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Stock-recruitment relationships for alewives and blueback herring
returning to the Mactaquac Dam, Saint John River, N.B.

by

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Abstract

Stock-recruitment relationships were found between the escapement to the Mactaquac Dam headpond on the Saint John River, N.B., of alewives (Alosa pseudoharengus) and blueback herring (A. aestivalis) in year X and the total returns to the fishway at the dam four or five years later. A relationship was also found between the escapement of alewives in year X to the return of virgin spawners of that year-class in years X+3 through X+6. A lack of adequate data prevented the examination of a similar relationship for blueback herring.

Résumé

On a découvert des rapports concernant le recrutement des stocks entre la quantité de gaspareaux (Alosa pseudoharengus) et d'aloses d'été (A. aestivalis) transmise (échappement) pendant l'année X au bassin d'amont du barrage de Mactaquac, situé sur le fleuve Sain-Jean (N.-B.) et le total des retours à la passe migratoire du barrage quatre ou cinq années plus tard. On a aussi constaté un rapport entre l'échappement du gaspareau pendant l'année X et le retour de reproducteurs vierges de cette classe d'âge entre les années X+3 et X+6. Le manque de données pertinentes n'a pas permis de vérifier s'il y a des rapports semblables chez l'alose d'été.

Introduction

The search for clupeid stock-recruitment relationships has been elusive although one has often been assumed eg., Saville (1980), Stocker et al. (1985). Marine clupeids have been characterized as having recruitment completely independent of spawning stock over a wide range of escapements and thus more influenced by density-independent than by density-dependent factors (Cushing 1971; Murphy 1977), although both factors have been found important (Nelson et al. 1976; Stocker et al. 1985; Anthony and Fogarty 1985). Both factors are also important for anadromous species such as American shad (*Alosa sapidissima*) (Leggett 1977; Creco and Savoy 1984; Creco et al. 1986). Leggett (1976) reported a stock-relationship for American shad from the Connecticut River but Creco and Savoy (1984) were unable to confirm a relationship, possibly due to their limited number of years of data and range of escapements. A relationship between juvenile shad abundance and subsequent adult return may exist (Creco et al. 1983) although its value is reduced by the fact that it depends essentially on one point. Richkus and DiNardo (1984) have concluded that, under normal conditions, shad recruitment is independent of stock size.

Havey (1973) found a fair correlation between the number of spawning female alewives (*A. pseudoharengus*) and juvenile production as well as a good correlation between juvenile production and subsequent adult recruitment for a moderate range of escapements. He concluded that the magnitude of adult escapement roughly forecast the return four years later. No relationship was found with a smaller range of escapements from fewer years (Havey 1961). Brown (1972) concluded that a stock-recruitment relationship did exist for landlocked alewives in Lake Michigan but Henderson and Brown (1985) could find no relationship for alewives from Lake Huron. Comparable information for blueback herring (*A. aestivalis*) seems unavailable.

Historically, no significant gaspereau (alewives and blueback herring combined) fishery existed in the Saint John River upriver of the present Mactaquac Dam site. Perley (1852) noted that "...the gaspereau and shad rarely ascend the Saint John higher than Fredericton four miles above which the swift water and strong rapids commence." In the recent past, relatively small numbers of gaspereau migrated past this site, as indicated by the 50 to 22,000 fish that annually used the Beechwood Dam fish hoist between 1958 when it was completed and 1967 when the Mactaquac Dam was completed. Between 1968 and 1978, the numbers of gaspereau passed through the fish-lift increased over 200-fold from approximately 22,000 fish to over 4.4 million fish (Table 1). A commercial fishery was begun in 1974 and returns have since declined somewhat.

This paper presents stock-recruitment relationships for alewives, blueback herring and for both species combined for stocks newly established in a headpond environment.

Materials and Methods

Annual estimates were made of the numbers of gaspereau released upriver of the Mactaquac Dam between 1968 and 1985. Numbers were visually estimated by the fish-lift crew as the hopper was loaded. Accuracy of these estimates was checked

from 1973 through 1976 by counts of tank-truck contents (range 27-55 counts) over the major part of the run. In 1979, a randomized estimation procedure was used in which counts were made of the contents of about 30% of the 443 trucks. The potential bias due to fall back of fish from the release site which is about 0.8 km upstream from the turbine intake canal was evaluate by a tagging program in 1973. Floy T-bar tags of various colors were applied to 8,230 fish released into the headpond during a five week period. Observations for tagged fish were made at the fish-lift and at the release site. Corrections to the estimated run size for estimation error or fallback were believed unnecessary because of the small size of the correction factors.

Weekly samples of 50 fish were collected from the fish-lift throughout the run from 1973 to 1977; in 1978, 50 fish were collected twice weekly while from 1979 onwards 100 fish were taken twice weekly. Species were identified according to peritoneal color and morphometrics (Scott and Crossman 1973) which, for 1978 and 1979, was checked using scale pattern criteria (MacLellan et al. 1981). Age compositions based upon majority agreement were determined following three independent scale readings, the third of which was made only if the first two did not agree.

Estimates of the number of fish harvested by the commercial fishery at the dam were obtained by dividing the weight of fish per truck load (determined from the buyers' weighing slips to the nearest 4.5 kg) by the mean weight per fish. Numbers and mean weight per fish of each species were based on a two sample unit moving average.

Empirical relationships between escapement in year X and return in year $X+t$ were calculated for each species and for both species combined using least squares linear regressions with both untransformed and logarithmically transformed (base 10) data. Analyses of variance (ANOVA) and coefficients of determination (r^2) were used to select the best relationships. Plots of standardized residuals were examined to determine the appropriateness of the regression model. Measurement errors in the escapement estimates (X variable) were shown to be minor and are believed to be much less than those in the estimates of total return and ordinary least squares regression was assumed to be appropriate.

