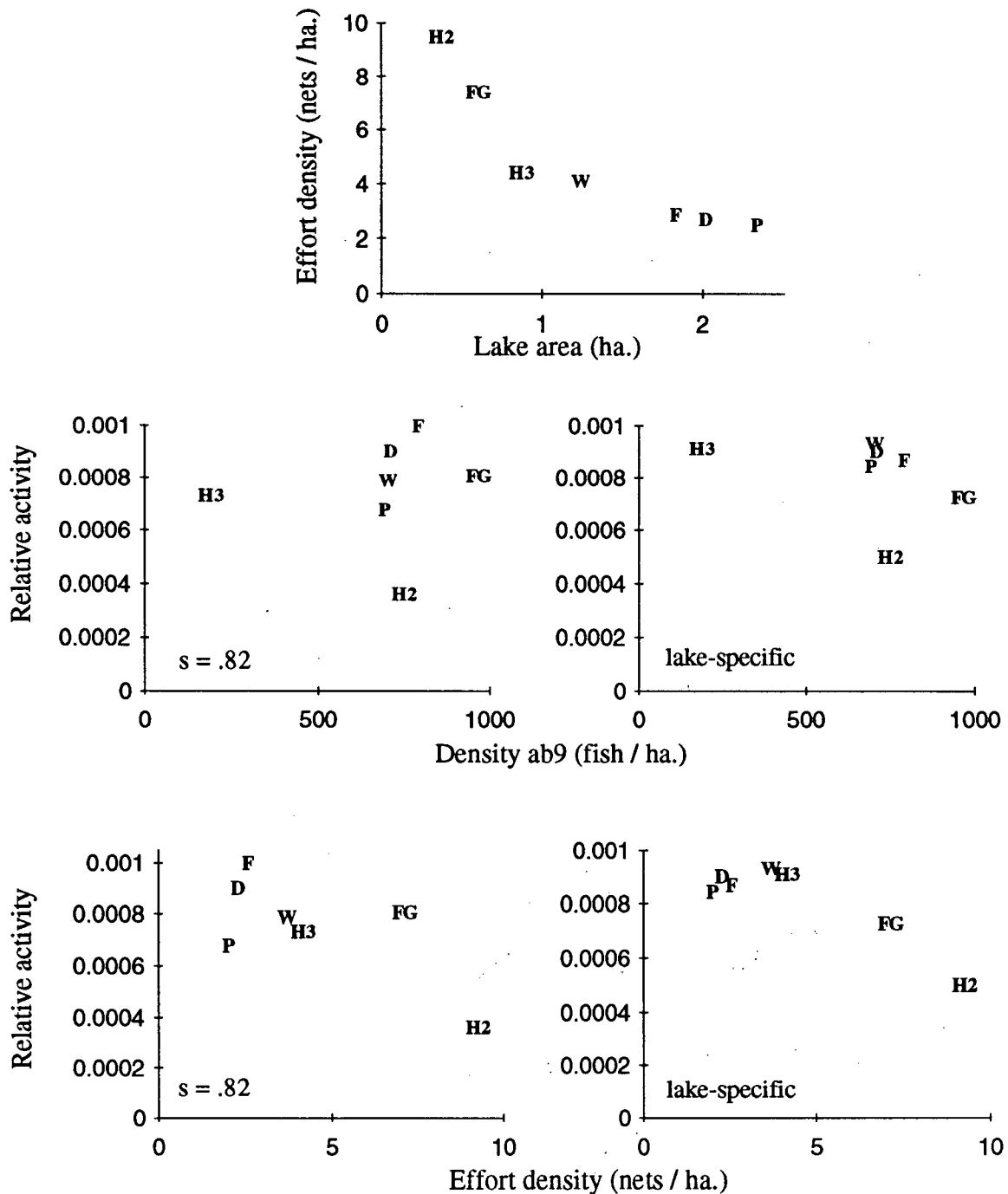


Figure 4.11. The top panel shows mean effort density, nets fished per area (ha), plotted versus lake area. Smaller lakes received much higher effort density. The center panels show relative activity, k , estimated from the WC encounter rate fitting, plotted versus mean adult density 1987 to 1992, using area above the 9m depth contour. The left panel shows the fitting made with age-invariant $s = .82$, while the right shows fittings made with lake specific age-varying survival. The single low density lake does not show k different than the other lakes. The bottom two panels show k versus effort density for the same area and survival parameters. High effort density may be associated with lower k , implying gear competition at high effort density. Plot symbols: H2 - Hell Diver 2; H3 - Hell Diver 3; D - Dingleberry; F - Flower; FG - Fishgut 1; P - Par Value; W - Wonder 3.

