FURTHER STUDIES OF PREDATOR AND SCAVENGER USE OF CHUM SALMON IN STREAM AND ESTUARINE HABITATS AT BAG HARBOUR, GWAII HAANAS

T. E. Reimchen
Islands Ecological Research
Box 970, Queen Charlotte City, B.C.

Prepared for Canadian Parks Service, April 1994.

Figure Captions

Table captions

Acknowledgements

Islands Ecological Research gratefully acknowledges the valuable field assistance of C. French and D. Seguin who contributed throughout the study and to D. Burles, T. Rutherford, K. Rowsell and P. Mylechreest for assistance in fish capture and other logistics. IER respectfully acknowledges Canadian Parks Service for transportation and equipment, and in particular for the night-viewing goggles as these were essential in evaluating nocturnal bear activity. P. Mylechreest provided the bear photograph in Figure 1.

Figure 1. Upper: View across Bag Harbour looking to the northeast. Middle: Black bear in stream channel. Lower: Partially-eaten chum salmon left by bear showing representative tissue loss and brain removal.

Introduction

Migrating salmon represent a major autumn pulse of energy for a broad assemblage of predators and scavengers in Gwaii Haanas. In October 1992, a pilot project was undertaken to quantify mammal and bird use of salmon at Bag Harbour near Burnaby Narrows (Reimchen 1992). Results of this study indicated that numbers of salmon returning to the stream greatly influence the carrying capacity of the riparian and associated estuarine habitats. Black bear which foraged on the salmon, were observed to transfer more than 80% of the entire run to the forest floor and in the process leave large numbers of partially eaten carcasses throughout the riparian habitat (Figure 1). The bear appears to be a keystone species in this habitat as these carcasses provided the major food source for numerous scavengers including crows, ravens, gulls, eagles and pine marten.

Various deficiencies remain in understanding the dynamics and significance of these interactions. The most important is whether the data observed during a two week period in 1992, particularly the high percentage of salmon transferred by the bear to the riparian habitat, are representative of other years. Accordingly, in the present study, the major components of the pilot project (species of predators and scavengers, numbers of carcasses) are re-surveyed for the salmon run in autumn 1993.

One of the results in the 1992 survey showed that less than ⅓ of the salmon taken by bear were females and most of these were spawned-out. Consequently, despite the large quantity of salmon taken, there appeared to be only a minor or effect on the reproductive potential of the salmon. This was an important finding because black bears have been destroyed for their alleged destruction of salmon runs. Studies in Alaska conclude that black bear target gravid female salmon and largely ignore males and spawned-out individuals (Frame 1974). Yet, the results of my pilot project can be criticised not only for the small sample size of carcasses examined (N=89) but because it was carried out during the latter half of migration when spawned-out salmon may have been the only choice. This could have led to incorrect conclusions on the impact of bear predation on the salmon run. To address this deficiency, I have monitored in the current study the sex and reproductive state of bear-killed carcasses throughout the spawning run.

While most of the salmon captured by the bear were eaten close to the stream, some salmon were carried substantial distances into the forest. The reasons for variability in distribution of carcasses is unknown but it greatly influences the activity of scavengers and the effective width of the riparian habitat. In this study, I record carcass position and examine whether particular attributes of the carcasses (size, condition) are correlated with transfer distances from the stream channel.

Following completion of spawning, the salmon that are not captured by the bear or consumed by scavengers in the stream channel are eventually swept downstream into the estuary. The ecological destination of these carcasses has not been described or determined. For example, what invertebrate scavengers utilize carcasses and how long do carcasses persist after entering the estuary. In this study, underwater surveys are conducted with SCUBA to consider these factors.

There is considerable variability in the amount of surface activity of salmon in the estuary (jumps, agitation) probably associated with disturbance or differences in total numbers of salmon. In the present study, I have quantified this activity as a measure of estimating relative or absolute abundance of salmon remaining in the estuary.

In 1992, there appeared to be extensive nocturnal foraging activity in the estuary by seals, sea lions and possibly bears but this could only be inferred from the sound of surface agitation by schools of salmon near shore. The inability to discern foraging activity at night limits the understanding of a potentially important aspect of the biology of the estuary. In this study, night-viewing devices are used to quantify nocturnal foraging activity in the estuary.

METHODS

The study extended from September 28 to October 26 with an additional site visit on November 13-14. Numbers of bear, seal, sea lion and all birds in the harbour were recorded daily. Birds were counted at 0900 from the west end of the harbour (Figure 2). Surface activity of salmon (jumps, swimming agitation of schools) was recorded during a 5 minute time block regularly at hourly intervals from 0700-2100 and then at four periods during the evening.

Night observations on black bear were made with helmet-mounted night-viewing glasses for 15 - 60 minute time blocks near 2000 h, 2200 h, 0100 h and 0400 h. Interactions, amount of foraging activity and numbers of salmon captured were recorded. Most of the night observations were made on the estuary but on two occasions, I also looked at nocturnal bear activity on the stream.

Diving surveys were undertaken in the estuary to identify scavengers on carcasses. In the initial dive (October 13), general occurrence of scavengers on salmon carcasses was recorded in various habitats such as the outflow channel of the stream, eel grass beds (Zostera) and sub-tidal mud flats in the middle of the harbour. Following this, 40 spawned-out carcasses were collected from the lower reaches of the stream, weighed, tagged and tethered at 3.4 meter intervals on three separate anchor lines. These lines were then placed in the estuary (outflow channel, eelgrass beds, centre of channel). Each day, for a 5 day period, the carcasses were re-examined using SCUBA and all scavengers recorded. Following each dive, the carcasses were raised into a boat, weighed and then returned to the bottom. By the 5th day, carcasses had begun to disintegrate and further weights were uninformative.

Stream observations follow the same protocol as in 1992 which involved daily surveys for carcasses on the east side of the stream and general observations on predators and scavengers. I also searched for fresh carcasses along the high tide line and adjacent forests around the estuary in areas where black bear had been observed foraging.

A total of 760 fresh carcasses were measured, most of which were from bear capture. On each of these, I measured lower jaw length, body length when possible, weight, sex, weight of testes or number of eggs in the body cavity and number of eggs on the ground, position of carcass (stream channel, forest floor and distance from stream), body condition at time of capture (new, medium, old), intactness of carcass (complete, tissues missing) and presence or absence of brain.

Lower jaw length was measured to allow an estimate of original size of the salmon. Among all carcasses examined, 53 were completely intact (no tissues removed). An exponential plot of jaw length against body weights of these intact carcasses is shown in Figure 3 and I will use these exponentials to estimate original weight from jaw length.

Body condition was categorized to give some general indication of the tissue quality. 'New' carcasses generally had red flesh and no loss of body pigmentation or fin deterioration. 'Old' carcasses had pale flesh and major depigmentation of the body, erosion of fins and may have been dead when the bear removed them from the stream.

I tagged one hundred fresh carcasses which were found in diverse localities in the riparian habitat on the east side of the stream and every 48 hours for 8 days, re-weighed the remaining tissues. Any scavengers in the region of the carcass were noted.

To quantify total transfer of salmon to the riparian habitat over the entire spawning run, a complete count of carcasses was made from the bank and forest on the west side of the stream. Search area extended from the estuary to 1.5 km upstream including banks and forests adjacent to all major and minor tributaries (Figure 2). Generally, the forest floor was surveyed to a distance of about 100 m from the stream. On some of the bear trails, carcasses were occasionally present at this distance and if so, the search was extended further along the trail until no further carcasses were detected. In addition to the forest floor, all carcasses in the stream channel were recorded throughout the length of the stream. These counts of all carcasses were initially done on September 29 near the beginning of the run and then again on October 7, October 17, October 25 and November 13. Total counts were also made on the east forest on October 25 and November 13.

All carcasses were 'marked' by cutting the lower jaw symphysis such that on subsequent surveys, these old carcasses could be differentiated from new material. This allowed a count of all carcasses over the entire spawning run. On each carcass, I attempted to ascertain gender, either from direct examination of gonads when these were present or from jaw characteristics when gonads were absent. I also recorded dominant features of the site (stream, forest) and general location between the estuary and upper most reaches of spawning gravels (Figure 2). The lowest region (below the waterfalls) is inundated during high tide and has primarily pre-spawned salmon that are holding for eventual movement past the falls into the stream.

To obtain information on movement of individuals from the estuary to the stream, 134 chum salmon were captured in the estuary on October 5th, tagged and released. Ninety seven fish were marked with a number opercular clip while 37 were marked with a small V cut on the posterior end of the operculum.

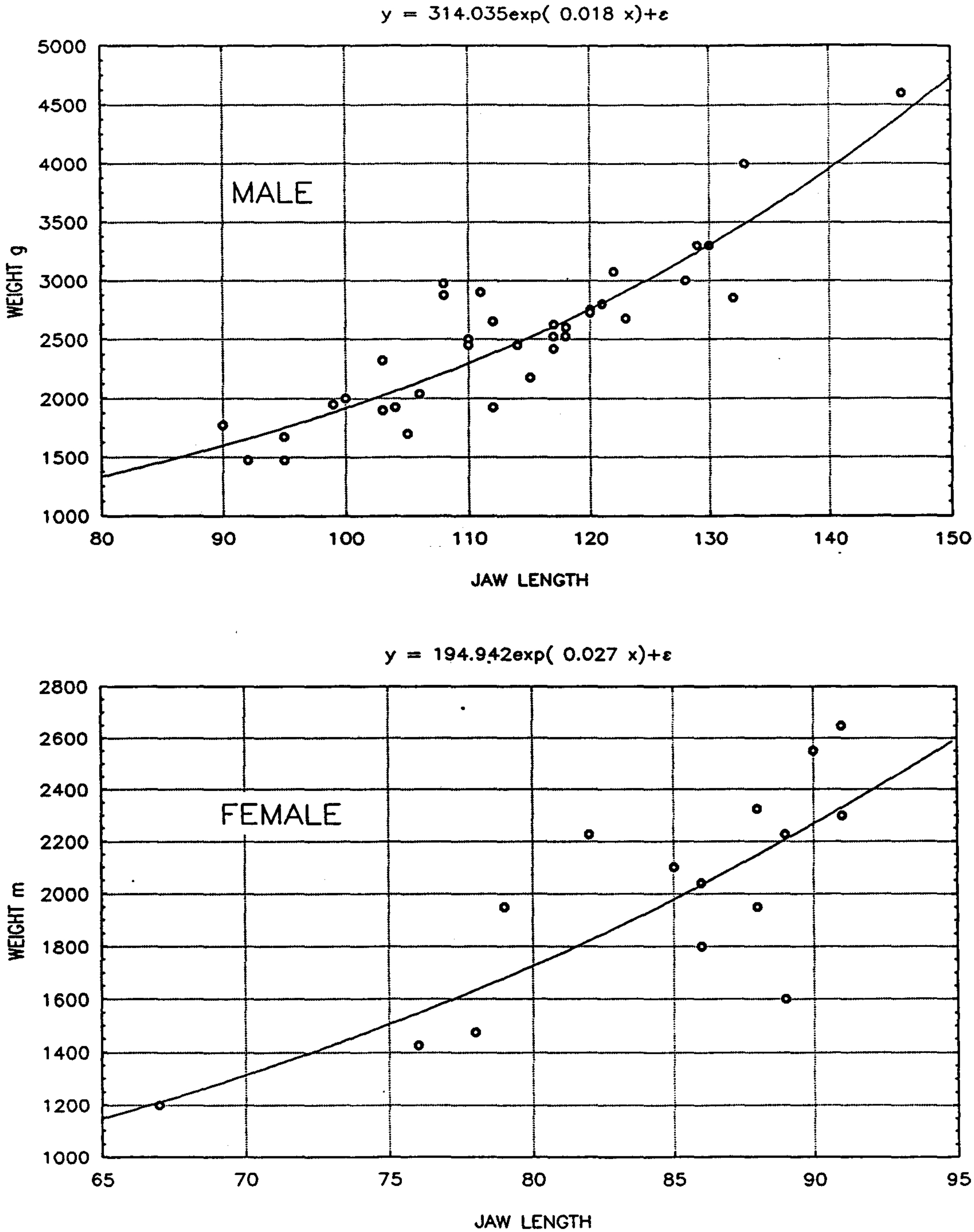


Figure 3. Relationship between lower jaw length and total body weight in male and female chum salmon.

RESULTS

Estuary

Salmon activity

Salmon began to congregate in Bag Harbour during the latter half of September; throughout October, small schools (20-100 individuals) were common along the shore in the western sections of Bag Harbour. Approximately 1000 to 3000 salmon were present in the estuary in the first half of October, with numbers declining as salmon moved into the stream. The two common types of activity of the salmon visible at the surface were occasional jumping and also brief periods of intense swimming commotion within the small schools. Incidence of these activities were clearly associated with total numbers of salmon in the estuary as numbers of jumps were highest during the early stages of the run and decline to zero by late October when most individuals have moved into the stream (Figure 4). Surface agitations show a similar trend but there is a suggestion of a bimodality with peaks occurring near the beginning and middle of October (Figure 5).

While incidence of jumps and surface agitations provide a visual index of salmon abundance, there is additional complexity to the timing of these activities. Frequency of jumping increased from dawn through to a maximum just before dusk and thereafter sharply declining during darkness (Figure 6). In contrast, number of agitations by schools demonstrates the inverse of this pattern with relatively low levels of activity occurring during the day, increasing prior to dusk and remaining common throughout the night and then declining shortly after dawn (Figure 7). Some of these diurnal trends in surface agitation appear to be responses to aerial disturbance as I occasionally observed intense swimming agitation when gulls flew low over schools.