The parent-progeny relationship for alewives was further examined for the 1968-1978 year-classes using adult recruitment estimated as the sum of virgin alewives of ages 3 to 6. The 1973 alewife age-composition was assumed applicable to the returns of 1971 and 1972 because relatively little change was observed in the first few years of sampling. This assumption was not made for blueback herring because the adequacy of age-composition sampling for them prior to 1978 (the 1968-1974 year-classes) was substantially less than for alewives. On average, 150 blueback herring were sampled annually versus 270 alewives. When coupled with the relatively small estimated annual return of blueback herring a potential exists for large errors when estimating the number of virgin fish. The 1975-1978 blueback herring year-classes are not considered because of the narrow range (about 20,000 fish) in escapements.

The equations (Table 2) relating escapement of each species to subsequent recruitment were used to estimate the available harvest (number of fish exceeding the replacement level) and the recruit/spawner ratio for a range of escapements.

Multiple linear regression was used to test the hypothesis that the escapement level of one species influenced the future recruitment abundance of the second species. The escapements of both species in year X were regressed against the return of the target species in year X+t. The lag t was that which provided the best linear relationship. All variables were logarithmically transformed when blueback herring was the target species.

Results

The difference between tank-truck counts and fishway visual estimates ranged from 3.1% overestimates in 1973 and 1974 to 7.7% and 5.6% underestimates in 1975 and 1976. In 1979, the most comprehensive evaluation of the accuracy of fishway estimation procedures resulted in a 3.8% underestimate. Over-estimation of the run size due to fallback was evidently minor because only two tags were reported from the fish-lift and none were observed among more than 80,000 counted or observed at the release site. The reported observation of tagged fish at the fish-lift undoubtedly somewhat underestimates their true abundance.

A scale sample of 800 to 1,400 fish per species was calculated to be necessary to estimate the abundance of fish at each age (range 3-11 years) with error rates of 15-20% at a probability of 0.8 (C.Vithayasai, Dept. Fisheries and Oceans, pers. comm.). Age composition estimates since 1979, when more intensive sampling was begun, are likely more accurate but error rates of > 20% may have occurred in previous years, particularly for the youngest and oldest age groups. The accuracy of estimates of the proportion of virgin fish in any age-group is further reduced at small sample sizes, which is a problem most acute for blueback herring.

Reproduction curves relating the returns four and five years after spawning and the spawning escapement in year X were found for alewives, blueback herring and both species combined (Fig. 1, 2, 3). Note that in each plot, the values for the three or four most recent escapements (1977-1980) tend to clump together at the lower edge of the distribution, perhaps indicating a downward shift in the relationship. The best relationship, for alewives and both species (combined), was based on returns four years after spawning and untransformed data (Table 2). A log-log transformation and returns after five years was best for blueback herring. These relationships were significant ($P < 0.005$) and explained from 55% to 67% of recruitment variation. Returns of alewives, by year-class, were also positively related ($r^2=0.65$; $P < 0.005$) to increasing escapement over the observed range of 20,000 to 1,160,000 fish (Table 2, Fig. 4). Note that year-classes after 1978 have not yet been fully recruited. The regressions relating the escapement of alewives to returns of virgin fish and to total returns had similar slopes ($F_{1,20}=2.12$; $P > 0.10$) but differed ($F_{1,21}=33.92$; $P < 0.001$) in elevation (adjusted mean).

Residual plots indicated no major systematic trends for the total return models, although they have recently tended to overpredict returns, and it was concluded that the regression model was satisfactory (Figs. 5,6). However, the virgin return model tended to underestimate for about the first half of the time

series and then to overestimate. Why this pattern occurs and its importance is uncertain but it may be related to a decline in productivity associated with ageing of the headpond. The single significant ($P < 0.05$) standardized residual of the alewife model can be attributed to the lag used; no blueback herring model residuals were significant.

As escapement increased, the return/spawner and recruits/spawner ratios declined (Table 3). The available harvest increased with increasing escapement on a total return basis but decreased on a virgin recruit basis.

No significant effect was found between the escapement abundance of blueback herring in year X and the recruitment abundance of alewives in year $X+4$ ($F_{1,10}=1.95$; $P > 0.10$), nor between the escapement of alewives and blueback herring return in year $X+5$ ($F_{1,9}=1.50$; $P > 0.25$). In each case, the escapement of alewives was highly correlated with the escapement of blueback herring ($n=13$, $r=0.67$ and $n=12$, $r=0.95$, respectively).

Discussion

Year-class strength, as evidenced by alewife returns four years later and blueback herring returns five years later, has been shown to be primarily determined by the size of the spawning escapement. Previous studies of anadromous clupeids such as American shad and alewives have produced conflicting conclusions on the existence of a stock-recruitment relationship (Leggett 1976; Creco and Savoy 1984; Havey 1961, 1973). Studies where no relationship was found suffered from either insufficient years of, or contrast in, the data. Creco et al. (1986) conclude that, although climatic events may overwhelm the weak relationship between parental stock size and year-class recruitment, accounting for these environmental effects greatly improves the relationship.

A downward shift in the stock-recruitment relationship in recent years could occur in response to a reduced productive capacity due to aging of the headpond and continued pollution abatement efforts (Rawson 1968; Ruggles and Watt 1975). A large increase in the predator population of smallmouth black bass (Micropterus dolomieu) and lesser increase in chain pickerel (Esox niger) may also have contributed although Kohler and Ney (1981) found that juvenile alewives were seldom eaten by black bass because of their littoral rather than pelagic residence. The black bass population peaked in the mid-to-late 1970's and is now at a "healthy" level and supporting an important sport fishery (P. Cronin, N.B. Dept. of Forests, Mines and Energy, pers. comm.).