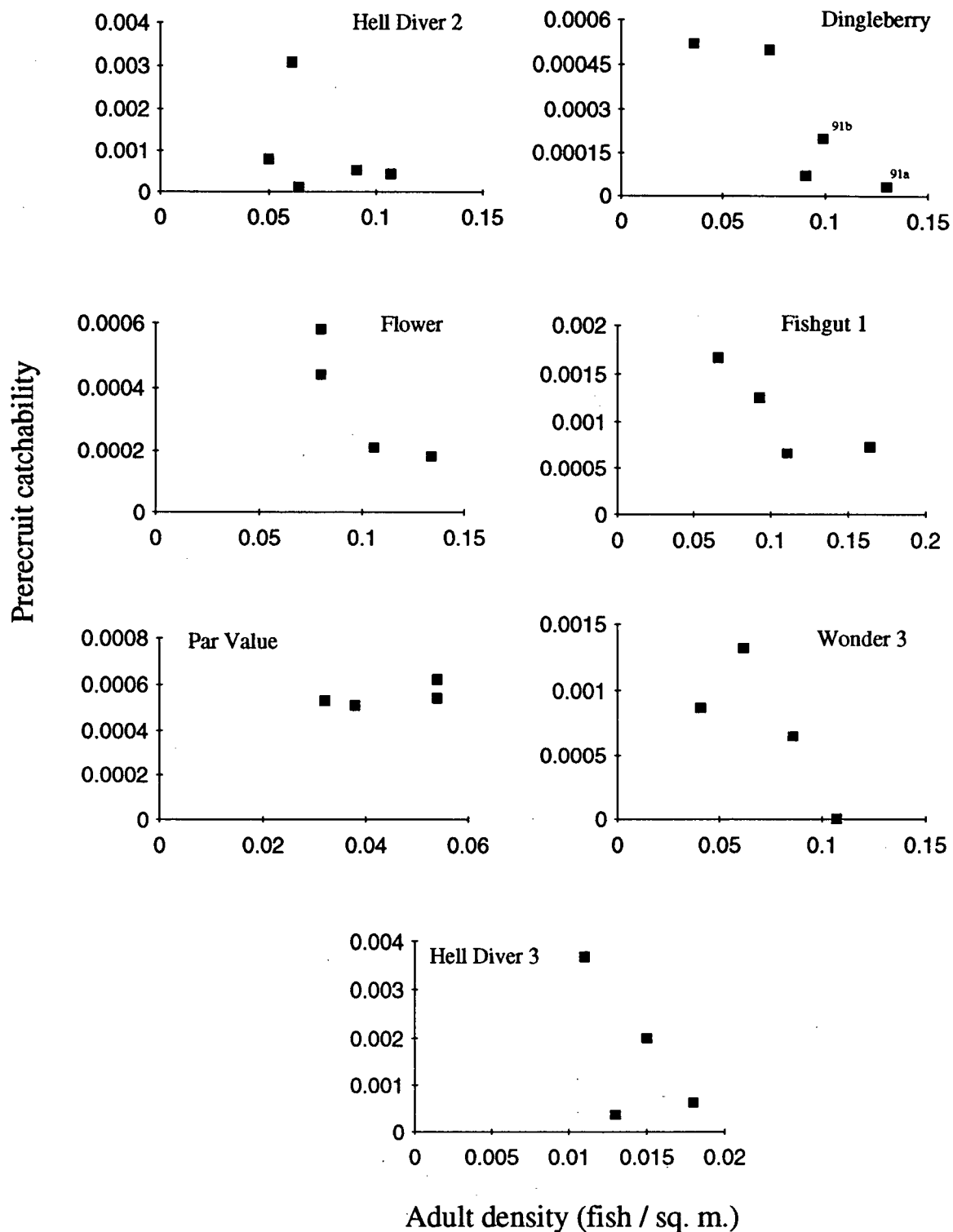


Figure 4.12 a. Pre-recruit q plotted versus adult density for seven study lakes, 1987 through 1991. Estimates made with the constant q WC method using $s = .82$; details provided in the text. With the exception of Par Value, most populations show an inverse relationship between prerecruit q and adult density. Two depletions were made for Dingleberry in 1991; the first is labelled '91a' and the second '91b'.