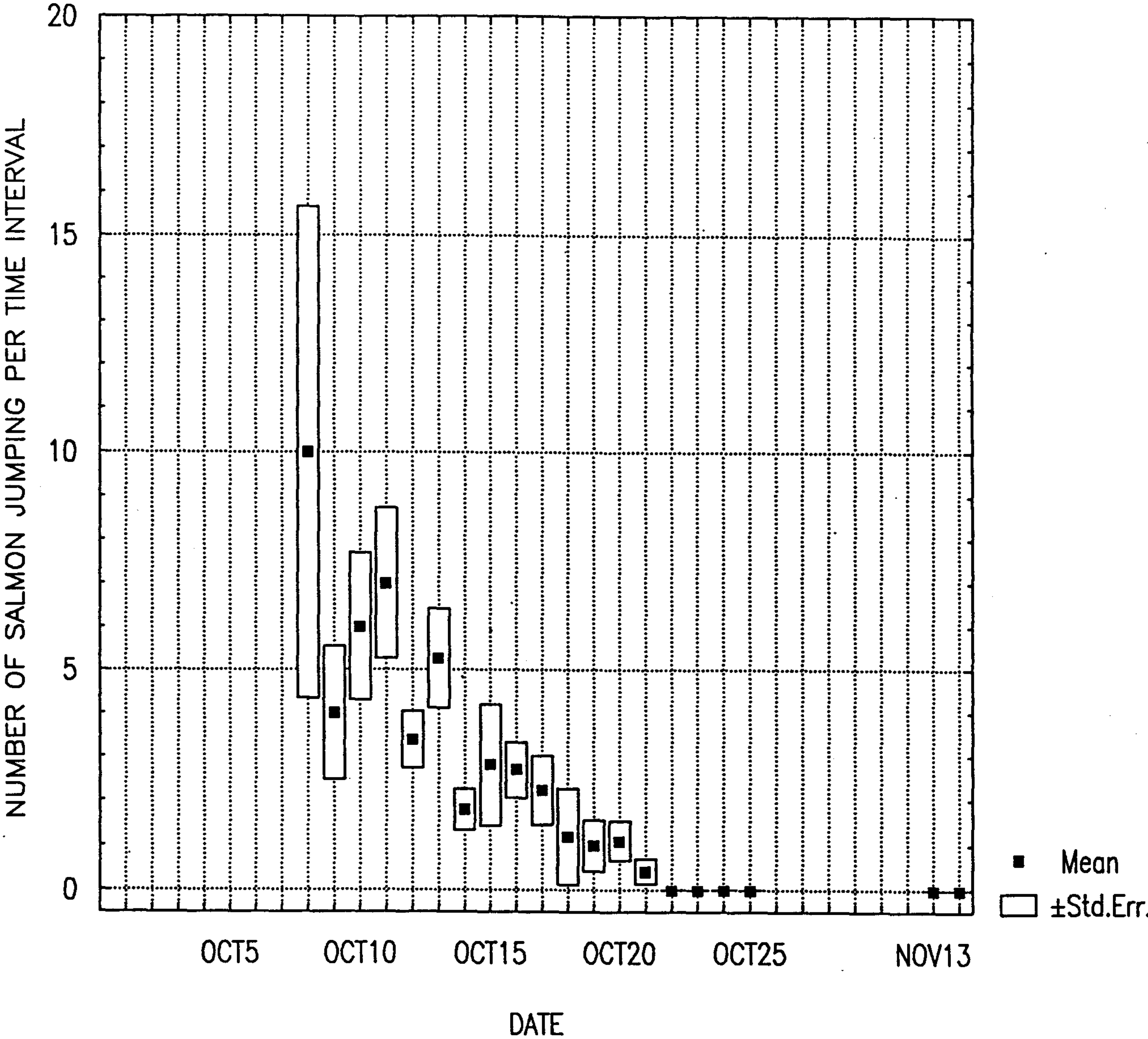


Figure 4. Average incidence of salmon jumping in the estuary over duration of the spawning run. Data represents average jumps over replicated 5 minute observation blocks.

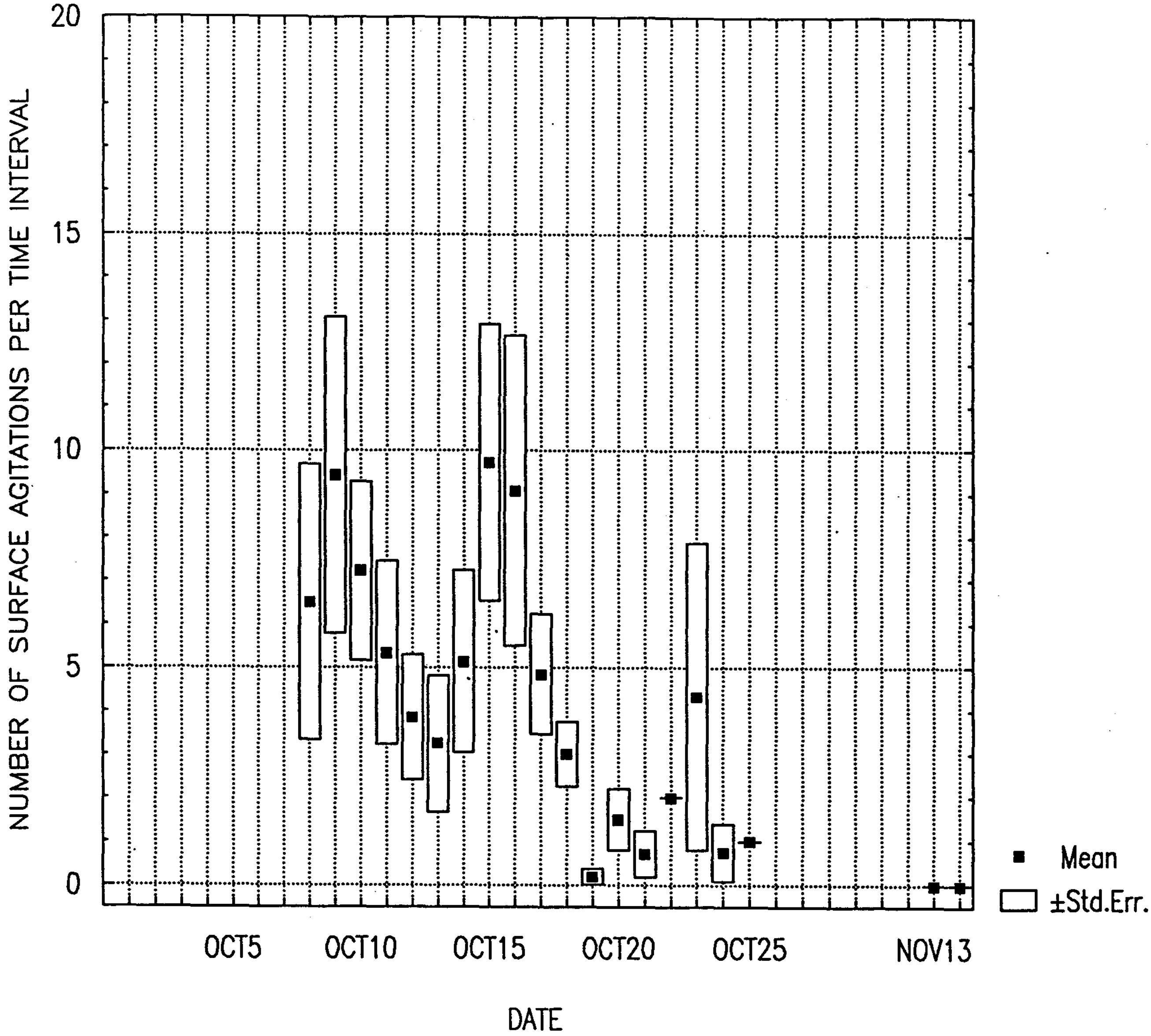


Figure 5. Incidence of surface swimming agitation in the estuary over duration of the salmon run. Data represents average jumps over replicated 5 minute observation blocks.

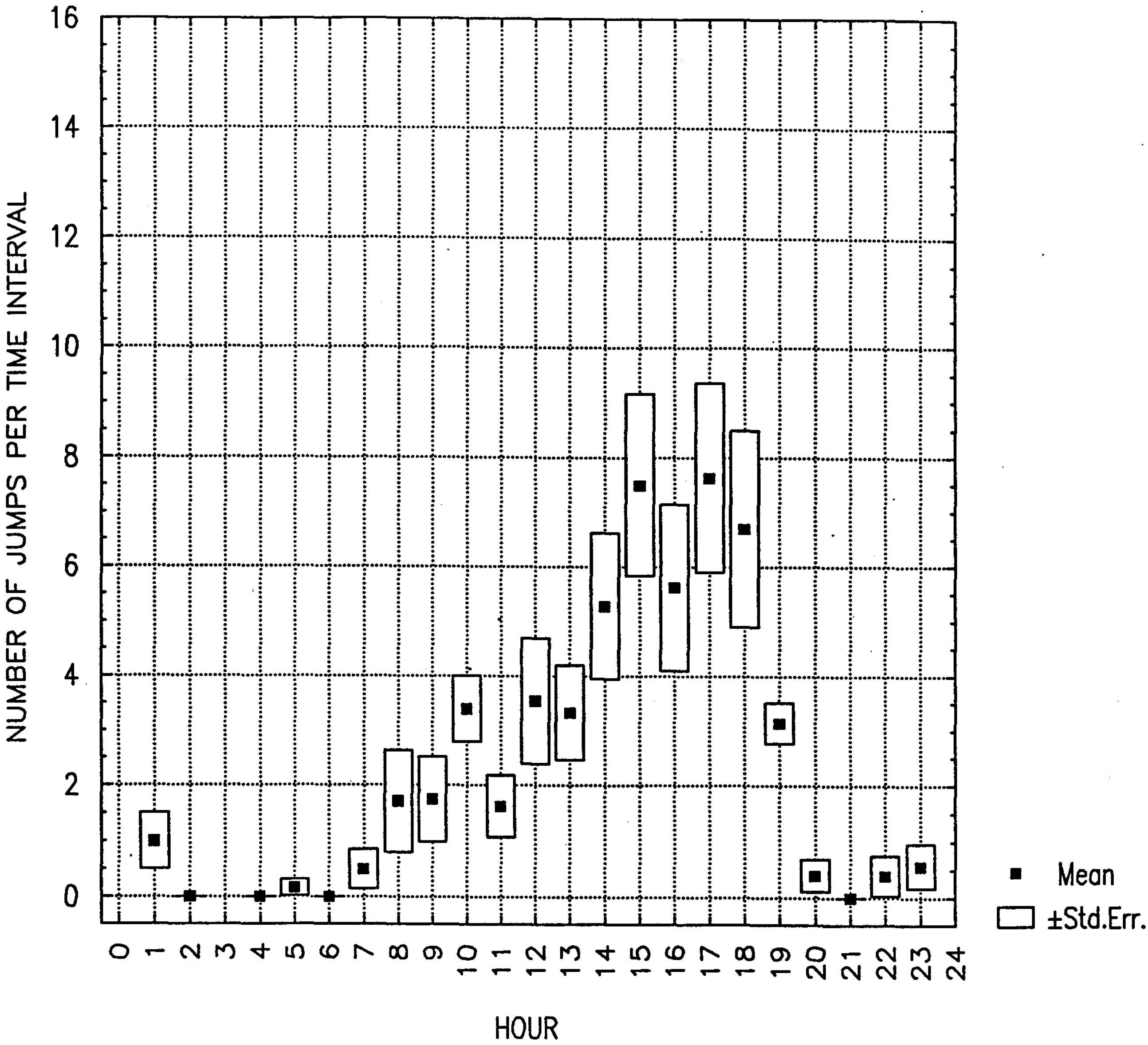


Figure 6. Hourly incidence of salmon jumping in the estuary.

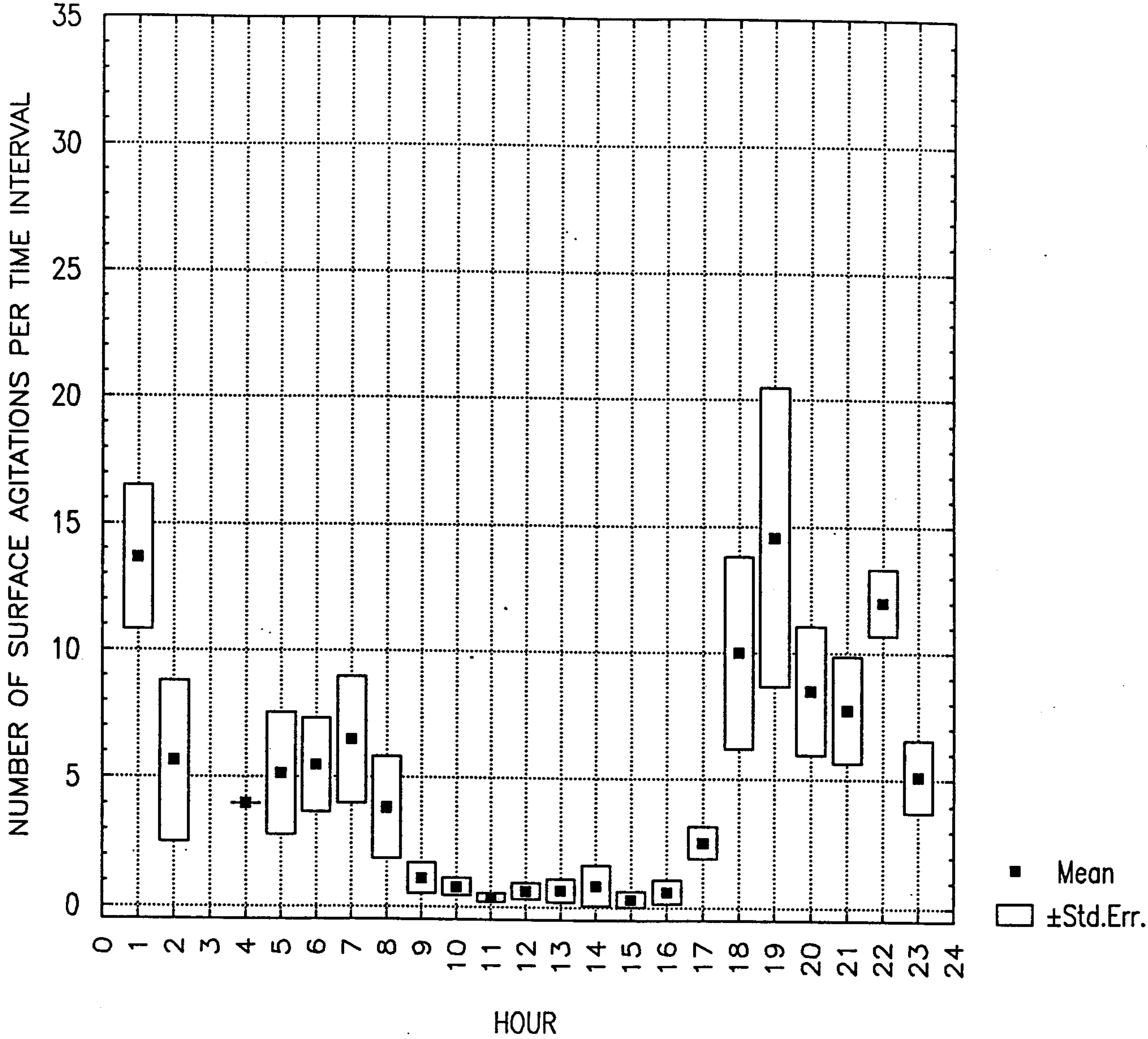


Figure 7. Hourly incidence of swimming agitation in the estuary.