The density dependent mortality necessary for a Ricker stock-recruitment relationship is a function of escapement (i.e., is stock-dependent) and operates at an early life stage (Cushing 1981). Creco et al. (1983) and Creco and Savoy (1984) have concluded that shad year-class strength is established before the juvenile stage and this may also be true for alewives and blueback herring. Environmental factors such as water temperature and flow may significantly influence recruitment (Marcy 1976; Creco and Savoy 1984; Creco et al. 1986) but were not evaluated in this study.

A high correlation between alewife and blueback herring escapements biases the multiple regression coefficients and creates difficulty in interpreting the "importance" of these predictors of future return. The apparent lack of interaction between alewife escapement and recruitment to the spawning stock of blueback herring derived from blueback herring escapement in a given year, and vice versa, implies that little competition-induced mortality exists between the young of each species during headpond residence. The juveniles of both species have similar feeding preferences and are thus potential competitors for the available food supply (Watt and Duerden 1974). The consumption by juvenile alewives and blueback herring of highly productive, macrobenthic organisms (up to 40% of the diet) in addition to zooplankton may minimize food competition in the Mactaquac Dam headpond. At the densities of juvenile gaspereau resulting from the observed adult escapement levels, food supplies may be in surplus due to the high biological productivity of the headpond.

At some level of escapement exceeding 1.5 million fish, density-dependent mortality should occur, thereby producing a Ricker-type stock-recruitment relationship. Alewife and blueback herring escapements were correlated mainly because both species increased in abundance over much of the period considered. The effect of species interaction on recruitment is probably best evaluated on a total annual return basis but such a comparison can not yet be made.

Just why the best (highest r^2 values) alewife stock-recruitment relationship occurred for returns at $X+4$ and the best blueback herring relationship occurred for returns at $X+5$ is uncertain. A reversed lag might be expected because the weighted mean age at first spawning was 4.8 years for alewife and 3.8 years for blueback herring. Weighting by run abundance would provide a more accurate mean age but would not likely change the relative age-composition of the two species.

Differences in the available harvest and production/spawner ratios when virgin recruits are used rather than total returns at year $X+t$ are due to the presence of large numbers of previous spawners in the total return. The most realistic stock-recruitment relationship should be achieved using virgin recruits; predicting returns is best achieved using the total returns relationship. At the escapement levels observed, density-dependent mortality has not clearly produced a decline in recruitment. However, the recruit/spawner relationship suggests that no harvestable surplus of virgin recruits occurs at escapements of about 1.1 million alewives. At higher escapements, the turning point in the stock-recruitment relationship may be passed. When total returns of both species are considered, the indicated harvest of over 2.4 million fish from an escapement of 1.1 million fish represents the accumulated surplus of previous spawners available at the harvest rates historically imposed upon this stock (1974-1984 mean exploitation rate=0.70, Jessop, unpublished data).

The validity of the observed stock-recruitment relationships rests upon the assumptions that (a) alewives and blueback herring home to a natal area of the river, (b) all fish returning to the Mactaquac Dam are passed through the fish-lift, and (c) accurate estimates of fish numbers and species composition are made, and (d) the mortality experienced by downstream migrant, post-spawning

adults and juveniles is relatively constant and multiplicative in nature, i.e., the proportion of fish killed is independent of fish abundance. The evidence is persuasive that anadromous clupeids can and do home, with considerable accuracy, to a natal area (Rounsefell and Stringer 1943; Walburg and Nichols 1967; Thunberg 1971; Carscadden and Legget 1975; Messieh 1977; Jessop unpublished data). However, the return to the Mactaquac Dam will inevitably be reduced by the degree to which fish ascending the river stray into tributaries and become exposed to the commercial fishery.

The methodologies for estimating the numbers of fish in the escapement and harvest, and the species composition and age distribution are believed to be acceptably accurate, but it is difficult to evaluate whether the fishway is completely efficient at passing all returning recruits and whether substantial numbers of strays from downriver contribute to the run. For each species, a ratio >1 of the sum of the return at age $t+1$ of each fully recruited age group (age ≥ 6) to the escapement in year t (ignoring natural mortality) indicates that quantities of "surplus" fish entered the fishway between about 1976 and 1981-83 (Table 4). The available evidence fits the hypothesis that fish delayed in passage spawned a short distance downstream of the dam and that the recruits contributed the "surplus". Alternatively, the combination of large sampling error in the estimates of numbers of fish at older ages and the progressively larger returns of fish until about 1980 could contribute. This possibility has not been evaluated.

During the early 1970's, before the 1974 development of the Mactaquac commercial fishery, returns and escapements increased steadily as did delay in passing the fish. Thus, prior to 1970 few fish were collected past late June but from 1971 through 1974 (peak 1972) substantial numbers of fish were passed in mid-July or later. From 1975 onward, the run has ceased by late June or early July. The delay in passage presumably prompted some fish to drop back and spawn downstream of the dam.

Immigrant fish could originate from either nearby or distant spawning areas. Tagging studies have shown that few fish from the downstream commercial fishing areas move upriver to the Mactaquac Dam, as would be expected of fish with good homing abilities (Jessop, unpublished data). A potential spawning area, particularly for blueback herring, exists in the inter-island channels at the mouth of the Keswick River, about 5 km downstream from the dam. Recruits from the downstream spawners contributed most to returns at the dam 3-6 years later as would be expected. The "surplus" of blueback herring was largest and lasted longest because its run is later than for alewives and probably experienced greater delay thereby permitting more fish a greater opportunity to spawn downstream. The spawning conditions in the inter-island channels were probably better for bluebacks than for alewives due to the current and level fluctuation of the river resulting from the diel discharge pattern at the dam. As the fishery harvest increased and stock size decreased, passage delay and downstream spawning evidently decreased and the "surplus" disappeared by the early 1980's. The installation in 1980 of two additional turbines at the dam may have further reduced downstream spawning success (and the surplus fish) due to adverse changes in the flow regime i.e., increased diel water level and velocity fluctuation.