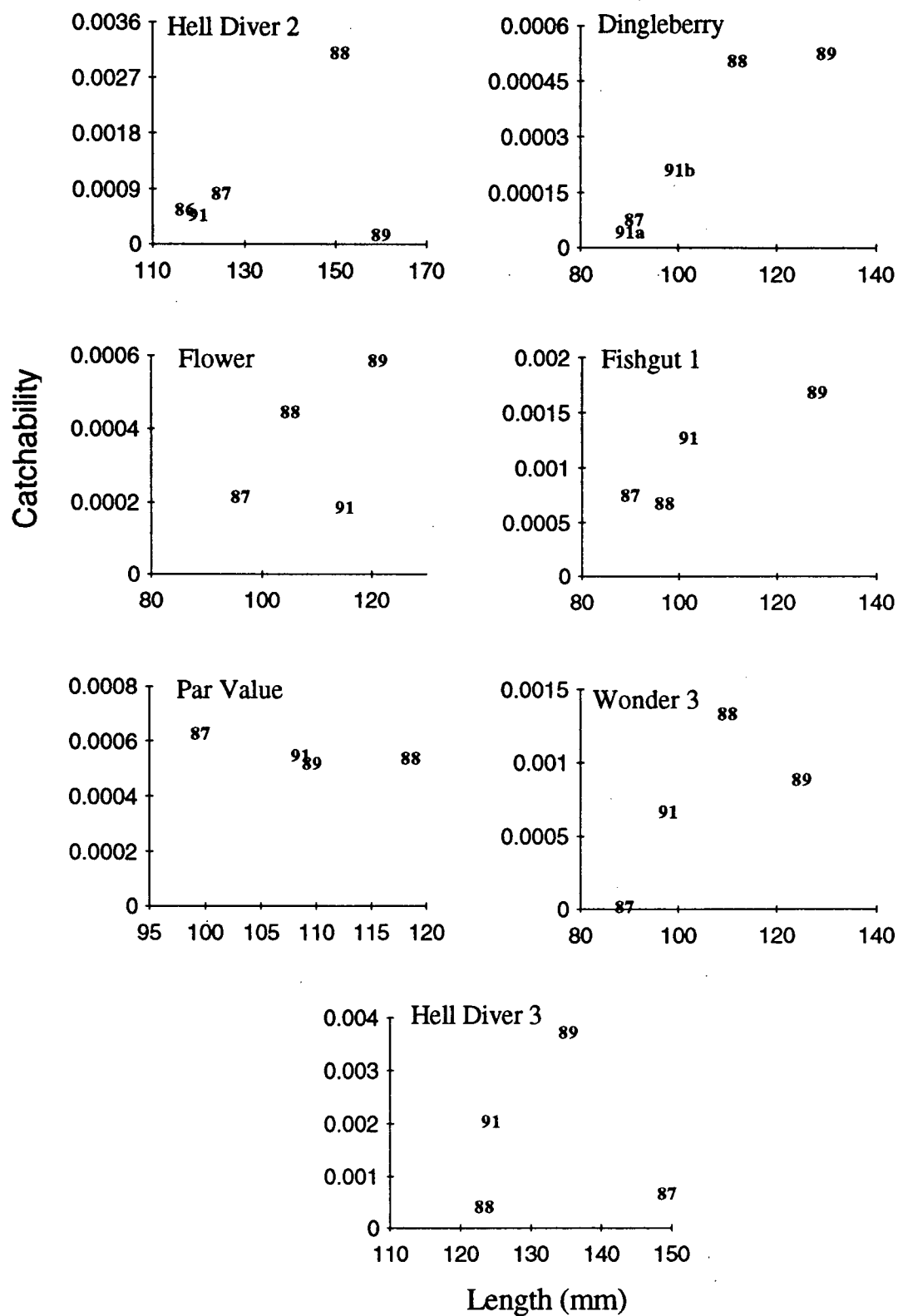


Figure 4. 12b. Estimates of prerecruit catchability plotted versus mean length of prerecruits for six study lakes. For most of the lakes, prerecruit q is positively related to prerecruit length.

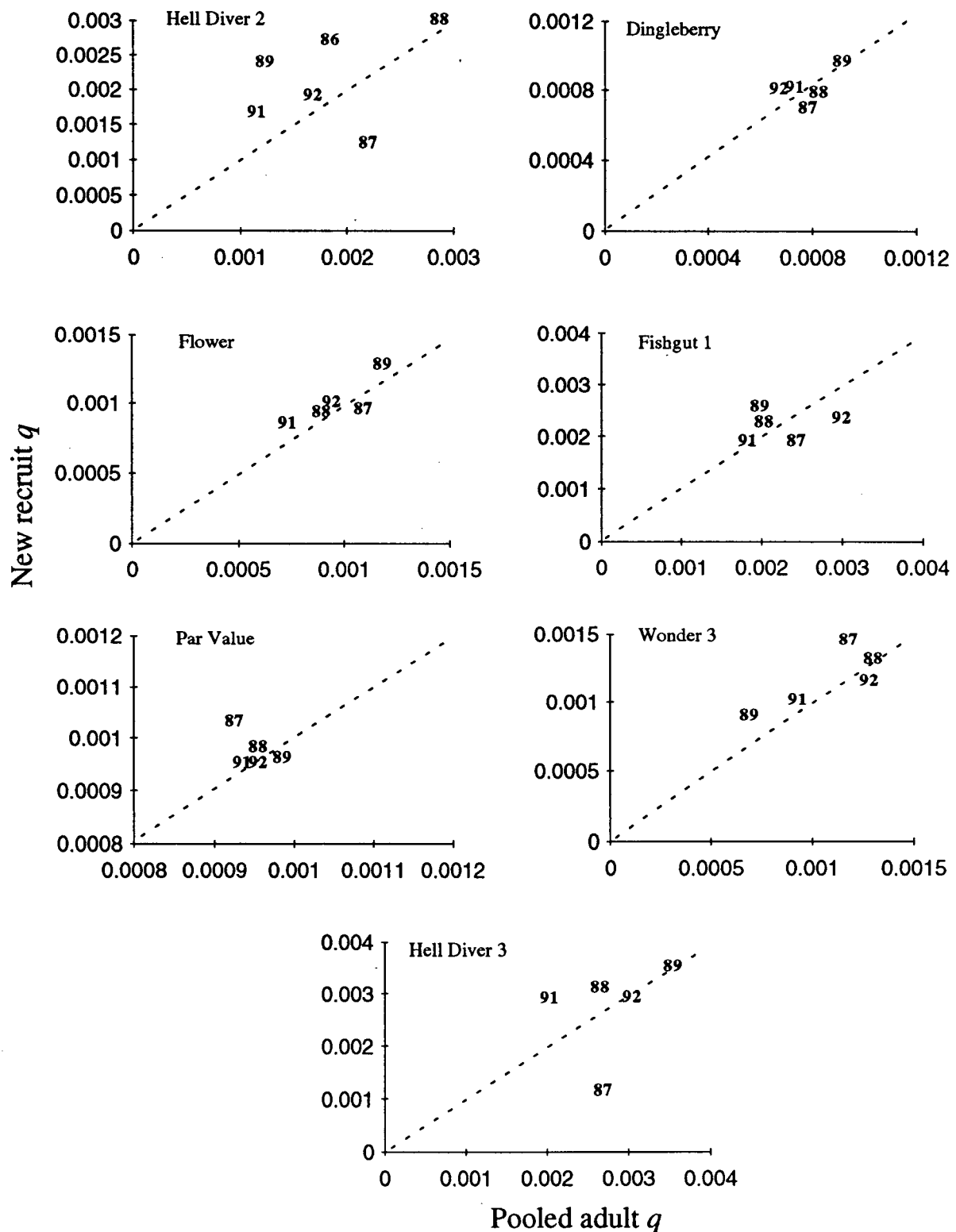


Figure 4.9. Estimated catchability of cohorts newly recruited to the sampling gear, plotted versus estimated pooled adult catchability in the same year, for seven study lakes 1986 to 1992. Estimates made by the WC method, $s = .82$. New recruit catchability does not differ in any systematic way from pooled adult catchability.

DISCUSSION

The results of this chapter confirm Hall's (1991) observation that as adult density declined due to the removals, large cohorts were produced by the study populations. Additionally, as those large cohorts matured, year class strength again declined. Because the treatments were not staggered, strong year classes in 1988 and 1989 might also have been interpreted as due to drought conditions. However, 1987 year classes which were not unusually strong and weak year classes in 1989 or 1990 also occurred during drought conditions. While year class strength in some years may have been exaggerated by weather conditions, the full results suggest that the observed variation is not explained primarily by weather but that adult population density plays a strong role in regulating year class strength.