Mammal activity

There were generally from one to four harbour seals daily in Bag Harbour over the study period (Figure 8) for an average of 2.8 daily (Table 1). Following several days of rain, numbers briefly rose to 10 seals on October 16 and to 19 seals on October 23 during a severe storm. These concentrations of seals did not appear to forage. Among the 'resident' seals, several spent considerable time near the stream mouth and in bays where salmon commonly congregated close to shore. Due to the shallow water and flat profile, seals were unable to capture salmon in these situations. This low capture rate persisted throughout the length of the salmon run. Several successful captures were recorded during the incoming tide where steeper shore profiles allowed seal access close to shore but no useful quantitative could be obtained on total salmon consumption. From studies on Vancouver Island, average daily consumption of salmon by harbour seal averages 1.9 kg (P. Olesiuk, DFO). Over the duration of the salmon run at Bag Harbour (ca. 45 days), there would be 239 kg of salmon consumed which comprises 80 salmon.

Number of bear on the estuary seen at any single time ranged from zero to six. Average numbers showed a bimodal distribution with the major peak on October 2 and a secondary peak on October 14 (Figure 9). No bear were seen on the estuary after October 22. The bear came from different geographical areas when first appearing on the estuary. Only one bear was regularly seen moving between the Bag Harbour stream and the estuary. Two bear regularly appeared from the forests near the mid-southern shore of the harbour while an additional bear generally approached from the forest on the northwest corner of the harbour. On two occasions, a bear came from the entrance of Bag Harbour suggesting an origin near Burnaby Narrows.

There was a major difference in the diel activity of bears. They were not normally seen on the estuary during daylight hours. However, around dusk, bears were occasionally observed at the forest edge moving towards the estuary and low tide line. Average number of bear was greatest from four to eight hours after sunset (Figure 10) but individuals occurred during all hours of darkness that were surveyed. By 0700 h, all bear had returned to the forests.

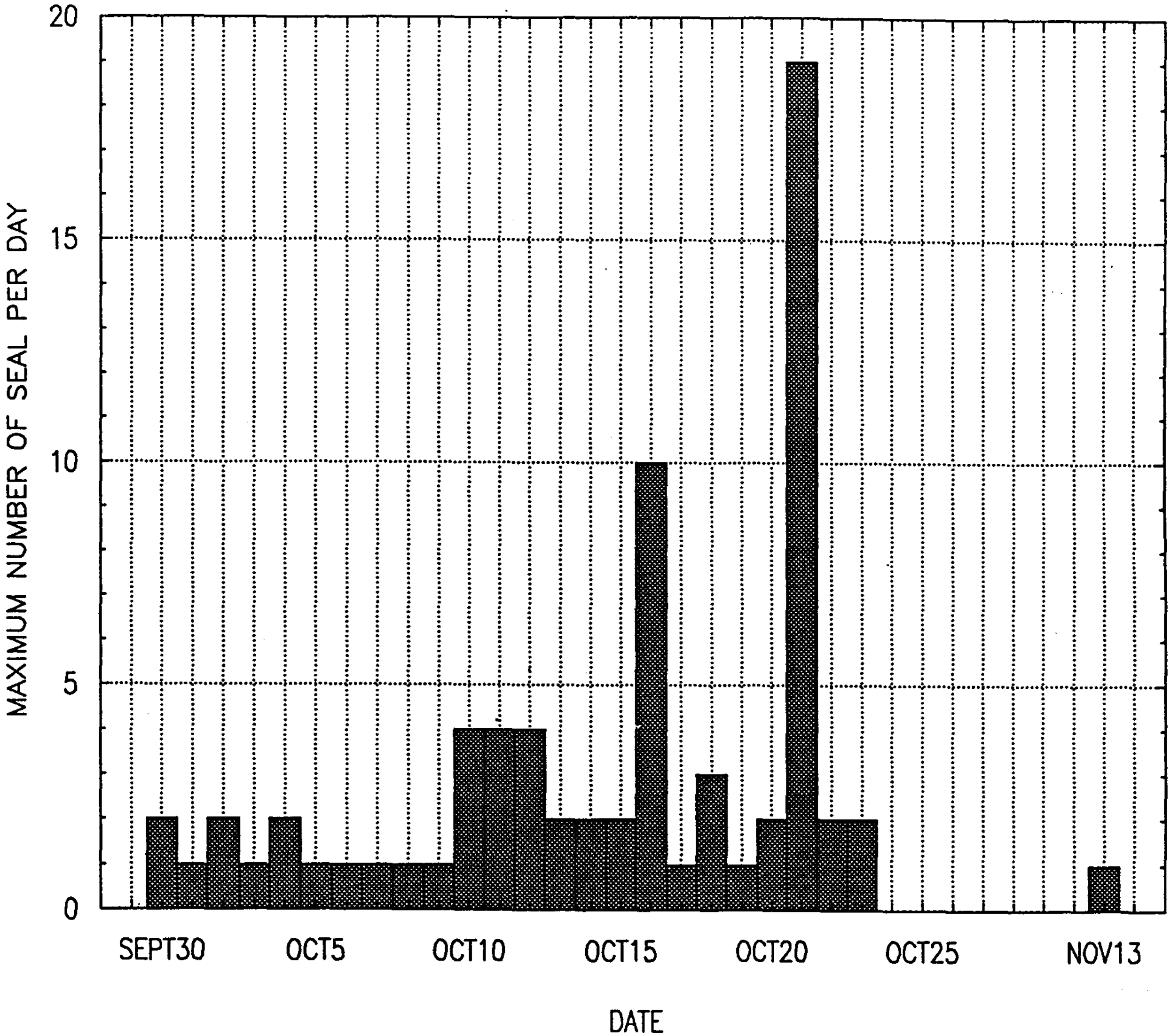


Figure 8. Maximum number of harbour seal seen daily over duration of the salmon run.

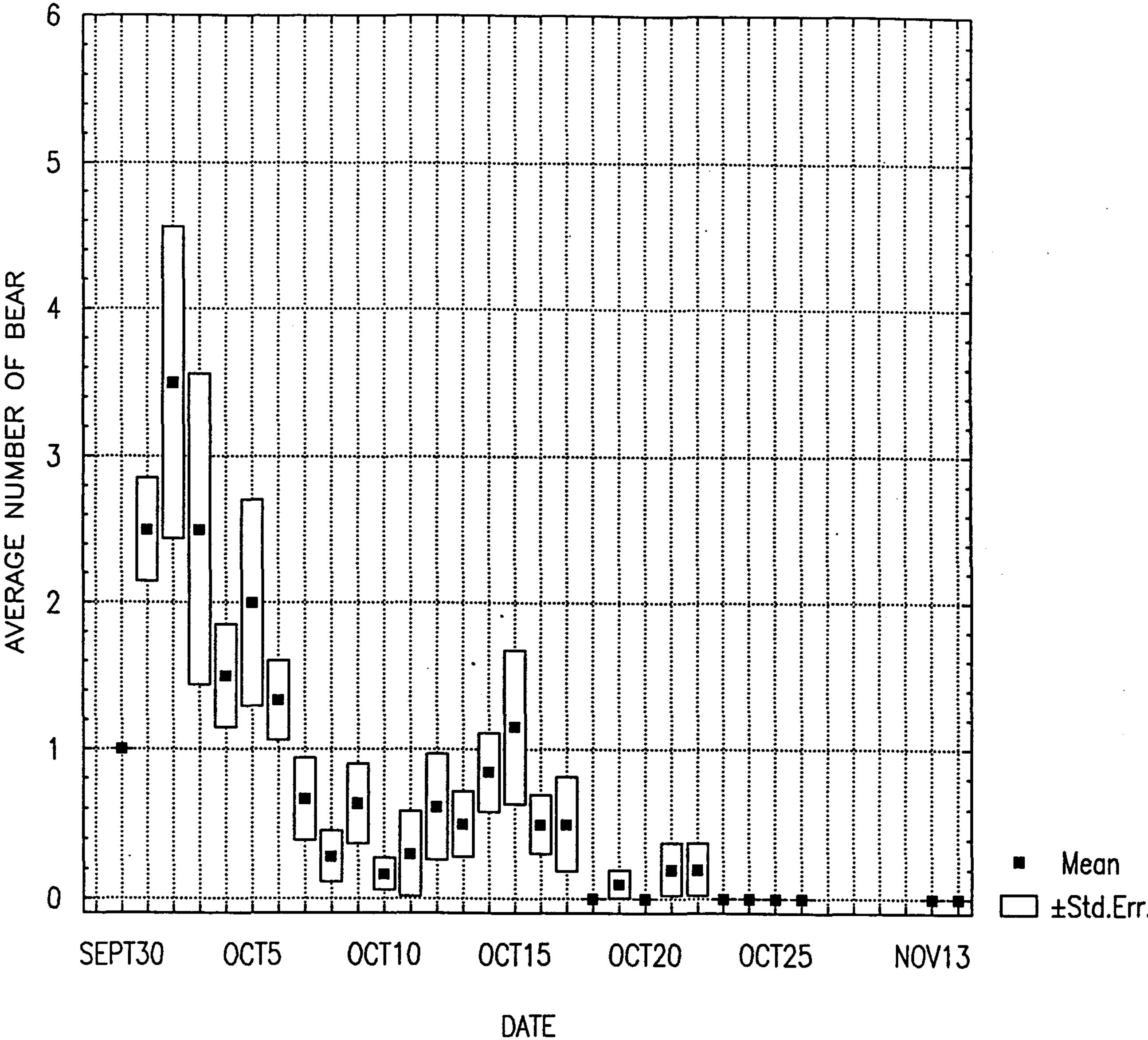


Figure 9. Average number of bear observed daily in the estuary over duration of the salmon run.

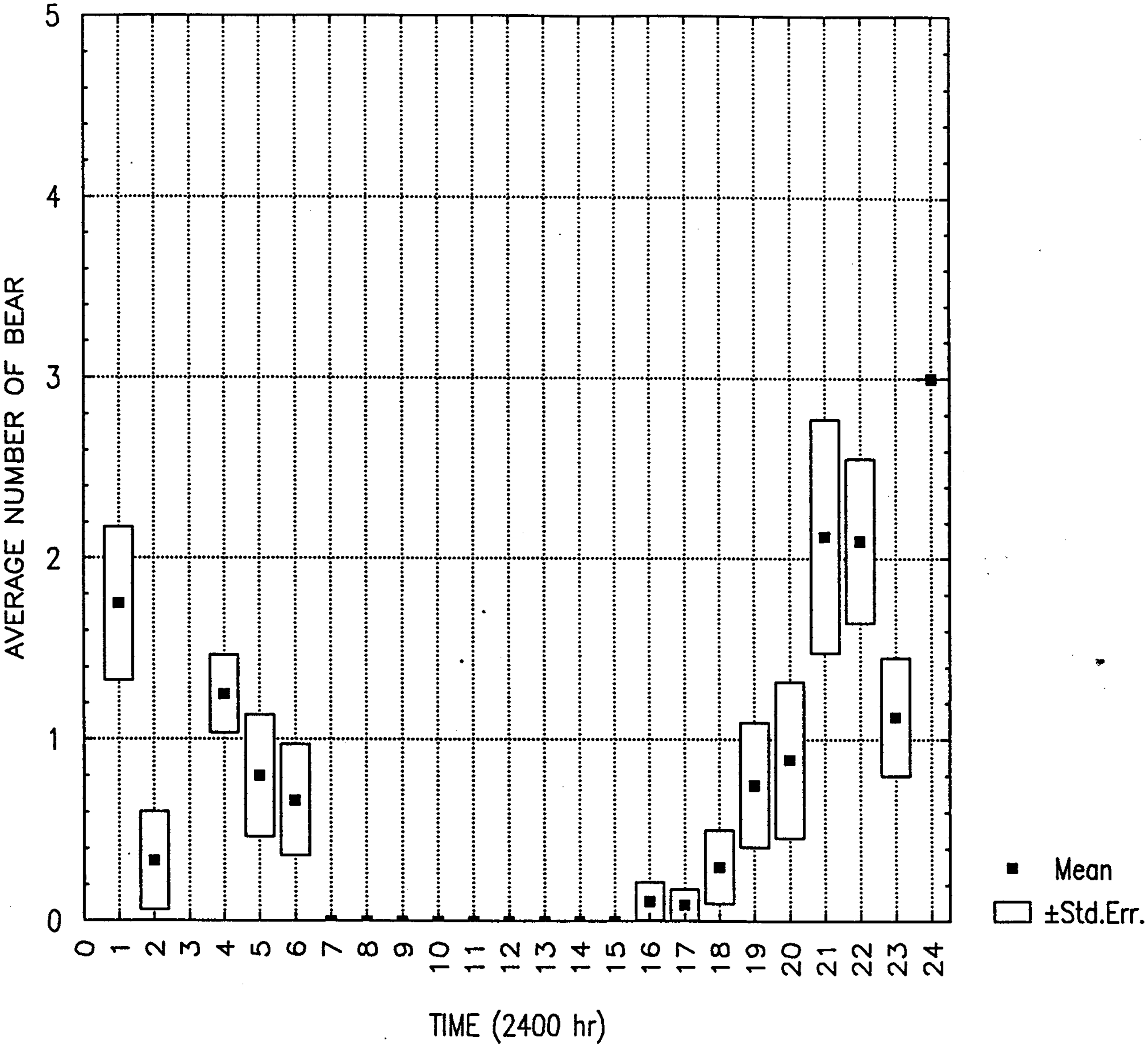


Figure 10. Average number of bear in the estuary at hourly intervals.

Most foraging activity by the bear occurred during low tide on the west end of the harbour. The mouth of the stream was a major focal area for the bear but additional foraging occurred on the large shallow northwestern bay and in the small bays on the south shore (Figure 2). For example, bear waded slowly into shallow water (<½ m) and stood motionless for several minutes. At some stimulus, the bear would leap forward and with a major splash, 'belly-flop' back into the water and rest on the bottom with all limbs extended. There was usually intense surface agitation of numerous salmon immediately adjacent to the bear indicating the presence of a school. In the majority of cases following the plunge, the bear stood up without a salmon and repeated the manoeuvre several meters further along the shore. Occasionally, after the plunge, the bear immediately stood up holding a salmon in its jaws while on other occasions it submerged its head and retrieved a salmon, presumably pinned under the feet. It was then carried back to shore, usually on to grasses above the high tide line where it was eaten. The salmon was usually taken into the forest if other bears were foraging in the estuary. Over a 20 day period, I was able to observe 129 plunges among different bear of which 31 (24%) were successful. Based on 59 separate observations blocks ranging in length from 13 to 160 minutes ($\bar{x}$ = 47 min), overall capture rate during darkness averaged one fish per hour.