Unknown mortality rates occur during downstream passage through the turbines by adult and juvenile fish. Although turbine-induced mortality rates for juvenile Aloasa can exceed 80% (Taylor and Kynard 1985), the rapid increase in stock abundance indicates that such high rates do not occur at the Mactaquac Dam (or that juvenile production is very high). The proportion of previous spawners (1975-81 mean of 69% for alewives and 81% for blueback herring), even given a 1974-1981 mean exploitation rate of 77% (species combined), implies that adult mortality rates are much lower than juvenile mortality rates.

The mortality of juvenile fishes during passage through Kaplan turbines (the type at Mactaquac Dam) is believed primarily due to cavitation (Ruggles et al. 1981) while adult mortality is mostly a function of the probability of impact by the turbine blades. (Montén 1985). Both factors would act in a multiplicative manner.

Manipulation of the escapement by a process of active management (Ludwig and Hilborn 1983) is being done to further validate the stock-recruitment relationship.

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TABLE 1. Total return of alewives and blueback herring to the Mactaquac Dam, Saint John River, N.B.¹

Year	Total return		
	Alewife	Blueback	Combined
1968	20,100	1,900	22,100
1969	92,800	13,500	106,300
1970	70,400	14,100	84,500
1971	313,200	81,300	394,500
1972	848,000	356,500	1,204,600
1973	1,158,000	286,600	1,444,600
1974	1,175,500	168,400	1,343,900
1975	2,037,000	363,700	2,400,700
1976	2,359,100	1,081,500	3,440,600
1977	2,991,600	1,221,800	4,213,400
1978	3,367,300	1,076,500	4,443,800
1979	1,803,200	1,258,700	3,061,900
1980	2,257,400	1,540,700	3,798,100
1981	1,631,500	710,500	2,342,000
1982	902,900	772,800	1,675,700
1983	698,000	764,000	1,462,000
1984	899,400	793,400	1,692,800

¹ Numbers in each column have been rounded and may not total.

TABLE 2. Linear regression statistics for the stock-recruitment relationships for alewives and blueback herring from the Mactaquac Dam, Saint John River, N.B.

Species	Return at	n	r ²	a	b	s ² _{y.x}
<u>Total return</u>						
Alewife	X+4	13	0.55	856.88 ¹	1.898	363,386
Blueback	X+5	12	0.67	4.1668 ²	0.3426	0.0307
Combined	X+4	13	0.62	1186.65 ¹	2.147	561,844
<u>Virgin recruits</u>						
Alewife	X+ 3 to 6	11	0.65	224.59 ¹	0.7995	51945

¹ scaled x 10³² log₁₀ transformedTABLE 3. Stock-recruitment relationship values for alewives and blueback herring from the Mactaquac Dam, Saint John River, N.B.¹

Escapement	Based on the total return			Based on virgin recruits		
	Return	Available harvest	Return· spawner ⁻¹	Return	Available Harvest	Recruit· spawner ⁻¹
<u>Alewife</u>						
20	895	875	44.7	241	221	12.0
50	952	902	19.0	265	215	5.3
100	1,047	947	9.5	305	205	3.0
300	1,426	1,126	4.8	464	164	1.5
500	1,806	1,306	3.6	624	124	1.2
700	2,185	1,485	3.1	784	84	1.1
900	2,565	1,665	2.8	944	44	> 1.0
1,100	2,945	1,845	2.7	1,104	4	1.0
1,300	3,324	2,024	2.6	1,264	0	< 1.0
<u>Blueback²</u>						
10	371	361	37.1			
20	471	451	23.6			
50	645	595	12.9			
100	817	717	8.2			
150	939	789	6.3			
200	1,036	836	5.2			
250	1,119	869	4.5			
300	1,191	891	4.0			
350	1,256	906	3.6			

¹ scaled x 10³² estimates corrected following Ricker (1975, p. 275).

TABLE 4. Ratio of return at age t+1 to escapement at age t, of fully recruited age-groups (ages ≥ 6), for alewives and blueback herring at the Mactaquac Dam, Saint John, N.B.

Years	Alewife	Blueback	Combined
1973-74	0.7	0.2	0.6
1974-75	0.7	0.5	0.7
1975-76	1.5	2.9	1.8
1976-77	2.1	3.5	2.3
1977-78	4.8	3.7	4.5
1978-79	1.7	4.3	2.7
1979-80	4.0	3.1	3.7
1980-81	1.2	1.5	1.3
1981-82	0.5	2.6	1.2
1982-83	0.4	2.1	0.8
1983-84	0.5	0.9	0.5