The uncertainty about age-specific survival for the study populations translates into greater uncertainty about year class strength for older cohorts. Depending on the survival parameterization, time series of year class strength may show old cohorts which appear stronger than those produced during experimental removals. The uncertainty in survival means that the strength of those cohorts, relative to those produced during the experiments, cannot be established. One approach to survival parameterization which I did not utilize, would be to estimate survival parameters which produce a "flat" time series of year class strength estimates prior to the removals, when analyzed with catch-age methods. Given the drought cycle of the Sierra, the influence of weather on year class strength, and the lifespan of alpine lake brook trout, I did not expect that year class strength would necessarily be flat across the relevant timespan.

One reason for attempting ageing error correction was to reverse the downward bias of recruitment estimates for large cohorts occurring in the decade prior to the start of the experiment. Better estimates of the size of the largest cohorts produced in the past might have provided additional evidence about whether strong recruitments during the experimental removals were an unusual occurrence, likely due to the experimental removals. Second, I wanted to ensure that true pattern of strong and weak year classes during the removal years was reproduced in the data. However, given the uncertainty about

natural mortality, the size of cohorts produced before the mid-1980's is highly uncertain regardless of ageing error correction. The low error rates for the youngest ages made the second point of minor importance. The tendency of correction to increase the variance of the estimates, and the differences between methods used for error estimation and procedures used for general ageing, led me to rely on uncorrected data for the analyses in this chapter.

Gillnet catchability of prerecruits appeared inversely related to adult brook trout density, and positively related to prerecruit size. But the results do not resolve how much direct effect adult density has on prerecruit catchability, independent of the presumed effect of adult density on prerecruit size and thus prerecruit encounter rate. Prerecruit size and adult density are confounded for this study, and statistical distinction of their (possibly nonlinear) effects on prerecruit q is not possible, given the limited observations for each lake. Multiple depletions made in the same year, as for Dingleberry in 1991, do little to resolve the two effects. The second depletion invariably has lower adult density co-occurring with greater prerecruit length since the prerecruits grow rapidly in the period between depletions.

The results leave open the intriguing question of which mechanism(s) are most important in the suppression of year class strength by adult brook trout. Young brook trout are occasionally found among the stomach contents of adult brook trout in Sierra Nevada lakes. It seems likely that cannibalism is an important mortality source for young brook trout, and it is quite possible that the observed relationship between adult stock and year class strength is driven mainly by cannibalism upon young brook trout. As noted previously, young fish are presumed to carry out a delicate balancing act, playing off the risk of being eaten against the need to feed, outgrow predation risk, and reach reproductive size (Walters and Juanes 1993). If the tradeoff is manifested in the habitats used by young brook trout, the amount of time spent in those habitats, or their activity or other behavior within those habitats, changes in gillnet q might reflect this. Such changes could be due to altered predation risk, foraging return or both. Regardless, the sensitivity of prerecruit q to adult density confirms that

earlier studies which did not account for the catchability response of juvenile fish in their population estimation, were unjustified in inferring a numerical recruitment response to adult removals.

The estimates of cohort-specific adult q might seem disconcertingly variable. Estimation of q using population estimates made by forward calculation from the WC N_0 (year class strength) parameters, could be variable within and between years for a number of reasons. Among these are ageing error, errors in survival parameterization or changes in survival, small sample size, and density- and size-dependence of q . Other variation in q might be due to year-to-year variation in sampling date, and unintended changes in nets or netting procedures. Any combination of these sources of variation could occur, and some sources, such as size and density, are likely confounded. Nor is there any particular reason to assume that such effects are linear. This combination of factors makes estimation of size- and density dependence in adult catchability implausible for the study. I have presented adult catchability estimates mainly to demonstrate that given the apparent variation in q , there is little positive evidence for density dependence using my data and methods. I cannot conclude that such mechanisms did not occur during the manipulations.

This discussion points to the inability of the field design to reveal such relationships in q . The removal method requires a distinct numerical decline in numbers in order to gain information about population size. As well, exploitation must produce contrast in density sufficient to overcome other error and allow detection of density-dependence in whichever parameter is under study. For small populations such as those used for this study, cohorts cannot persist for more than 2 to 3 years under such exploitation. To detect trends in catchability without reliable information about population size from within-year catch, cohorts must be abundant across several years' data and must be "interwoven" in abundance.

Producing sufficient contrast in density is difficult given the demonstrated numerical response and may destroy the interwoven structure needed to detect or reject density-dependence in q .

Nevertheless, the observed relationships between stock and year class strength, and between stock and prerecruit catchability, are fairly robust to errors in survival parameterization and to variation in

catchability. This is due to the short duration (generally three years or less) over which most cohorts contribute significantly to the catch, and the short period (1984 to 1990) used in the adult density - year class strength comparison. Only major changes in catchability and survival could produce the pattern of catch at age observed, without implying the relationships between adult stock, year class strength and prerecruit q which I have estimated. Detection of such changes generally requires longer catch time series and auxiliary data which were not available.

My encounter rate model for q neglects other size-based variation in behavior. As well, as a two dimensional model it does not account for differences in morphometry of the study lakes, which were intentionally selected for such heterogeneity. However, the similarity in k across lake morphometries and population densities suggests that a simple encounter rate model, which assumes that brook trout use benthic areas to roughly 10m depth, can explain much inter-population variation in q . Some studies have modeled swimming speed, and thus encounter probability, as a power function of length (Rudstam et al. 1984; Henderson and Wong 1991) rather than the simple linear function I chose. The parameters used by those studies resulted in length-encounter probability relationships which were nearly linear over the observed range of fish lengths, so the distinction does not appear important.