During daylight, I searched for carcasses above the tide line and the adjacent forest over all areas where bear had been seen in order to estimate total numbers of salmon captured in the estuary. In total, 142 carcass remnants were found. In addition, from the night observations, about ¼ of the salmon captured by the bear were eaten in the intertidal region and therefore these carcass remnants would not have been detected in the surveys above the tide line. Combining these two values yields an estimate of approximately 200 salmon captured by bear in the estuary over the salmon run.

Table 1: Mammal and bird use of Bag Harbour estuary, Moresby Island during chum salmon migration. Numbers show daily maximum and averages. *: can include Glaucous-winged Gull (Larus glaucescens), Herring Gull (L. argentatus), Mew Gull (L. canus) and California Gull (L. californicus). Numbers in brackets show data from Bag Harbour, October 1992 (see Reimchen 1992).

Species	**MAX**	**AVG**
Harbour Seal Phoca vitulina	19(8)	2.8(3.3)
Steller's Sea Lion Eumetopias jubatus	1(4)	
Black Bear Ursus americanus	6(4)	1.7(0.9)
Common Loon Gavia immer	3(5)	1.5(7.5)
Pacific Loon Gavia pacifica	30*(65)	1.4(10.5)
Horned Grebe Podiceps auritus	3(3)	0.4(0.5)
Red-necked Grebe Podiceps grisegena	4(5)	1.1(1.8)
Western Grebe Aechmophorus occidentalis	8(1)	2.0(0.8)
Doubled-crested Cormorant Phalacrocorax auritus	1*(0)	0.04(0)
Mallard Anas platyrhynchos	45*(4)	2(0.3)
Green-winged Teal Anas crecca	0(23)	0(2.5)
Redhead Aythya americana	0(1)	0(0.8)
Scaup Aythya spp	1(10)	1(2.2)
Common Goldeneye Bucephala clangula	0(3)	0(0.2)
Bufflehead Bucephala albeola	4(14)	1.4(3.5)
Harlequin Histrionicus histrionicus	13(10)	4.6(4.7)
White-winged Scoter Melanitta deglandi	20(68)	11.6(44.0)
Surf Scoter M. perspicillata	16*(0)	0.7(0)
Common Merganser Mergus merganser	0(15)	0(3.0)
Red-breasted Merganser M. serrator	6(0)	0.4(0)
Hooded Merganser Lophodytes cucullatus	5(14)	0.6(3.8)
Sharp-shinned Hawk Accipiter striatus	1(1)	.09(0.1)
Bald Eagle Haliaeetus leucocephalus	4(4)	1.5(1.3)
Great Blue Heron Ardea herodias	1(0)	.09(0)
Gulls*	375(300)	121.6(64.9)
Black-legged Kittiwake Rissa tridactyla	0(8)	0(1.7)
Common Murre Uria aalge	0(3)	0(0.5)
Belted Kingfisher Ceryle alcyon	1(1)	0.3(0.6)
Common Raven Corvus corax	1(4)	0.2(0.2)
Northwestern Crow Corvus caurinus	200(300)	49.2(102.5)

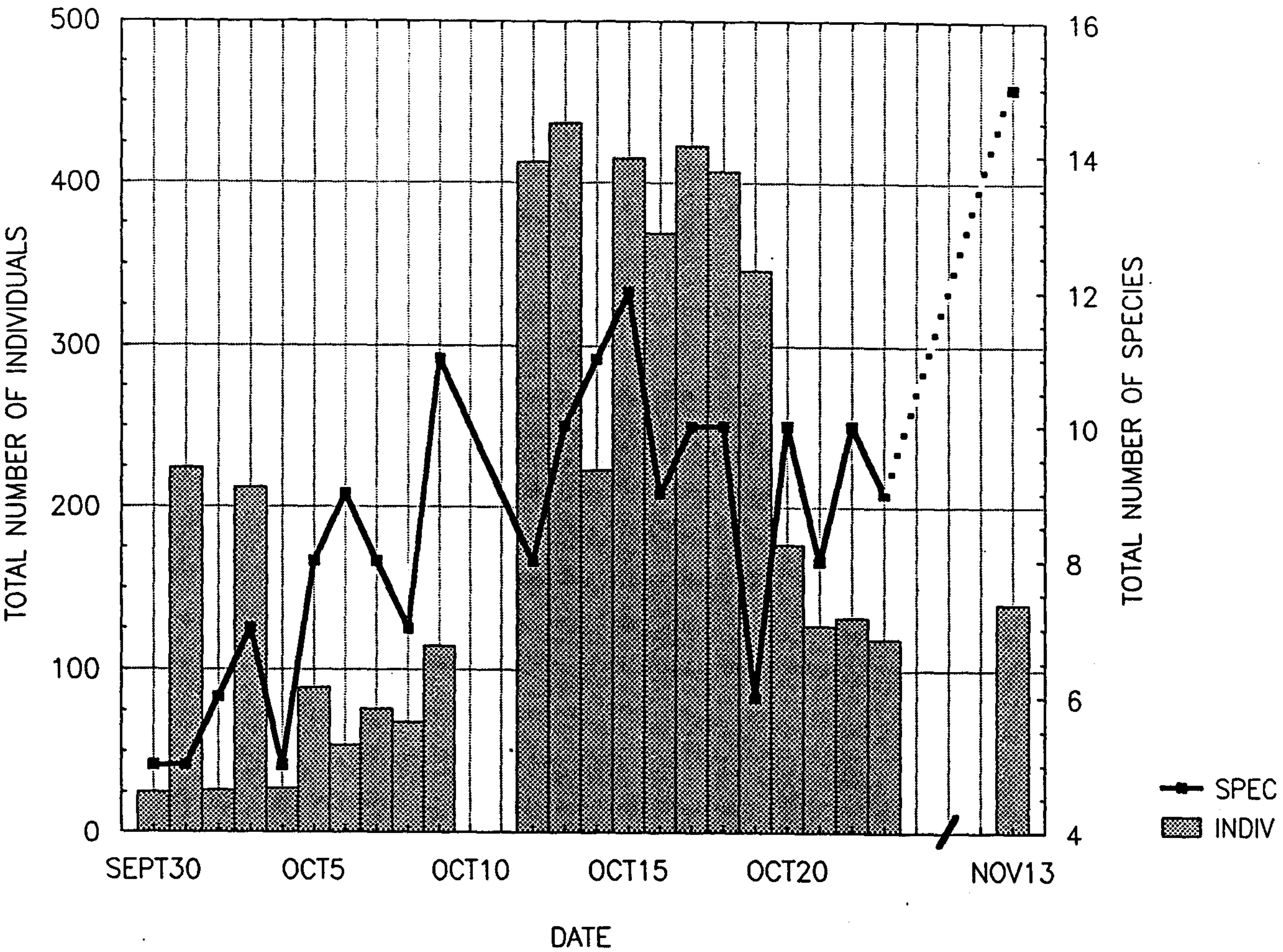


Figure 11. Occurrence of birds in Bag Harbour during salmon migration.

Bird activity

Twenty one species of birds occurred on the estuary over the study period including grebes (2 spp), loons (2 spp), cormorant (1 sp), ducks (8 spp) and gulls (4 spp) (Table 1). Number of species increased over the duration of the salmon run and was highest in early November after completion of the run while number of individuals was greatest near the middle of the run (Figure 11). Partitioning into several major groups indicates different trends. Piscivores, of which Western Grebe was the most common (Figure 12), were generally uncommon (<15 individuals) with a weak mode near the middle of the month, although after the salmon run in early November, Pacific Loon were common in the harbour. Number of ducks, of which White-winged Scoter and Harlequin Duck were the dominant species, was also low (<30 individuals) and relatively constant throughout October (Figure 13); Mallards, which were absent in October, were common in November. As well, a group of five Trumpeter Swans circled the estuary on November 14 and landed on Lutea Lake which forms the headwaters to Bag Harbour stream. Gulls (app. ¾ Herring Gull, ¼ Glaucous-winged Gull and occasional California Gull and Mew Gull) and Northwestern Crow were the most common birds during the salmon run (Figure 14). Crows were more prevalent on the estuary during early October and foraged on partially-eaten carcasses remaining from bear predation. In the latter half of the run, crows were most prevalent in the riparian habitat. Gulls were uncommon at the beginning of the salmon run but then increased to a maximum in the middle of October when salmon carcasses from downstream drift became prevalent in the estuary. All crows and the majority of gulls were absent from Bag Harbour two weeks after the salmon run ended.

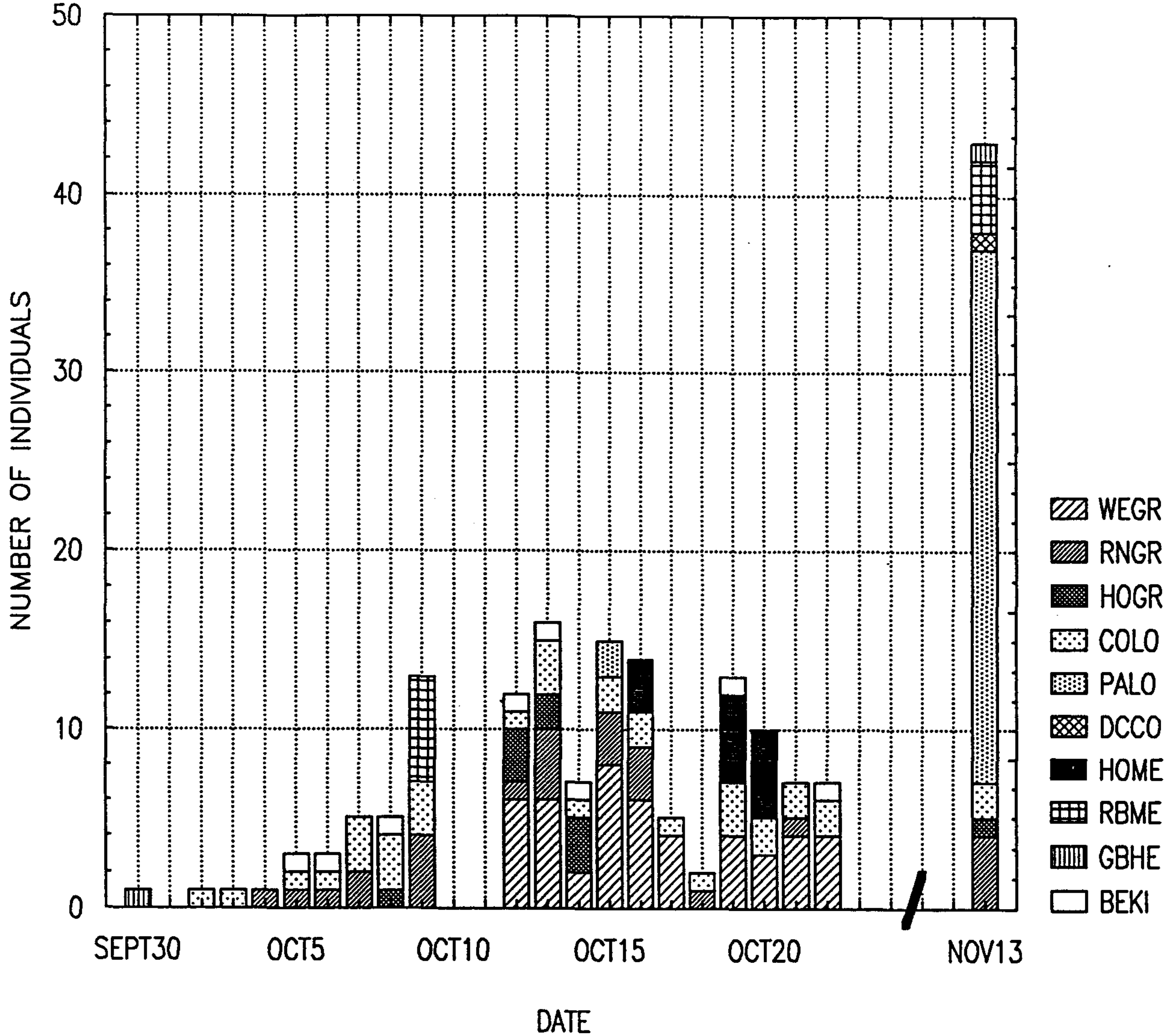


Figure 12. Occurrence of avian piscivores in Bag Harbour.