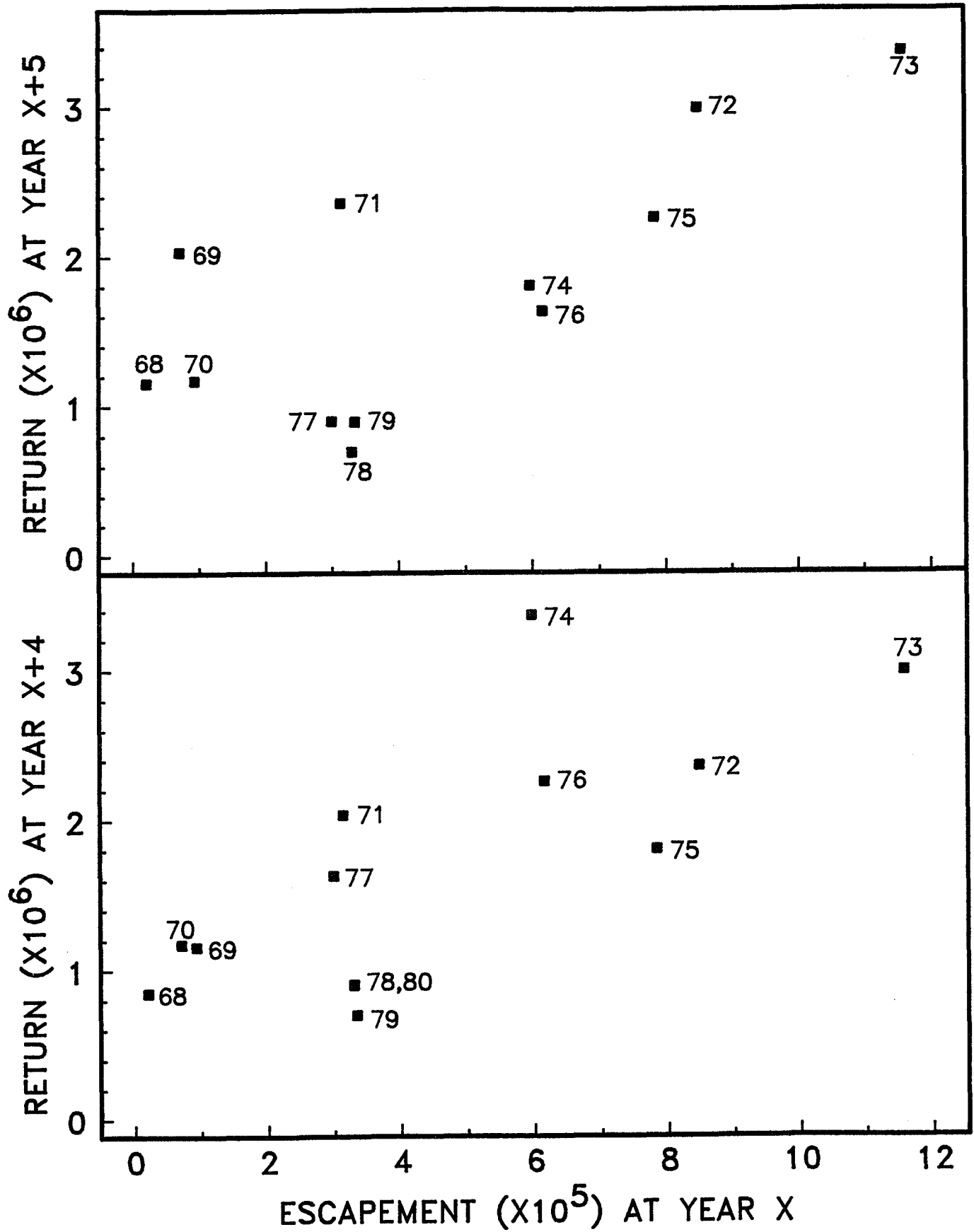


Fig. 1. Return of alewives in years X + 4 and X + 5 in relation to escapement at year X at the Mactaquac Dam, Saint John River, N.B. Numbers at each symbol indicate escapement year.