Other gillnet selectivity studies have also attempted to account for size-based variation in retention probability (Helser et al. 1991; Henderson and Wong 1991; Borgstrom and Plahte 1992). Such studies have modeled wedging as the dominant retention mechanism. "Wedging", the retention of fish encircled by the mesh posterior to their gillcovers, is an important retention mechanism which may be easily explained by the geometry of the mesh and fish girth (Borgstrom and Plahte 1992). However, other forms of entanglement are common. "Tangling" of fish by their mouthparts or other protrusions leads to retention in mesh sizes which do not necessarily have any simple correspondance to fish girth. Generally, to limit tangling the cited studies have used a narrower range of mesh sizes relative to the range of fish sizes captured, as well as simply excluding tangled fish from their analyses. Compared to the cited studies, the number and range of mesh sizes used in this study was greater relative to the range of fish sizes. I did not record mesh size of capture or mode of retention but tangling was

certainly an important retention mechanism (Figure 2.3 in Hall 1991) and may imply that retention probability was positively related to size. However, any resulting bias in k should have been similar across lakes.

Density dependence in q has been reported for other gillnetted fish populations (Henderson et al. 1983; Borgstrom 1992) including montane small lake stunted brown trout populations similar to Sierra brook trout (Borgstrom 1992). Although most of the lake populations for this study were apparently similar in density, the single population whose density was much lower, Hell Diver 3, did not show q variation unexplained by the simple encounter rate model. One lake, Hell Diver 2, did show q variation unexplained by the encounter rate model and a parsimonious explanation is that high effort density for Hell Diver 2 depletions led to gear competition.

The results of this chapter do not provide an explanation for the full pattern of variation in gillnet catchability shown by most cohorts across multiple years' catch. The downward bias of within-year population estimates suggests that a fraction of each cohort is virtually invulnerable to gillnets in any year. However, the fraction vulnerable appears generally consistent across years. This result rules out only innate, maintained differences in capture probability of individuals across years. Fish which are apparently invulnerable to gillnetting during a depletion become vulnerable by the next year's depletion, and the total fraction vulnerable appears relatively independent of population density. I am unable to distinguish between density-independent turnover of the population between active and inactive states as hypothesized by Hall (1991), the spatial hypothesis which holds that the invulnerable population occupies unfished pelagic areas of the lake (Chapter 3 of this thesis), or simply poor resolution in the estimation. Other studies, which have used both benthic and pelagic gillnets to capture salmonids in small lakes, have also found an apparent significant invulnerable fraction (Kelso and Shuter 1989; T. Johnston, pers. comm.), evidence which weakens the spatial hypothesis.

Despite the importance of gillnets as fishing gear and as tools for gathering information about fish abundance and behavior, the literature is surprisingly devoid of direct observations of fish behavior

with regard to gillnets. Increasingly parameterized models of catchability have been proposed (Helser et al. 1991; Henderson and Wong 1991; Borgstrom and Plahte 1992). Such models have been tested on wild populations for which there are essentially too many unknowns to allow convincing distinction of the specific importance of size- and density-dependent encounter and retention rates. Both encounter and retention are complex emergent properties of fish behavior and gear configuration/deployment. While models of these processes are suggestive, they will remain unconvincing without concurrent direct observations of lake fish individual behavior.

Chapter 5. Summary, conclusions and future research

The resilience of Sierra Nevada small lake brook trout populations to gillnet exploitation appears due to at least three distinct phenomena operating on different time scales. First, at any time a significant density-independent proportion of the adult population is apparently invulnerable to bottom-set gillnets. Second, removal of adults leads to increased year class strength of ensuing cohorts. Third, faster growth of young fish following removals probably leads to earlier maturity (Hall 1991). Acting together, these phenomena frustrate attempts to reduce adult population density. Following three years of removals, in 1991 length at age of gillnetted brook trout was similar to or lower than length prior to the experiment, and total adult densities were similar or even higher. This result reinforces the conclusions of several authors that increased exploitation of stunted salmonid populations is unlikely to alleviate stunting unless recruitment is inhibited (Langeland 1986; Donald and Alger 1989; Hall 1991; Borgstrom 1994). The results of the current study are more convincing due to replication, duration of the experiment and more rigorous estimation methods.

"Stunting alleviation" studies (Langeland 1986; Donald and Alger 1989; Hall 1991) have not clearly stated prior expectations with regard to the growth response to density reduction. A theoretical or even empirical approach to predicting how fish size might relate to population density has been lacking until recently (Walters and Post 1993). Stunted populations have been explicitly or implicitly considered abnormal, because larger adult body size occurs for lake populations elsewhere in the species' range (Hall 1991). Brook trout stunting cannot be considered abnormal unless it is demonstrated that theory would predict a different life history, given adult and juvenile growth and mortality rates and size-specific fecundity (Hutchings 1993).

Due to the paucity of information about exploitation rates for Sierra lakes, it is unclear whether low productivity lake populations could produce much larger fish, without high vulnerability to overexploitation at lower density. Of eight lakes I netted in both 1991 and 1992, all were visited at least once by anglers while I was working. Some of these lakes are relatively distant from developed trails. It is clear that

anglers often return to such lakes year after year and have the expectation of retaining fish to eat. As noted by Hall (1991), "few lakes on the eastern side of the Sierra Nevada crest contain large brook trout." He observed that "these populations are usually in the most remote lakes suggesting that periodic catastrophic events such as avalanches or partial winter-kill regulate population abundance." Instead, I propose that lakes with large brook trout tend to be those with infrequent recruitment, and that such lakes are those with spawning habitat only occasionally capable of supporting eggs and sac fry through the winter to emergence. Some may be remote, high elevation lakes near the "top" of watersheds and thus without permanent inflow and outflow streams to produce spawning habitat. Others, however, are accessible lower elevation tarns which lack year-round inlet and outlet streams. The evident persistence of some low-density populations suggests that the idea of producing larger brook trout in small alpine lakes was not completely unfounded. The recruitment response makes the point irrelevant for wild brook trout in most Sierra lakes.