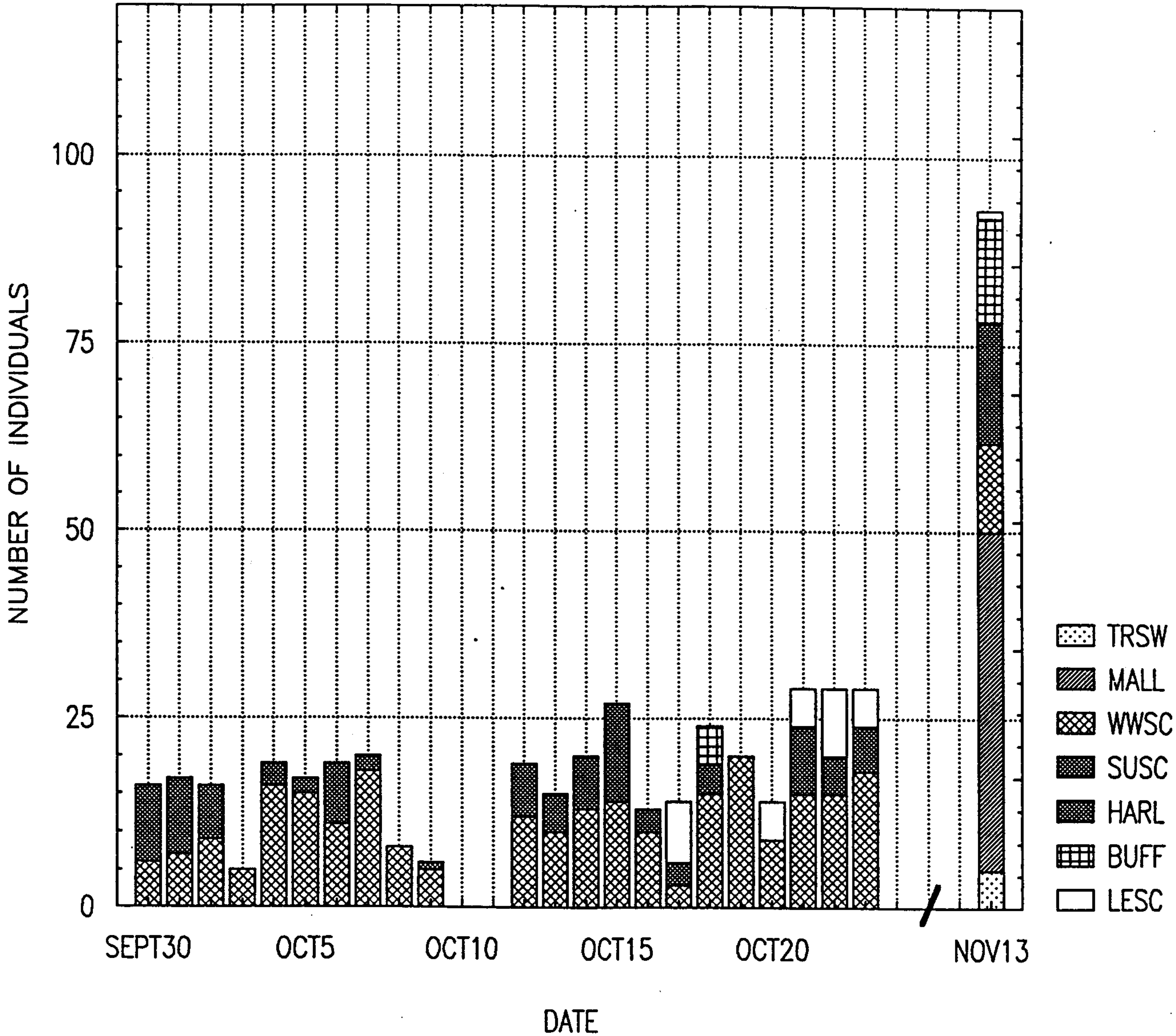


Figure 13. Occurrence of ducks in Bag Harbour.

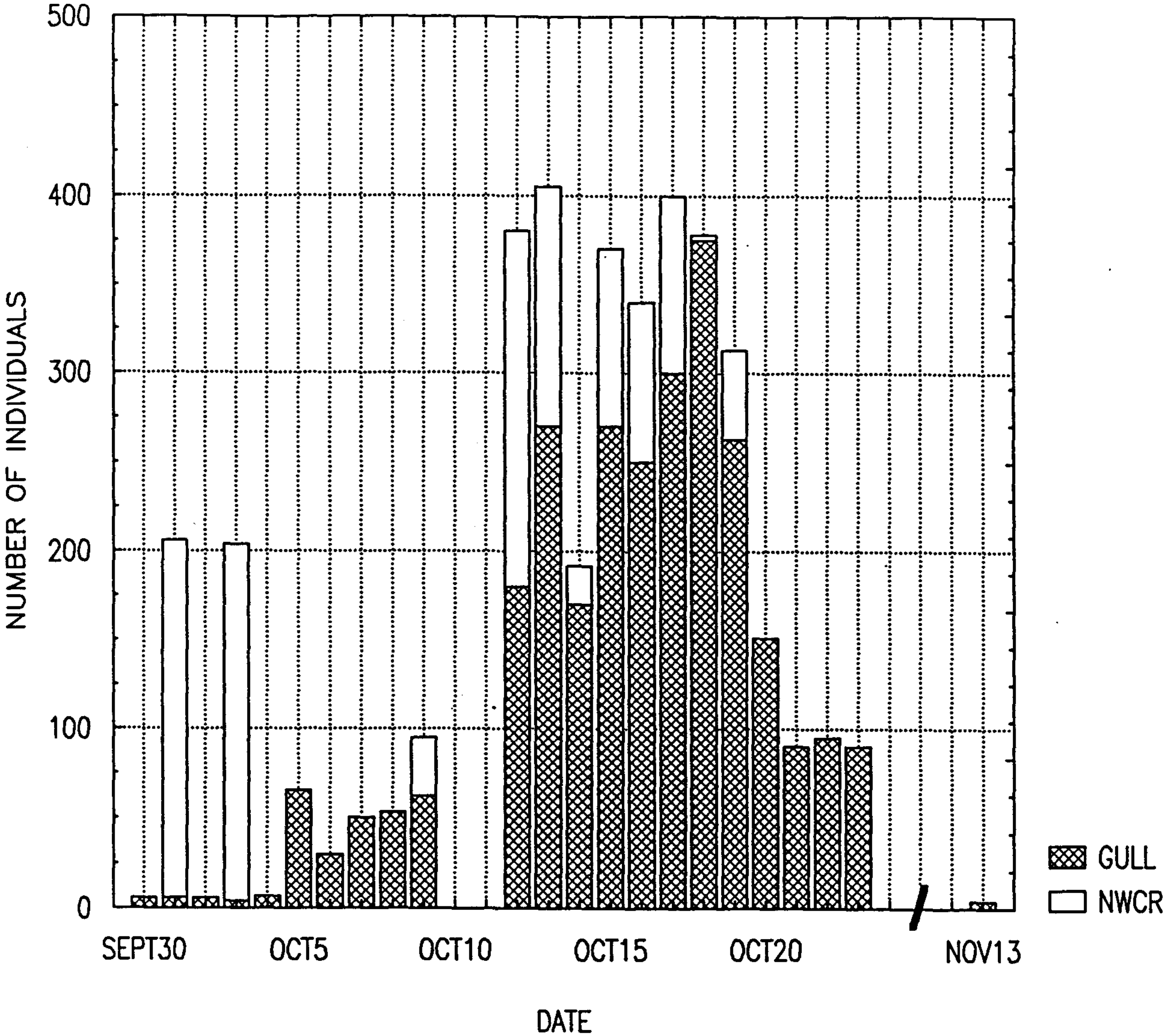


Figure 14. Occurrence of Northwestern Crow and gulls in estuary.

Diving transects

About 10 species of invertebrate scavengers were associated with salmon carcasses, the abundance of each dependent on substrate and depth (Table 2). The most common scavenger at shallow depths was the spindle shell (Searlisia dira). On some carcasses, >95% of the surface area was covered with these snails. Several hundred additional snails usually occurred on the substrate adjacent to the carcasses with decreasing densities at greater distances. At intermediate depths such as in eelgrass beds, spindle shells were much less common but remained important scavengers on carcasses close to rock substrates. Broken-back shrimp (Heptacarpus) were present on most of the carcasses in the eelgrass. On two carcasses, a small fish (Pholis laeta) occurred in the empty eye cavities of the head of the salmon. In sub-tidal habitats near the middle of the harbour, starfish and small crabs were the dominant scavengers. Juvenile bat stars occurred on the majority of carcasses and were occasionally abundant.

Some scavengers were common in the estuary but were rarely seen on the carcasses. The large starfish Evasterias was very abundant in brackish habitats of the stream channel but was rarely observed close to the carcasses. There were large schools of juvenile herring (Clupea pallasii) in the estuary, particularly in the eelgrass beds. These fish are planktivores rather than scavengers and no direct association with carcasses was evident. However, the major plankton abundance in the estuary will be associated with the nutrient loading from salmon carcasses.

A brief intertidal survey of the estuary on November 13 indicated a major increase in numbers of crab-predated spindle shells relative to that observed in late October. As most of the broken shells were greater than 20 mm length, only large-bodied crabs, such as Cancer, would have been capable of breaking these shells (Reimchen 1982). This suggests that nutrients transferred from the salmon carcasses to gastropods can quickly move to another trophic level.

Table 2. Marine invertebrate scavengers found on 40 salmon carcasses at different depths in Bag Harbour. Each carcass was surveyed for a minimum of 4 consecutive days.

Taxon	Shallow $\bar{x}$ (range)	Medium $\bar{x}$ (range)	Deep $\bar{x}$ (range)
Searlisia dira (spindle shell)	7 (0-250)	20 (0-125)	0
Pagurus spp. (hermit crabs)	2.5 (0-10)	1.2 (0-4)	0
Hemigrapsus nudus (beach crab)	0.4 (0-10)	0	0
Cancer gracilis	0.9 (0-4)	0	1.4 (0-6)
Heptacarpus (broken-back shrimp)	0.1 (0-5)	2.7 (0-15)	0
Evasterias (starfish)	0.1 (0-1)	0	0
Pisaster (starfish)	0	0	0.1 (0-2)
Asterina (bat star)	0	0	1.1 (0-9)
Pycnopodia helianthoides (sun star)	0	0	0.1 (0-1)
Dermasterias imbricata (leather star)	0	0	0.1 (0-1)
Number of carcasses	15	15	10

Carcasses anchored in the estuary showed 50% weight reduction over 5 days for an average loss of 200 g daily (Figure 15). Those in shallow water with high densities of spindle shells were consumed at a greater rate than those in deeper water with starfish and crabs. In both habitats, however, the tissues became progressively softer each day such that by the 5th day, some of the carcasses disintegrated on contact and could not be weighed. Movement of the carcasses produced a whitening to the water from the fine suspension or possibly from tissues entering solution. From these observations, all of the nutrients associated with these carcasses were re-incorporated into the marine system within one week.

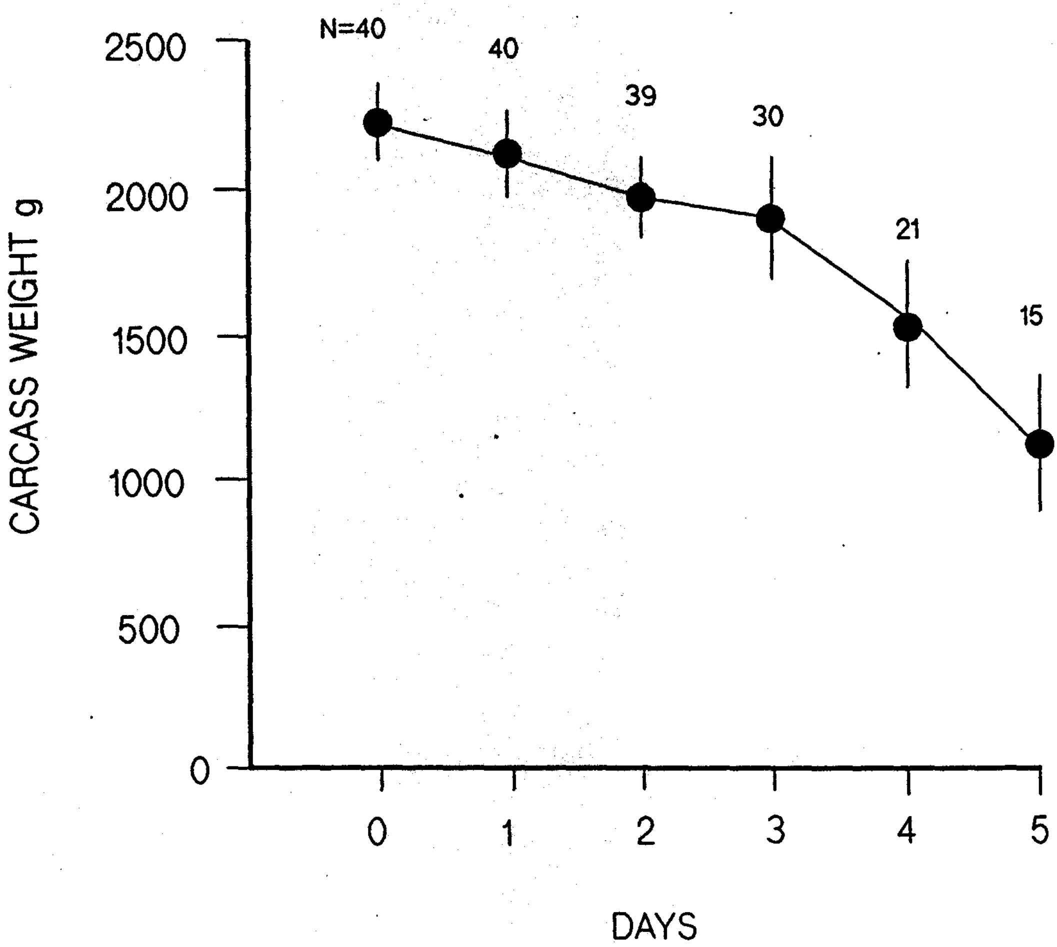


Figure 15. Daily weight loss of submerged carcasses from marine invertebrate scavengers.

Stream

Salmon activity

Department of Fisheries and Oceans (DFO) personnel surveyed Bag Harbour stream on 6 occasions from September 23 to November 4. Salmon first entered the stream September 24 and reached peak numbers of 2190 by October 24 after which numbers declined steadily (Figure 16). I visited the stream on November 13 and there was a single coho salmon and no living chum salmon in the stream.

Movement from the estuary into the stream was not a daily occurrence but rather occurred in pulses separated by several days with no entry. The major pulses of movement other than at the end of September occurred on October 4-5, October 15-16 and then on October 22-25. These pulses followed periods of high rainfall with the resultant increased discharge of the stream.

Of the 134 chum salmon marked in the estuary on October 5, recoveries were too low to evaluate any pattern in useful dispersal distance or longevity on the spawning gravels. In total, ten marked salmon (7.4%) were recovered over the following three weeks. These had each been captured by the bear and were found primarily adjacent to the estuary rather than beside the stream. Some, which were still in fresh condition, were captured as late as October 16. This indicates that at least some of the salmon present near the beginning of the run remained in the estuary for two weeks rather than migrating up the stream.

Total size of run estimated by DFO was 5115 chum, 60 coho and 3 pink salmon which included all living and dead salmon in the stream channel and adjacent banks. Based on total carcass counts (see below), I derive a marginally higher estimate of about 5800 chum in the estuary. Yearly number of salmon in the stream over the last 46 years have ranged from 1000 to 35000 individuals (Reimchen 1992b).