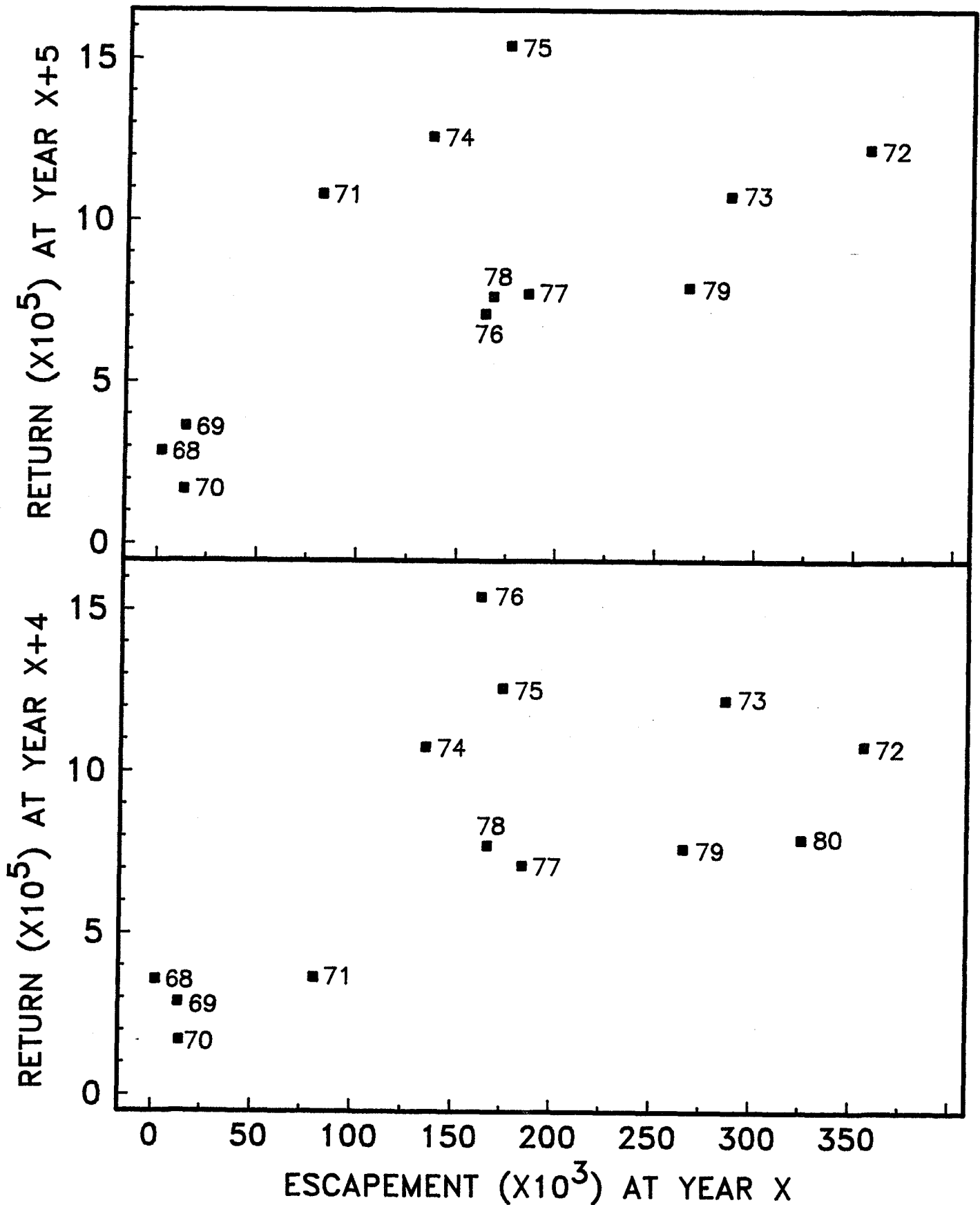


Fig. 2. Return of blueback herring in years X + 4 and X + 5 in relation to escapement at year X at the Mactaquac Dam, Saint John River, N.B. Numbers at each symbol indicate escapement year.

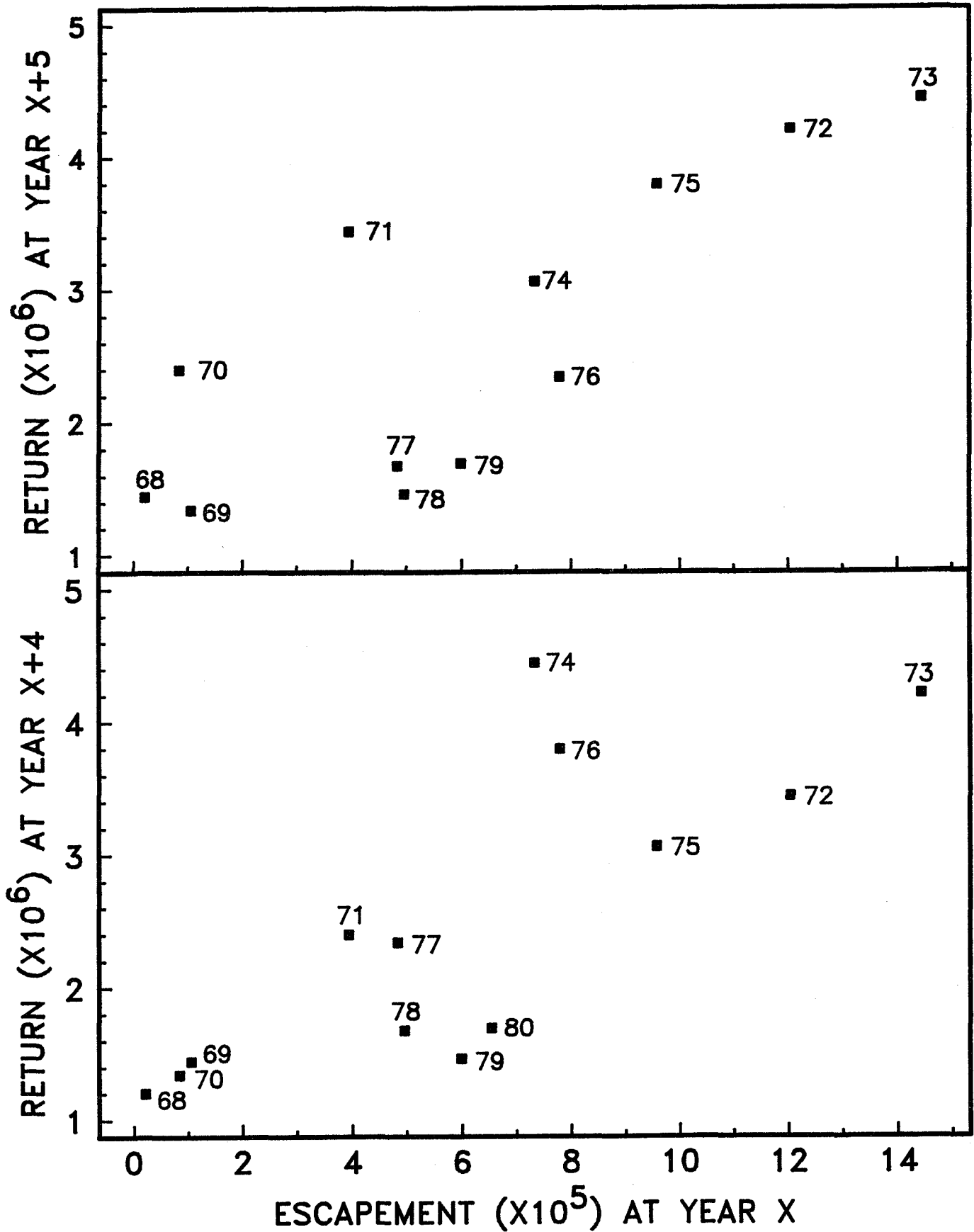


Fig. 3. Return of alewives and blueback herring (combined) in years X + 4 and X + 5 in relation to escapement at year X at the Mactaquac Dam, Saint John River, N.B. Numbers at each symbol indicate escapement year.