While biologists may consider 200 mm brook trout undesirable, I met few anglers who expressed outright dissatisfaction with the size of mountain small lake brook trout. Most appeared to appreciate the ability of wild brook trout to thrive in an unproductive environment. Nevertheless, there is continued interest in manipulating brook trout populations. Fish managers wish to replace brook trout with species which do not reproduce in alpine lakes, so that density and fish size can be controlled. As well, introduced fish have been implicated in the decline of native aquatic species, and agencies are interested in eliminating fish from some watersheds to attempt to restore aquatic communities. At least six methods for extirpation of self-sustaining brook trout populations have been suggested. Among these are piscicides, gillnetting, stocking with other salmonids, introduction of sterile brook trout to reduce population fecundity, blocking access to spawning areas (Hall 1991), and introduction of a species-specific disease. At this time the least disruptive and most reversible manipulation techniques are considered most desirable. Agencies are currently reluctant to use piscicides, and some lakes are simply too deep for poisoning. In the past, other salmonids have been airplane stocked "over" brook trout populations in the hope that large non-brook trout adults would be produced and consume young brook trout, reducing brook trout density and improving their growth. This approach appears to have failed in most cases (Hall 1991). Gillnetting now appears likely to succeed only in lakes where recruitment is irregular.

Future research

This study and its predecessor have yielded minor returns toward improved management of stunted brook trout populations, for the effort expended. I hesitate to claim that advances in the ability to manage, manipulate, and enhance the size and yield of lake salmonids will be best achieved by further intensive study of recruitment dynamics. Nevertheless, experimental manipulation of Sierra lake brook trout populations has verified a seldom demonstrated inverse relation between adult density and year class strength, at least partly because recruitment appears less "noisy" than for most freshwater fish populations. Other characteristics of the lakes also make them ideal for further research on recruitment dynamics: ease of replication, freedom of manipulation, and lack of other disturbances (Hall 1991). Future research will likely be directed to determining which mechanisms that suppress year class strength for natural populations, respond to adult density reduction. In particular, testing of ideas about how individual behavioral mechanisms of young fish lead to whole population dynamics (Walters and Juanes 1993) may be tractable. While gillnet sampling has also suggested the sensitivity of young fish to either adult-associated risk or adult effects on foraging return, further understanding of recruitment dynamics will be contingent on the use of methods other than gillnetting to observe their numbers and behavior.

Major conclusions

1. Repeatability of brook trout age estimates decreases with estimated age
2. Ageing error correction, using the methods of Richards et al. (1992), relieves much of the bias for age composition and year class strength estimates, but results in increased variance of the estimates
3. For age-specific period level removal estimates, initial period catchability does not differ systematically from catchability for the remainder of the depletion
4. Period-level removal data give downward-biased estimates of population size

5. Effort-adjusted catchability is often higher for night than day removal periods, and the disparity may increase with fish size or age
6. Year class strength appears inversely related to adult density
7. Gillnet catchability of young fish is positively related to size or inversely related to adult density, or both

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Appendix A

Table A.1a. Catch -at-age, corrected catch-at-age and standard errors for corrected catch-at-age for Hell Diver 2 removals, 1987 to 1992. For years with more than one depletion, the depletion number follows the year. Correction methods are given in the text. Standard errors cannot be estimated when corrected catch-at-age is 0.

	age															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Hell Diver 2 1986																
catch	1	1	1	3	23	11	11	6	18	14	10	4	3	0	0	0
corrected	1	1	1	1	26	10	12	2	22	15	11	3	2	0	0	0
S.E.	4	4	4	8	16	11	10	10	13	12	9	10	8	-	-	-
Hell Diver 2 1986-2																
catch	3	0	0	0	5	2	2	3	5	3	3	4	0	0	0	0
corrected	3	0	0	0	5	2	2	3	6	3	3	4	0	0	0	0
S.E.	5	-	-	-	5	4	5	5	3	5	5	5	-	-	-	-
Hell Diver 2 1987																
catch	0	12	1	0	5	4	4	8	8	2	3	4	1	2	0	0
corrected	0	12	1	0	5	4	3	9	10	0	3	5	0	2	0	0
S.E.	-	4	8	-	8	8	7	7	7	6	7	7	-	5	-	-
Hell Diver 2 1988																
catch	1	40	27	2	0	3	6	4	1	4	5	2	2	0	0	0
corrected	0	41	28	1	0	3	7	4	0	4	7	1	2	0	0	0
S.E.	4	16	14	6	-	7	9	9	-	8	9	8	7	-	-	-
Hell Diver 2 1989																
catch	152	1	52	17	0	1	1	1	0	0	4	3	0	0	0	0
corrected	152	0	54	16	0	1	1	1	0	0	4	3	0	0	0	0
S.E.	19	-	15	4	-	4	5	5	-	-	9	8	-	-	-	-
Hell Diver 2 1991																
catch	0	56	133	6	10	0	0	0	0	1	0	0	0	0	0	0
corrected	0	52	143	0	10	0	0	0	0	1	0	0	0	0	0	0
S.E.	-	27	11	4	13	-	-	-	-	4	-	-	-	-	-	-
Hell Diver 2 1992																
catch	8	60	102	61	7	1	1	1	0	0	0	0	0	0	0	0
corrected	7	58	106	64	4	0	1	1	0	0	0	0	0	0	0	0
S.E.	10	15	5	16	10	5	5	5	-	-	-	-	-	-	-	-

Table A.1b . Catch -at-age, corrected catch-at-age and standard errors for corrected catch at age for Dingleberry Lake depletions, 1987 to 1992. For years with more than one depletion, the depletion number follows the year. Correction methods are given in the text. Standard errors cannot be estimated when corrected catch-at-age is zero.