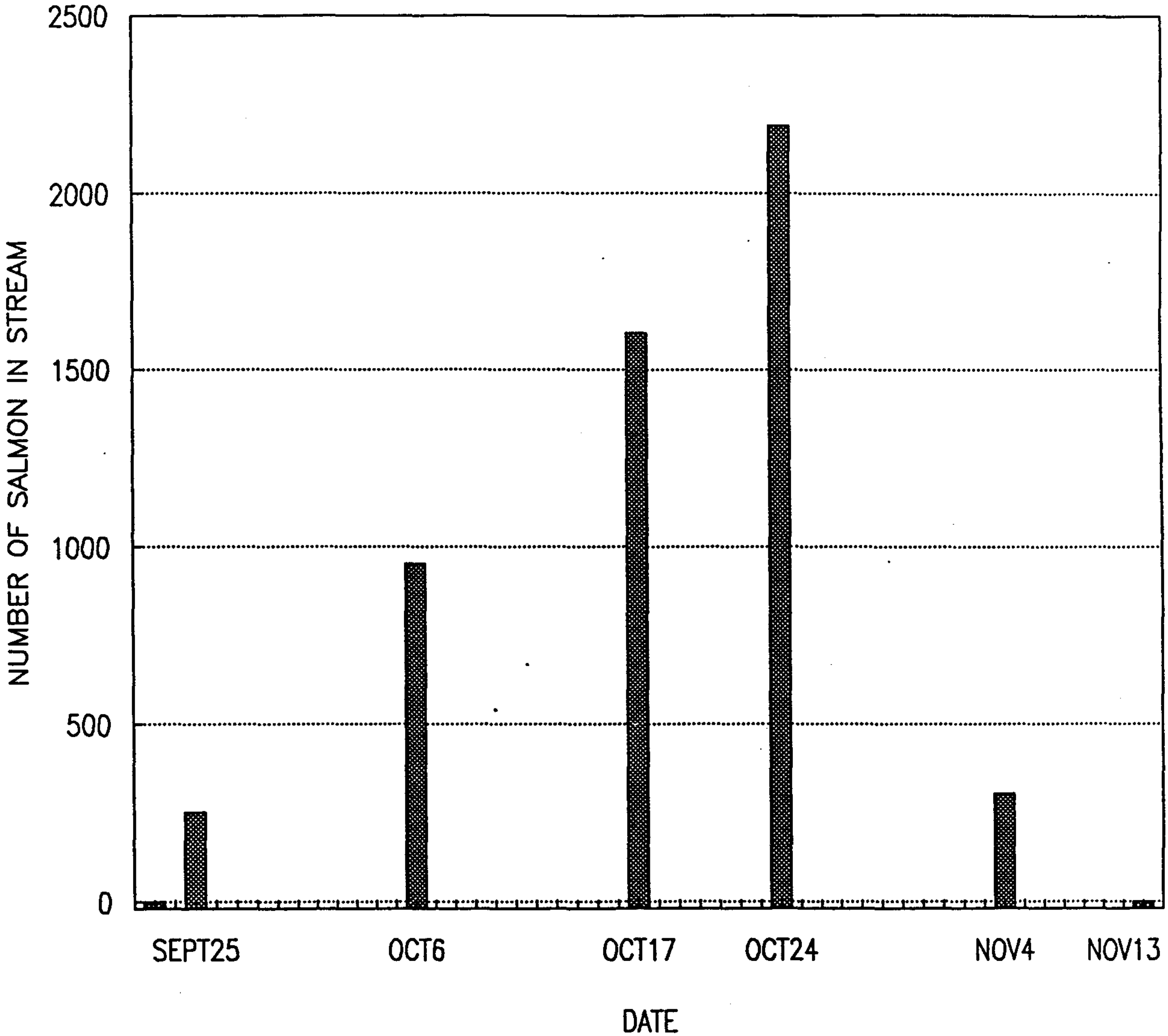


Figure 16. Number of chum salmon in the stream during the spawning run (records from B. Rowsell, DFO).

General behaviour of black bear

Throughout the study period, one or two black bear, occasionally three, were encountered daily on the stream. The three areas where each bear tended to occur were about 300-400 m from each other and the bears were seldom within visual range of each other. On a single occasion where two bears encountered each other during daylight, the smaller of the two rapidly ran into the forest so I suspect that at least during daylight there were a maximum of three foraging territories on the stream. On two occasions using night-viewing devices near dusk and dawn, I surveyed the lower reach of the stream where I had invariably seen only a single bear during daylight. On each occasion, two adult bears were foraging within 20 m of each other so I suspect that as in the estuary, nocturnal foraging is greater on the stream as well. During daylight or dusk, distance between bears appears to be maintained largely by visual cues yet during darkness, the absence of visual acuity seems to allow greatly reduced individual distance between bears.

Bear predation on salmon

Daylight foraging behaviour of the bear in the stream is quite different to that used during darkness in the estuary. The bears did not use the plunge manoeuvre as in the estuary nor pursue salmon on the spawning gravels but rather would wade into the stream, search under overhanging banks and under logs and on occasion, without any substantive motion, seize a salmon. Approximately ¾ of all the stream observations on bear involved this type of foraging. Also, for a two day period following heavy rains, the bear that foraged near the waterfalls stood in the centre of the channel and successfully seized salmon that were swimming up the falls.

Following capture, black bear carried the salmon either to a gravel bar, to a log or to the forest. Similar to observations in 1992, bear ate only part of the carcass, usually the dorsal musculature and the brain, before moving elsewhere in the forest or back to the stream. Bear generally returned to the carcass within a day and consumed more tissues.

Carcass abundance and estimates of total bear predation

Summarized data on number of salmon carcasses on the forest floor and in the stream channel are shown in Table 3. On September 29, five days after the first salmon entered the river, the west forest contained 220 carcasses and by October 7 contained 548 additional carcasses for an approximate transfer rate from the stream of 100 salmon daily. Over the next 18 days, 716 new carcasses occurred in the west forest or approximately 40 salmon daily. The final count of carcases on November 13, following completion of the spawning run, yielded 344 new carcasses or approximately 35 salmon daily. Cumulative transfer from the stream to the west forest for the entire autumn spawning run was 1828 salmon. During this period, there were an additional 1030 carcasses found in the stream channel.

Some proportion of carcasses are undetected during the surveys as remnants are dragged under logs by scavengers or totally consumed. In 1992, the rate of loss was estimated at 2% per day. I obtained further estimates in 1993 from mark and recapture values. Among the 220 carcasses marked on September 29, 189 were 'recovered' on October 7. This translates into a 1.56% loss daily. On October 17, a total of 737 fish had been marked (189 recoveries from October 7 + 548 fresh carcasses marked October 7) and 10 days later, 626 carcasses were recovered for a 1.51% carcass loss. Over longer periods the older carcasses are often not identifiable. For calculating number of lost carcasses on the west bank, I will use the average value (1.53% per day). This gives an estimate of 289 lost carcasses over the entire spawning run. Therefore, black bear transferred a total of 2117 salmon to the forest on the west side of the stream.

Black bears also transfer salmon to forests on the east side of the stream. A partial count of carcasses in 1992 suggested similar occurrence on both sides of the stream. To obtain a more detailed estimate, I made total carcass counts on the east side of the stream on October 25 and November 13 for comparisons with total counts from the west side of the stream during the same period. During this survey of the east forest, it became evident that there were no additional tributary streams draining into the main channel as were present on the west of the stream and this leads to reduced amount of riparian habitat bordering spawning gravels.

Table 3. Carcass surveys from west forest and stream channel at Bag Harbour (Sept to Nov 1993). M-male, F-female, UP-upper stream, IUP- intermediate upper stream, ILO-intermediate lower stream, LOW-below waterfalls (see Figure 2). All values represent number of carcasses in each site for each sex. PREDATED-bear captured salmon, SENESCENT-post-reproductive carcasses without bear injuries.

DATE	SITE	PREDATED FOREST		TOTAL	PREDATED STREAM		TOTALS		SENESCENT		TOTAL
		M	F	∑	M	F	∑	∑∑	M	F	∑
29/10/93	UP	30	14	44	2	3	5	49	2	0	2
	IUP	76	21	97	19	11	30	127	7	3	10
	ILO	29	16	45	3	1	4	59	0	1	1
	LOW	16	8	24	0	0	0	24	0	0	0
	∑	151	59	220	24	15	39	259	9	4	13
7/10/93	UP	102	31	133	36	14	50	188	2	7	9
	IUP	180	36	216	129	52	181	397	1	2	3
	ILO	89	39	128	44	32	76	204	0	1	1
	LOW	36	35	71	29	35	64	135	0	0	0
	∑	407	141	548	238	133	371	919	3	10	13
17/10/93	UP	40	25	65	27	8	35	100	24	10	34
	IUP	102	37	139	43	11	54	193	55	35	90
	ILO	68	56	124	17	2	19	143	27	37	64
	LOW	58	41	99	110	50	160	259	47	77	124
	∑	268	159	427	197	71	268	695	153	159	312
25/10/93	UP	106	55	161	52	14	66	227	106	28	144
	IUP	65	45	110	17	9	26	136	152	75	227
	ILO				4	7	11	11	40	38	78
	LOW	9	9	18	11	5	16	34	39	30	69
	∑	180	109	289	84	35	119	408	337	171	508
13/11/93	UP	90	57	147	15	14	29	176	1	3	4
	IUP	72	44	116	44	27	71	187	3	14	17
	ILO	27	35	62	49	35	84	146	12	16	28
	LOW	11	8	19	26	23	49	65	14	23	37
	∑	200	144	344	134	99	233	577	30	56	86
	∑∑	1206	612	1828	677	353	1030	2858	532	400	932

Numbers of carcasses reflect this difference as the east side has about 71% the number of carcasses (range 58-83%) found on the west side (Table 4).

Table 4 . Comparison of carcass abundance on west and east sides of Bag Harbour stream.

Date	West	East
25/10/93	923	764 (82.8%)
13/10/93	916	534 (58.3%)
Total	**1839**	**1298 (70.55%)**

Therefore, combining counts from the west and east sides of the stream yields a total of 3611 salmon (2117 + (2117*.7055)) that were transferred from the stream to the riparian habitat. This averages about 80 salmon daily over the 45 days of the autumn spawning run and represents approximately 63% of the entire run. There were an additional 1030 salmon that were captured by bear but eaten in the stream channel. Summation of these carcasses with those on the forest floor gives a total of 4641 salmon or about 81% of the salmon run that are captured and partially consumed by bear. In 1992, total consumption was estimated at 87% of the run.

Carcass weights

During the study period, I weighed 689 carcasses that had been left by bear. The majority of these salmon would have been captured within the previous 24 hours as I had surveyed the same areas and marked all carcasses on the previous day. Average weight of all carcasses was 1331 g (range 40 - 4600 g) or approximately 46% of the original weight of the salmon (Figure 17). Daily weights of fresh carcasses fluctuated over the spawning period in a cyclical fashion. Near the onset of the spawning run, approximately 60% of each carcass was left uneaten but by October 5 the bear was leaving less than 40% of the carcass (Figure 18). Over a period of several days, bears began to leave a greater portion (up to 75%) which again began to decline to near 35% over the next 13 days.

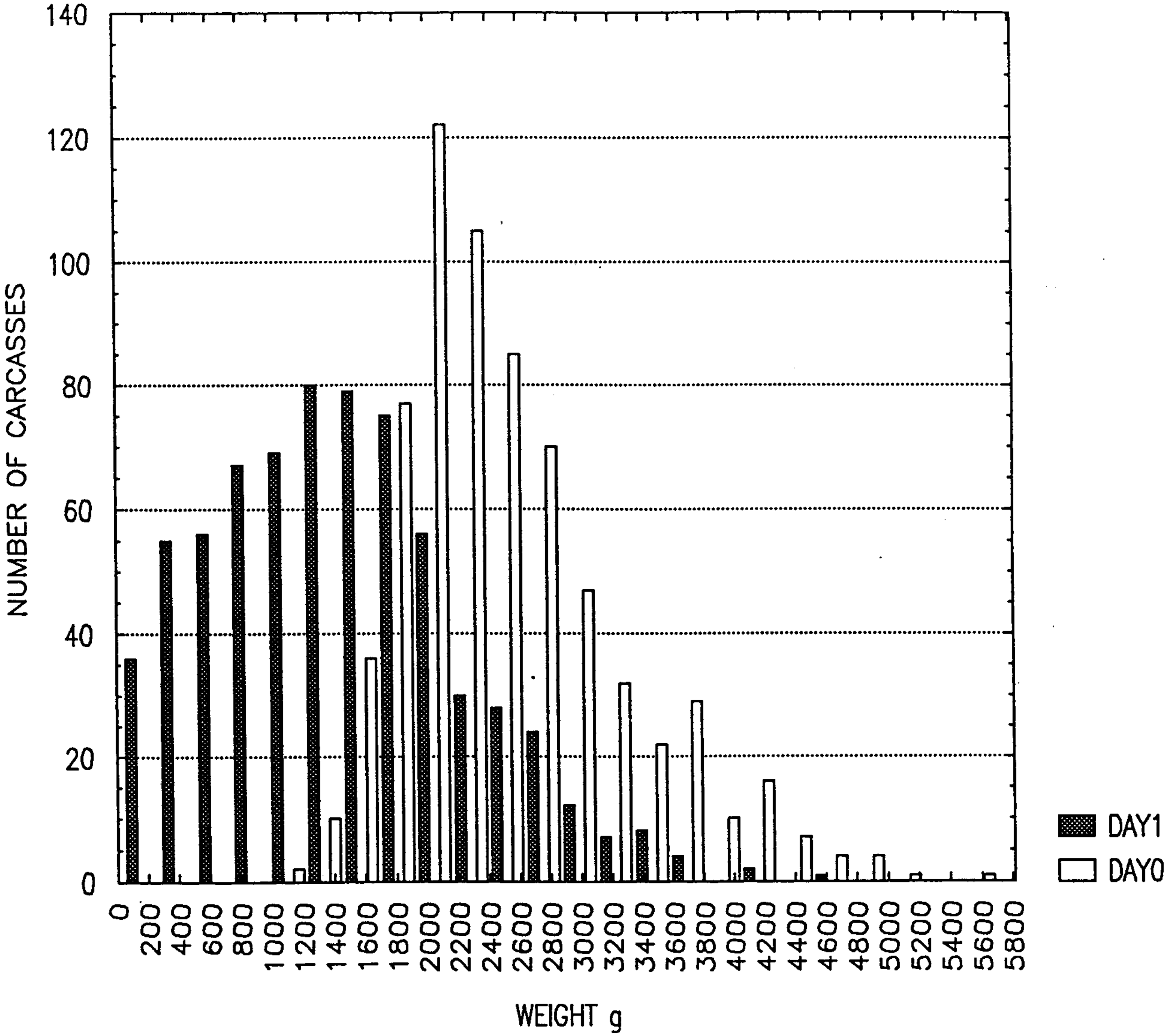


Figure 17. Weight frequency distribution of bear-captured salmon carcasses found in Bag Harbour estuary, stream and forest habitats. Open histograms represent original weight of carcass calculated from jaw length.