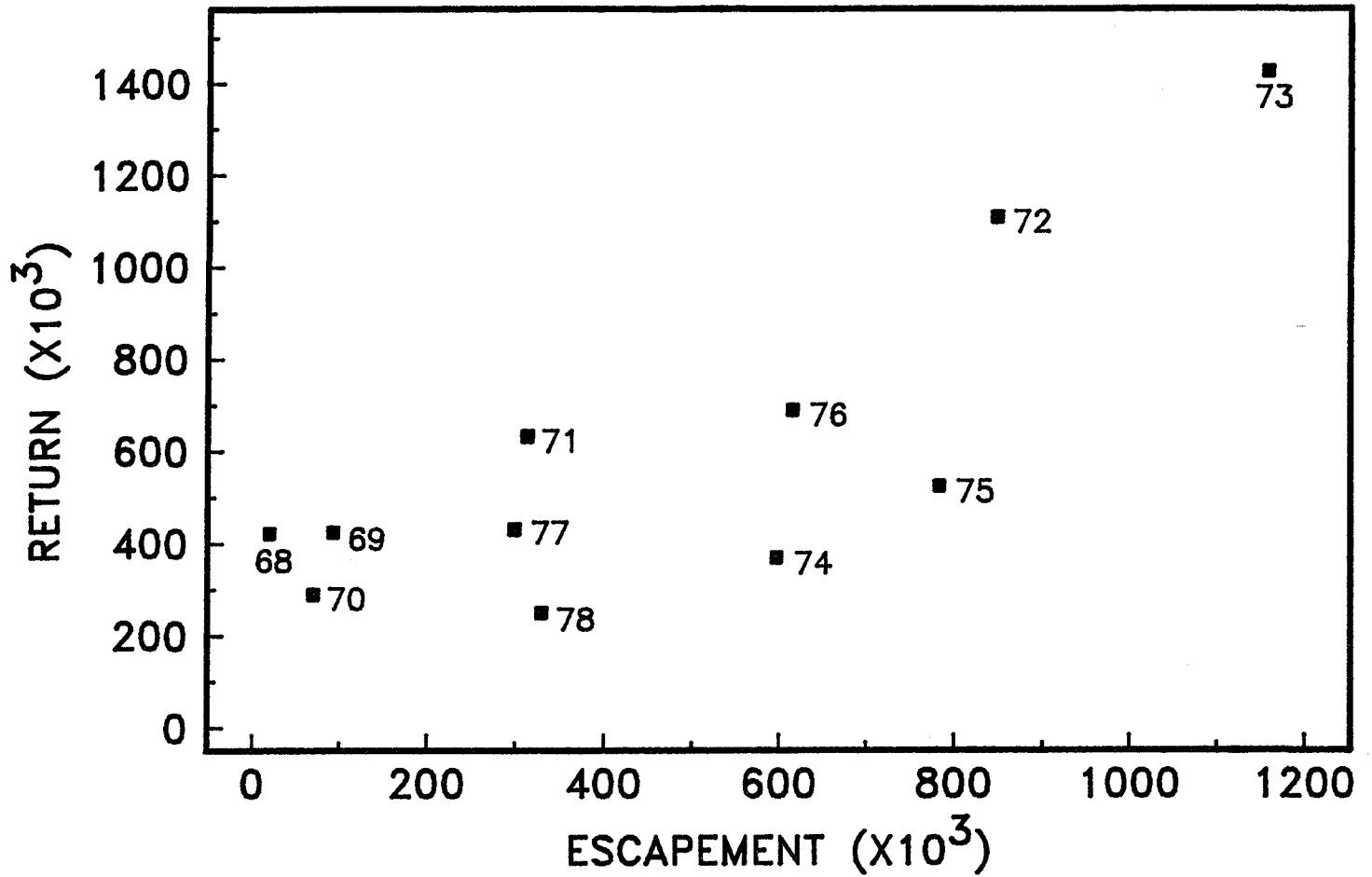


Fig. 4. Return, by year-class, of virgin alewives at ages-3 through 6 in relation to escapement at year X at the Mactaquac Dam, Saint John River, N.B. Numbers at each symbol indicate year-class.