	age															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Dingleberry 1987																
catch	23	225	120	37	83	53	25	32	23	20	1	2	1	0	0	0
corrected	18	229	123	29	90	54	20	35	23	21	0	1	1	0	0	0
S.E.	19	41	12	26	28	28	21	20	22	19	-	8	5	-	-	-
Dingleberry 1988 -1																
catch	92	231	246	88	18	49	25	18	16	15	15	3	0	1	1	0
corrected	87	230	257	87	9	56	23	17	16	15	19	0	0	1	1	0
S.E.	28	36	16	27	17	25	19	18	17	18	17	-	-	6	6	-
Dingleberry 1988-2																
catch	5	20	20	14	2	5	1	4	1	1	2	0	0	0	0	0
corrected	5	20	20	15	1	6	0	5	0	1	2	0	0	0	0	0
S.E.	7	5	10	10	6	7	-	7	5	5	6	-	-	-	-	-
Dingleberry 1989																
catch	409	56	81	55	17	6	15	7	7	4	2	5	1	0	0	0
corrected	408	55	83	58	16	4	18	6	8	4	1	7	0	0	0	0
S.E.	35	24	13	25	17	12	17	13	14	12	10	12	-	-	-	-
Dingleberry 1991-1																
catch	6	303	302	14	7	6	2	1	1	2	1	0	0	0	0	0
corrected	0	303	321	2	6	7	2	1	1	3	1	0	0	0	0	0
S.E.	-	46	16	12	12	12	7	6	6	9	5	-	-	-	-	-
Dingleberry 1991- 2																
catch	85	421	241	7	5	4	2	1	3	1	0	0	1	0	0	0
corrected	76	429	250	0	5	4	2	0	4	1	0	0	1	0	0	0
S.E.	29	37	15	-	10	10	7	6	10	5	-	-	4	-	-	-
Dingleberry 1992																
catch	150	163	177	78	4	6	3	3	0	0	1	0	0	0	0	0
corrected	146	162	184	79	0	6	3	3	0	0	1	0	0	0	0	0
S.E.	28	30	11	24	-	11	9	8	-	-	4	-	-	-	-	-

Table A.1c . Catch -at-age, corrected catch-at-age and standard errors for corrected catch at age for Flower Lake depletions, 1987 to 1992. For years with more than one depletion, the depletion number follows the year. Correction methods are given in the text. Standard errors cannot be estimated when corrected catch-at-age is 0.

	age															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Flower 1987																
catch	28	126	103	89	92	56	18	19	6	6	8	3	0	0	0	0
corrected	25	126	103	88	97	59	13	22	3	6	11	1	0	0	0	0
S.E.	18	25	26	25	26	21	16	16	12	12	13	8	-	-	-	-
Flower 1988																
catch	156	111	113	55	37	34	47	14	12	3	1	0	2	1	0	0
corrected	154	111	117	54	36	32	55	9	14	1	0	0	3	1	0	0
S.E.	28	29	30	23	18	23	21	15	15	9	5	-	8	5	-	-
Flower 1989																
catch	237	177	53	38	31	19	23	11	4	5	1	3	0	0	0	0
corrected	233	182	51	38	32	17	26	11	2	6	0	3	0	0	0	0
S.E.	27	24	22	19	19	17	18	16	11	12	-	8	-	-	-	-
Flower 1991																
catch	25	394	470	66	27	16	11	5	5	4	1	0	1	0	0	0
corrected	16	391	499	52	25	16	12	4	5	5	0	0	1	0	0	0
S.E.	18	42	41	28	20	17	16	12	12	11	-	-	4	-	-	-
Flower 1992																
catch	242	65	218	198	35	14	5	8	1	4	2	1	2	0	0	0
corrected	240	58	223	213	26	13	3	9	0	5	2	0	2	0	0	0
S.E.	32	25	30	26	21	15	10	12	-	10	9	7	7	-	-	-

Table A.1d. Catch -at-age, corrected catch-at-age and standard errors for corrected catch-at-age for Fishgut 1 depletions, 1987 to 1992. For years with more than one depletion, the depletion number follows the year. Correction methods are given in the text. Standard errors cannot be estimated when corrected catch-at-age is zero.

	age															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Fishgut 1 1987																
catch	6	48	98	24	38	16	9	1	3	1	0	1	0	0	0	0
corrected	5	46	104	20	42	15	9	0	4	1	0	1	0	0	0	0
S.E.	9	20	21	15	18	15	11	-	9	5	-	4	-	-	-	-
Fishgut 1 1988																
catch	37	32	115	100	27	29	22	7	6	7	1	0	0	0	0	0
corrected	36	28	118	106	22	30	24	5	6	8	0	0	0	0	0	0
S.E.	18	18	23	21	16	17	15	11	12	11	-	-	-	-	-	-
Fishgut 1 1989																
catch	215	81	12	33	46	15	20	9	3	8	5	1	0	0	0	0
corrected	213	84	9	33	51	11	23	9	0	10	5	0	0	0	0	0
S.E.	23	20	13	17	19	14	14	12	9	13	11	-	-	-	-	-
Fishgut 1 1991																
catch	93	169	105	12	8	10	11	12	15	5	1	1	0	0	0	0
corrected	90	172	110	8	7	10	11	12	19	4	0	1	0	0	0	0
S.E.	23	24	23	13	11	13	13	14	17	11	-	5	-	-	-	-
Fishgut 1 1992																
catch	136	61	88	42	12	3	10	10	3	2	3	2	0	0	0	0
corrected	135	60	92	43	11	1	11	12	2	1	4	2	0	0	0	0
S.E.	24	22	23	20	14	8	12	14	9	8	10	7	-	-	-	-

Table A.1e. Catch-at-age, corrected catch-at-age and standard errors for corrected catch-at-age for Par Value removals, 1987 to 1992. For years with more than one depletion, the depletion number follows the year. Correction methods are given in the text. Standard errors cannot be estimated when corrected catch-at-age is zero. Corrected catch and standard errors are rounded to the nearest integer.