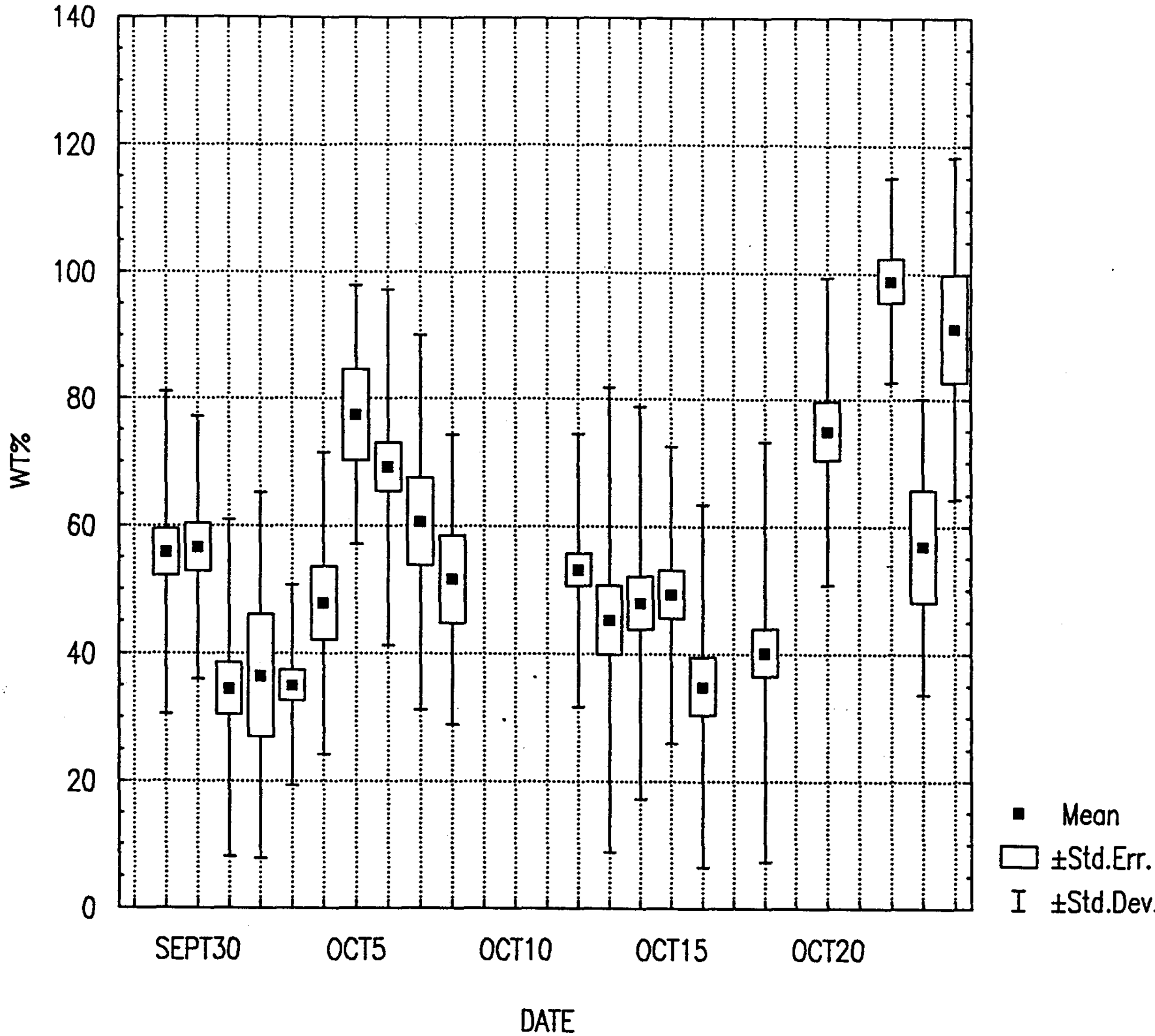


Figure 18. Average amount of carcass left uneaten by bear in estuary, stream and forest habitats. WT% represents actual weight of carcass divided by total weight estimated from jaw length.

over the next 13 days. However, near October 22, about 80% of each carcass remained. These fluctuations basically correlate to the abundance of salmon in the stream as higher weights of carcass occur immediately following one of the pulsed migrations into the stream. When salmon are uncommon, the bear consume a greater proportion of each carcass than if salmon are abundant in the stream.

Spatial distribution and carcass quality

Distribution of carcasses is shown in Figure 19. About ⅓ of the salmon captured by the bear were consumed directly in the stream channel while the majority were transferred to the forest floor. Numbers of carcasses were greatest adjacent to the stream and declined with increased distance from the stream. The furthest carcasses were found 150 m into the forest.

Presumably, the reason that the bear carried occasional salmon well back into the forest may simply reflect disturbance near the stream, for example from human activity or other bears. Several times when I encountered a bear on the stream, it took the carcass back into the forest. However, there may be some additional factors such as higher quality of particular salmon that on capture warrant greater transfer distance independent of whether there is any proximal disturbance. This is predicted from optimal foraging theory (Krebs 1978). For example, size of salmon captured by the bear might comprise a measure of quality. One predicts that larger fish would be carried further into the forest. Plot of average size against stream distance (Figure 20) is consistent with this suggestion as the data indicate that the smallest size classes of salmon are consumed either in the stream channel or on the stream bank. This trend occurs for both male and female salmon.

Towards the middle of the spawning run, there are increased proportions of senescent salmon which are spawned out and have atrophied soft tissues and decayed fins. One might suspect that these would have lower nutrient value and be of lower quality than fresh individuals. If optimal foraging processes are applicable here, senescent fish should be eaten closer to the stream than fresh fish. The data demonstrate that the majority (87%) of senescent fish were eaten directly in the stream channel compared with 30% for fresh salmon (Table 5).

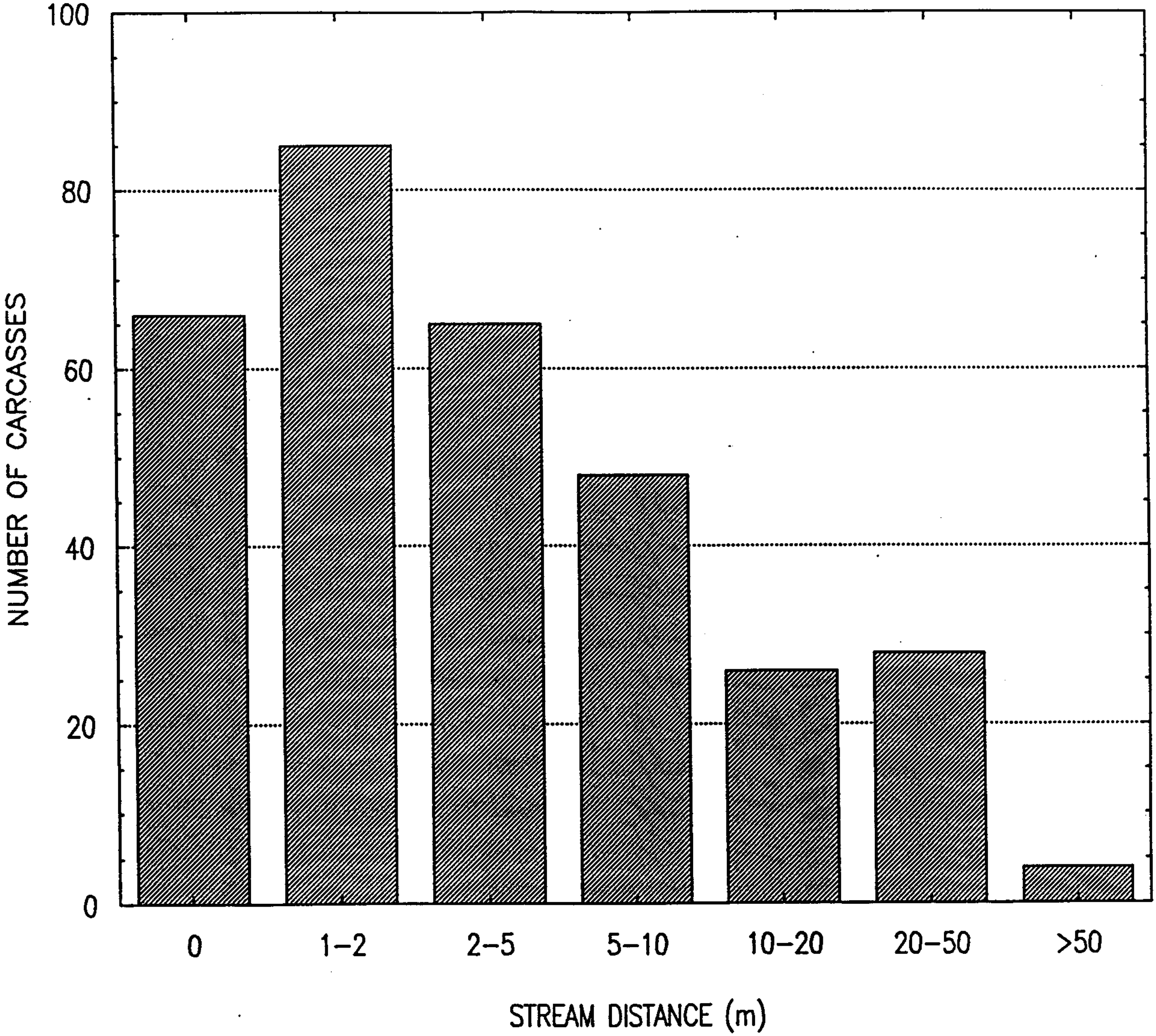


Figure 19. Frequency distribution of bear-captured carcasses over different distances from the stream.

Table 5. Relationship between carcass condition at time of capture and distance from stream. Period of capture is the same for the two groups (October 8-Oct 24).

Body condition	Stream distance (m)		
	0	1-2	>2
Fresh	19	22	21
Senescent	76	10	1

χ^2 =52.6, P<0.001

By transferring higher quality salmon further from the stream, the bear minimize potential interference during ingestion and, as well, will reduce secondary loss from scavengers such as gulls which are most active close to the stream.

One of the distinguishing features of many salmon carcasses that have been taken by bear is the absence of the cranium. This behaviour has been observed in grizzly bears (Mossman 1958) and black bear (Frame 1974) from Alaska. Occasionally, the brain case is the first and only part of the carcass consumed after capture, the remainder being taken during secondary visits. On several occasions where I observed at close range this tissue consumption, the bear held the carcass down with a paw and then delicately bit off the top of the head, occasionally including the orbits and nares. Extensive licking of the brain cavity after the main tissue was removed further suggested a strong preference for this tissue, perhaps due to the fats on the nerve fibres. On several instances, I noted that senescent carcasses in the stream channel had an intact cranium yet other tissues such as trunk musculature were removed. Consequently, in subsequent carcass measurements, I also recorded presence/absence of brain. These data (Table 6) demonstrate that for both sexes, the brain is consumed primarily on fresh salmon but rarely on senescent fish. Among males in prime condition, 69% had the brain missing compared with 6.9% of senescent males (χ^2 = 60.0, P<0.001). For females, 62% of those in prime condition had the brain missing compared with 4.9% of senescent fish (χ^2 = 37.9, P<0.001). This finding contrasts with that of Frame (1974) who noted that black bear seldom ate the brain of fresh salmon but regularly did so for senescent carcasses.

Table 6. Relationship between salmon carcass condition factor and brain consumption by black bear. Body Condition 1(new), 2(medium), 3 (senescent). Numbers show percentages.

		Body Condition			
	Brain	**1**	**2**	**3**	**N**
♂♂	Present	31	67	93	127
	Absent	69	33	7	180
	N	239	39	29	307
				χ^2 = 60.0, P<0.001	
♀♀	Present	38		95	75
	Absent	62		5	61
	N	95		41	136
				χ^2 = 37.9, P<0.001	

From the ongoing examination of carcasses, I suspected that small fish captured by bear were more likely to have an intact brain. Excluding all senescent carcasses and grouping for size class demonstrates that for both males and females, the largest carcasses had increased incidence of brain removal but this was only significant in male salmon (Table 7). Perhaps this is simply a matter of handling dexterity in which the bear is unable to properly hold and grip small carcasses. If so, then small bodied species such as pink salmon could be expected to have lower incidence of brain removal and as Frame (1974) has shown, represent for black bear a less-preferred prey than chum salmon.

Table 7. Relationship between size class of salmon and brain consumption by black bear. Body weight g 1000 - 2000 =1, 2000 - 3000 =2, >=3000 =3. Numbers show percentages and totals.

		Size class			
♂♂	**Brain**	**1**	**2**	**3**	**N**
	Present	42	37	21	109
	Absent	58	63	79	221
	N	38	116	95	330
				χ^2 = 7.6, P<0.022	
♀♀	Present	50	38	14	36
	Absent	50	62	86	59
	N	14	74	7	95
				χ^2 = 2.5, P=0.28	

Sex ratio of carcasses

In the 1992 survey, which was carried out in the latter half of the spawning run, about ⅓ of the salmon captured were female and most were spawned out. Direct observations in 1993 on foraging by bear initially suggested quite a different pattern. Near the lower reaches of the stream channel, there are several pools where salmon collect prior to moving up a narrow water falls into the stream proper. On several days following rains, black bear were quite active in these pools and were commonly observed to move slowly among the salmon which were frequently visible at the surface. The bear would seize a salmon, hold it a few seconds, release it and then repeat the pattern. Of 16 examples where the salmon was released, all of the fish were male. Only when a gravid female salmon was caught would the bear take fish onto the bank, step on the salmon's belly, extrude and lick up the eggs. The bear applied additional pressure to the belly with its nose and forced out additional eggs. After eggs were consumed, the bear would return to the pool and the pattern was repeated. The salmon on the bank were not eaten during these foraging bouts but generally within 24 hours, the bear returned and consumed more of the carcasses. Targeting females in this manner clearly for the high nutrient values of the eggs indicates that the bear could have a significant effect on numbers of females that reached the spawning grounds if this behaviour was representative over the entire month when salmon were moving into the stream. Such a generalization is prevalent among managers of these resources.