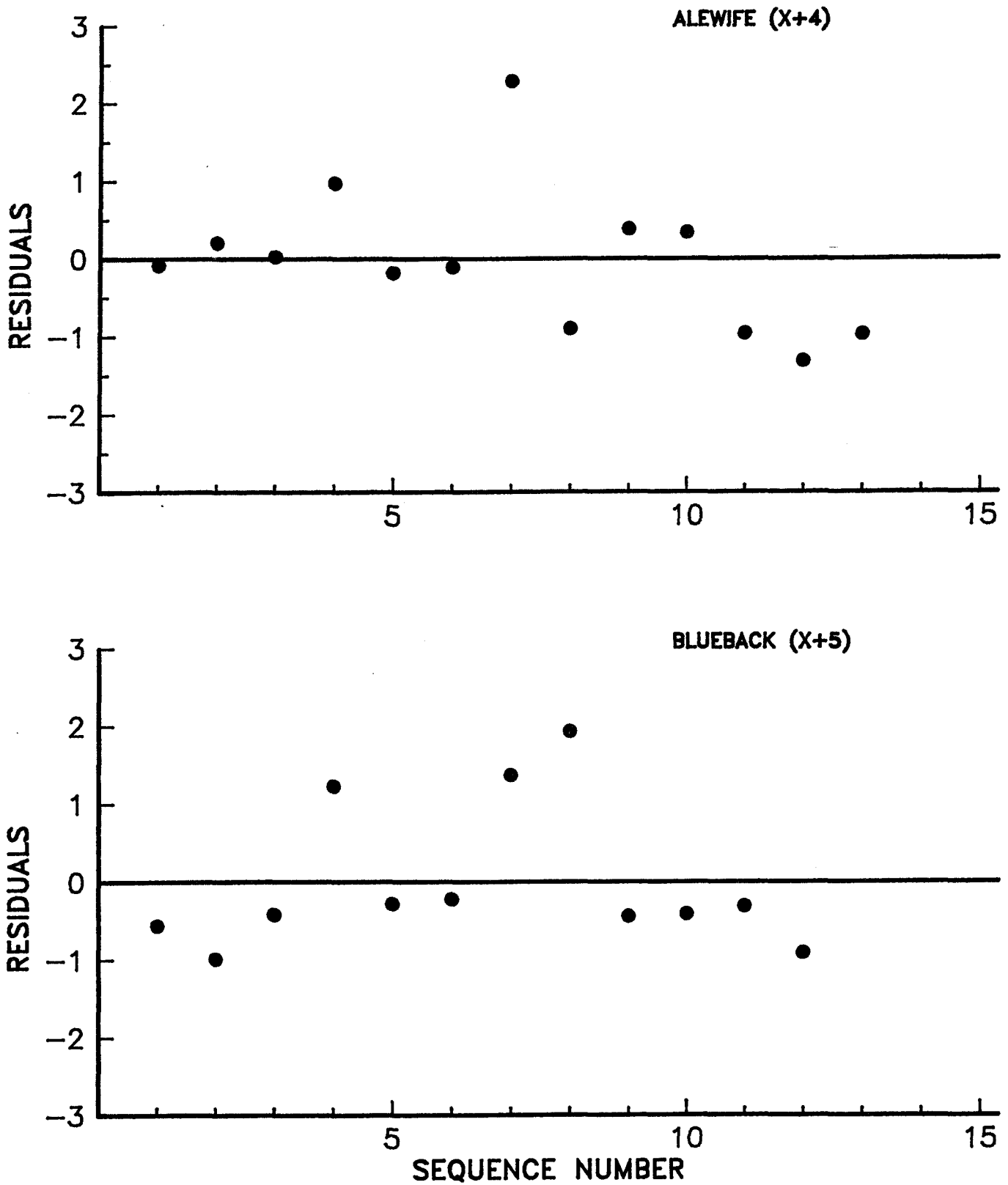


Fig. 5. Residual plots from the linear regression of return at year $X+t$ on escapement at year X for alewives and blueback herring at the Mactaquac Dam, Saint John River, N.B.

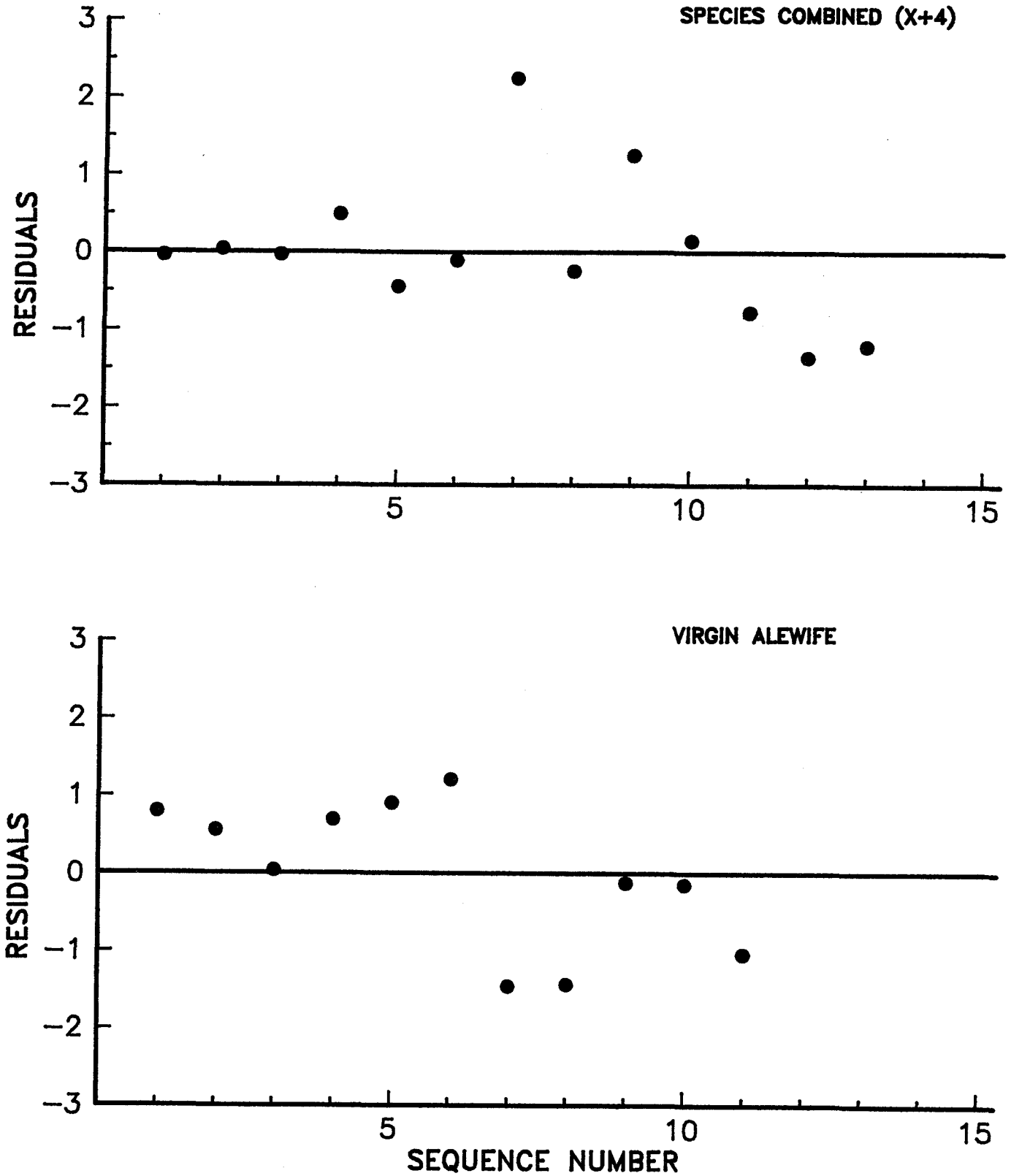


Fig. 6. Residual plots from the linear regression of return at year $X+t$ on escapement at year X for alewives and blueback herring combined and virgin alewife at the Mactaquac Dam, Saint John River, N.B.