	age															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Par Value 1987																
catch	82	88	36	9	23	101	26	70	54	86	37	6	2	0	0	1
corrected	80	90	36	6	15	120	8	80	44	111	31	0	0	0	0	1
S.E.	23	22	19	12	17	21	16	21	17	17	17	-	-	-	-	4
Par Value 1988-1																
catch	319	73	38	23	16	7	52	5	21	32	45	22	15	1	1	0
corrected	317	74	38	23	16	0	62	0	18	32	58	19	13	0	0	0
S.E.	35	30	24	19	17	-	23	-	20	22	23	22	20	-	-	-
Par Value 1988-2																
catch	49	6	0	2	0	0	5	2	2	2	4	1	2	1	0	0
corrected	49	6	0	2	0	0	5	2	2	2	6	0	3	1	0	0
S.E.	15	9	-	6	-	-	2	7	7	7	9	-	7	5	-	-
Par Value 1989																
catch	415	302	28	12	9	2	4	28	14	15	16	27	9	0	0	1
corrected	409	313	23	12	10	1	0	35	11	15	13	39	2	0	0	1
S.E.	33	29	20	14	13	7	-	23	19	19	19	22	15	-	-	4
Par Value 1991																
catch	286	190	296	86	8	7	5	3	2	6	4	1	0	5	3	0
corrected	282	185	312	84	2	7	5	3	1	8	4	0	0	6	2	0
S.E.	34	34	33	27	12	12	11	9	8	13	11	-	-	12	9	-
Par Value 1992																
catch	288	223	72	104	36	7	5	0	0	3	3	1	1	1	3	1
corrected	283	229	67	112	35	4	5	0	0	3	4	0	1	0	5	0
S.E.	31	31	28	27	22	13	10	-	-	8	10	7	7	-	11	6

Table A.1f. Catch -at-age, corrected catch-at-age and standard errors for corrected catch-at-age for Wonder 3 depletions, 1987 to 1992. For years with more than one depletion, the depletion number follows the year. Correction methods are given in the text. Standard errors cannot be estimated when corrected catch-at-age is zero.

	age															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Wonder 3 1987-1																
catch	0	63	37	19	12	51	17	11	8	6	6	4	2	1	2	0
corrected	0	63	38	18	7	60	14	11	8	6	7	4	2	0	2	0
S.E.	-	19	15	14	13	16	12	11	11	10	10	9	8	7	7	-
Wonder 3 1987-2																
catch	23	75	29	12	16	56	17	22	15	11	6	2	0	1	0	0
corrected	21	77	29	10	12	66	11	24	15	12	6	1	0	1	0	0
S.E.	13	18	16	12	12	15	13	13	13	13	11	7	-	4	-	-
Wonder 3 1988																
catch	106	39	28	85	46	8	39	25	19	14	10	4	1	0	0	0
corrected	105	39	24	91	47	0	45	24	19	14	11	3	0	0	0	0
S.E.	19	18	17	18	15	-	13	14	13	13	12	9	-	-	-	-
Wonder 3 1989																
catch	392	58	16	28	15	14	3	26	8	6	7	8	3	2	0	0
corrected	391	60	14	30	14	14	0	32	5	5	7	11	2	1	0	0
S.E.	29	22	15	19	15	15	-	18	14	14	13	15	11	8	-	-
Wonder 3 1991																
catch	146	237	146	28	9	19	6	3	0	9	3	0	1	0	0	0
corrected	141	241	152	25	6	22	5	2	0	11	2	0	1	0	0	0
S.E.	24	27	27	19	12	17	12	8	-	13	9	-	4	-	-	-
Wonder 3 1992																
catch	38	92	104	72	16	8	3	1	2	2	0	1	0	0	0	0
corrected	36	91	107	76	13	8	3	0	2	2	0	1	0	0	0	0
S.E.	18	25	27	22	15	12	9	6	8	7	-	4	-	-	-	-

Table A1g. Catch -at-age, corrected catch-at-age and standard errors for corrected catch-at-age for Hell Diver 3 depletions, 1987 to 1992. For years with more than one depletion, the depletion number follows the year. Correction methods are given in the text. Standard errors cannot be estimated when corrected catch-at-age is zero.

	age															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Hell Diver 3 1987																
catch	8	2	2	9	3	5	15	7	12	10	2	1	0	0	0	0
corrected	8	2	2	10	2	4	18	5	14	12	0	0	0	0	0	0
S.E.	7	5	6	10	7	7	7	7	8	9	7	4	-	-	-	-
Hell Diver 3 1988																
catch	6	25	4	3	1	3	1	3	8	5	1	2	0	0	0	0
corrected	6	26	4	3	1	3	0	2	10	5	0	2	0	0	0	0
S.E.	7	5	6	10	7	7	7	7	8	9	7	4	-	-	-	-
Hell Diver 3 1989																
catch	22	22	6	2	2	0	2	3	1	2	4	1	0	0	0	0
corrected	22	23	6	2	2	0	2	4	0	2	6	0	0	0	0	0
S.E.	10	10	7	5	5	-	5	7	5	6	6	-	-	-	-	-
Hell Diver 3 1991																
catch	67	50	9	5	3	1	0	0	2	0	1	0	1	1	0	1
corrected	66	52	8	5	3	1	0	0	2	0	1	0	1	1	0	1
S.E.	16	12	10	9	7	4	-	-	5	-	4	-	5	5	-	4
Hell Diver 3 1992																
catch	6	22	9	7	6	1	0	1	0	0	0	2	0	0	0	0
corrected	6	23	9	7	7	1	0	1	0	0	0	2	0	0	0	0
S.E.	7	9	6	6	7	4	-	4	-	-	-	4	-	-	-	-