Average sex ratios in salmon streams is highly variable but males tend to exceed females. In streams of eastern Asia, sex ratio of adult chum salmon is approximately 4♂♂:1♀♀ (Khorevin 1987) while in Alaska it averaged 1.45♂♂:1♀♀ near the beginning of the run and 1♂♂:1♀♀ near the end of the run (Salo 1991). In Oregon, the ratio was 1.7♂♂:1♀♀ at the beginning of the run, 1♂♂:1♀♀ near the middle and by the end, there was a slight excess of females (1♂♂:1.2♀♀)(Salo 1991). Consequently, the variability in sex ratio is sufficiently broad among different streams that sex ratio in Bag Harbour stream cannot be predicted a priori.

I determined sex ratio of the 692 bear-killed carcasses on the east side of the stream. Overall ratio was 2.3♂:1♀. This can be partitioned for habitat to yield ratios of 3♂:1♀ in the estuary, 1.8♂:1♀ in the stream and 2.2♂:1♀ in the forest (Table 8). These values are not statistically different from each other.

Table 8. Sex ratio of bear-captured salmon from estuary, stream and east forest.

		Estuary		Stream		Forest	
♂♂		75	162	65	105	69	217
♀♀		25	54	35	56	31	98
	N	216		161		315	

I also recorded sex ratio of 2858 carcasses from the west side of the stream and the stream channel as part of the survey of total carcasses (Table 3). These data demonstrate a consistent excess of males during each of the five survey dates and in both forest and stream habitats. Overall sex ratio of salmon taken by bear was 2.0♂:1♀. Sex ratio on the forest floor ranged from a high of 2.9♂:1♀ on October 7 to a low of 1.4♂:1♀ on November 13. In the stream, it ranged from 2.1♂:1♀ on October 17 to a low of 1.4♂:1♀ on November 13. Within the 4 survey zones along the length of the stream, sex ratio was close to unity only in the lower reaches of the stream and the adjacent forest, and occasionally (October 7) reaching a slight excess of females.

Following completion of spawning, adult salmon die and these carcasses collect under logs or at the bottom of pools. I examined 932 of these spawned-out carcasses and 57% were males for a sex ratio of 1.33♂♂:1♀♀. This varied from 1♂♂:1.2♀♀ (N=24) during the first two weeks of the run, 1♂♂:1♀♀ (N=312) near the middle of the run, 2♂:1♀ on October 25 and 1♂:1.9♀ on November 13. If bear were targeting female salmon throughout the run, then the salmon that survive to the end of the run such as these spawned-out carcasses, should exhibit a marked deficiency of females relative to the total sex ratio. This does not occur.

Among the 4957 salmon that were examined, which is close to 90% of the entire run, population sex ratio was 1.8♂♂:1♀♀. Because the sex ratio of salmon captured by bear averaged 2.0♂♂:1♀♀, it is evident that bear are not targeting females but rather exhibit a slight excess of predation on males relative to their frequencies in the population.

Reproductive condition of carcasses

In view of the large number of salmon captured by the bear, it would be useful to ascertain their reproductive state at the time of capture, for example, whether it was pre-spawned, partially spawned, or spawned-out. In the examples where I observed bear capturing gravid females, I examined the carcass after the bear departed and in each case found eggs still present in the body cavity. Subsequently I examined 19 post-reproductive female carcasses from the bottom of pools. Three of the fish (14%) still had substantial number of eggs (200-450) while the majority (84%) had fewer than 5 eggs. Egg retention, as observed in the former group, is common in post-reproductive salmon and is greatest on females that have had delayed access to the spawning gravels (Sandercock 1991). Examination of all female salmon captured by bear shows that 69% had fewer than 5 eggs in the intact ovaries and are presumed to have been effectively spawned-out at the time of capture. However, because bear consume the entire ovaries in some carcasses, the lack of eggs is at best ambiguous information on the reproductive state of the female. I also closely examined the substrate around the carcass of the freshly captured gravid females and noted from 20-100 eggs scattered and lodged in mosses and under sticks and suspected that egg count on the ground might provide a secondary estimate of reproductive state. Consequently, on all further carcasses, presence or absence of eggs was recorded and if present, numbers recorded.

Among the 176 female carcasses examined, 29% had some eggs on the ground (number of eggs $\bar{x}$ = 26.3, range 1 - 300) and are presumed to have been captured before completion of spawning. Yet this will be a maximum estimate as the analyses is confounded by egg retention in post-reproductive females. The majority of carcasses (71%, N=125) had no eggs on the ground and had probably completed spawning at the time of capture.

Male chum salmon are the major prey of black bear throughout the autumn spawning run at Bag Harbour and presumably the captured males comprise a range of reproductive states from pre-spawned to spawned-out. Each males attempt to spawn with many females and releases only a small proportion of total sperm during each fertilization event. I used relative testes weights as an index of spawning condition. Testes from pre-spawned males captured by bear in the estuary some 0.5 km from the stream mouth and well outside of the freshwater channel averaged 3.1% of body weight (range 2.1 - 4.3, N = 22). While the sample sizes are small, this value is similar (3.13%) to that obtained by Khorevin (1987), one of the few other published studies on testes weight in chum salmon. However, Khorevin also noted that smaller fish have slightly but significantly higher relative testes weight than larger fish (regression equation y = 4.547 - 0.000369 * body wt). Therefore, on a male that is partially spent, original testes weight can be predicted from body size and as such allow an estimate of the extent of relative weight loss in the testes. Testes were also weighed on 17 post-reproductive and senescent males found dead in pools below spawning gravels. These testes averaged 1.2% of the body weight. Therefore ratio of the relative body weights of testes provides an index of reproductive state of the male salmon at the time of capture. Values close to unity indicate that the bear are capturing pre-spawned salmon while values approaching 0.28 suggest that predation was on spent males.

Based on a sample of 338 bear-killed male salmon, average testes ratio was 0.64 (range 0.10 - 1.4, Figure 21). The ratio was highest in the estuary ($\bar{x}$ = 0.80), intermediate in the forest ($\bar{x}$ = 0.68) and lowest in the stream channel ($\bar{x}$ = 0.42) (F = 49.6, df = 335, P<0.001, ANOVA). On the criteria that ratios of 1.0 or greater represent a pre-spawned condition, then 89% of the males captured by the bear have spawned at least once. Using a ratio of 0.9 would indicate that 81% of the males have spawned at least once. A plot of average daily testes ratio over the spawning run is shown in Figure 22. Departures above and below average values probably reflect differences in abundance of salmon. Two of the three periods with marked increases in testes ratio (October 2, 15 and 22) occur following rains. Presumably, bear are capturing fresh salmon that have just entered the stream. Lowest testes ratio occurred near the middle of October near the end of an extended period without rain when no new fish had entered the stream and most were probably spent.

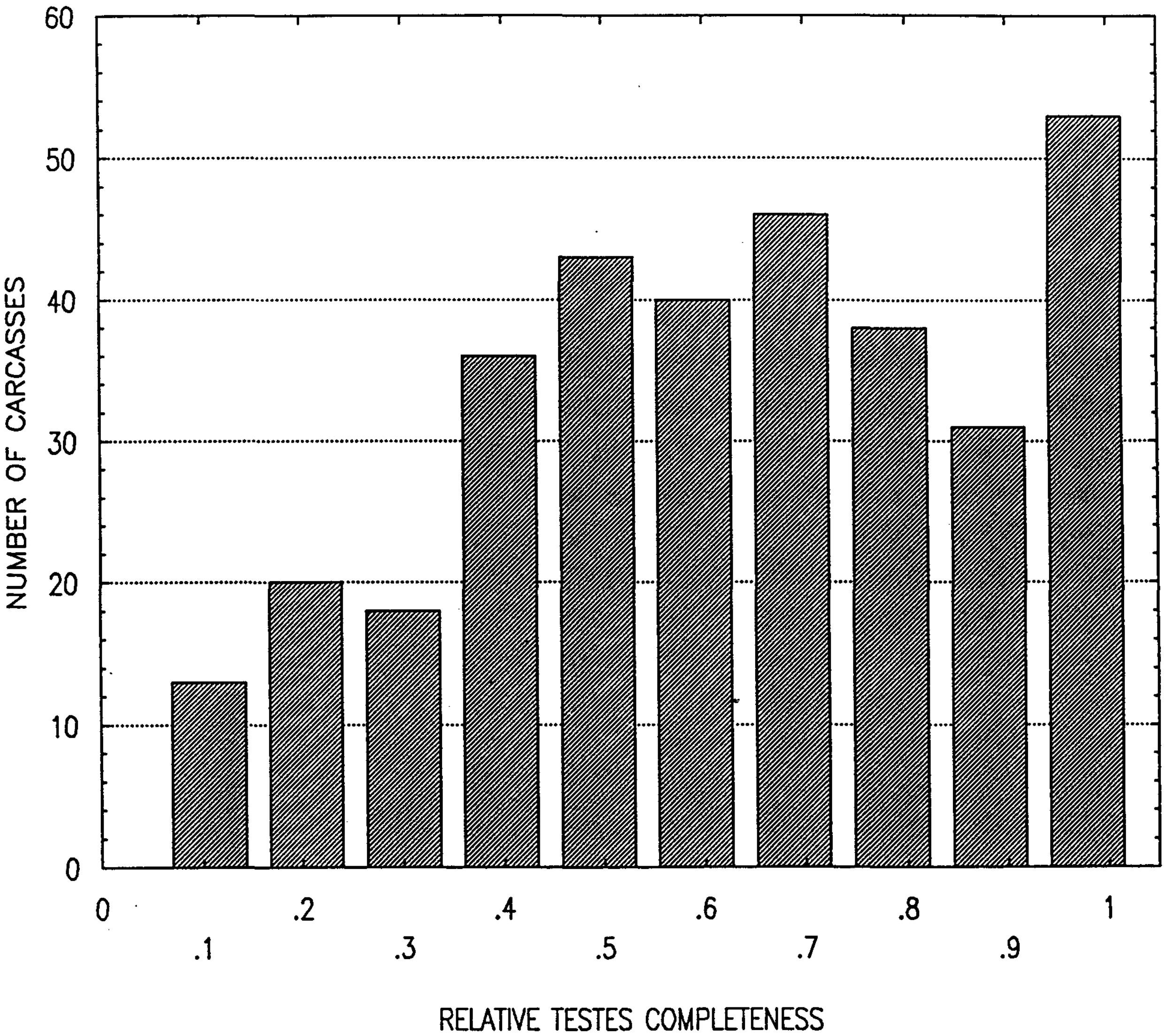


Figure 21. Frequency distribution of relative testes weight of bear-captured carcasses.

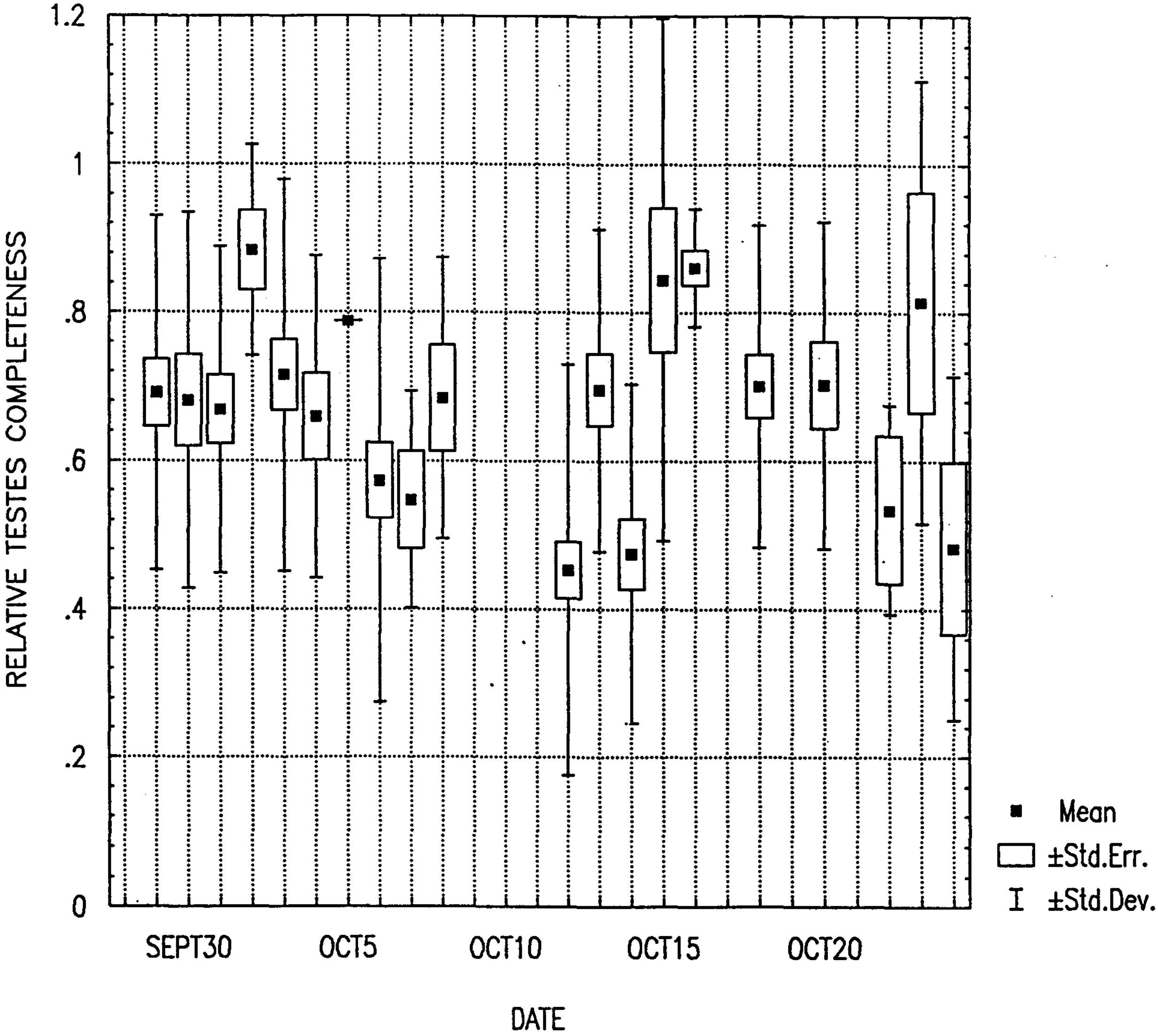


Figure 22. Testes ratio of bear-captured salmon over the study period.

Scavengers on carcasses

Pine marten were observed on four occasions on the stream (close to the waterfalls) pulling a fresh bear-killed carcass under a log and on two occasions eating salmon eggs that had been scattered near the carcass. As in 1992, the marten did not take any decaying tissues but only fresh material. River otter were not present on the stream but two individuals were seen in the headwaters at Lutea Lake and probably utilize coho salmon that spawn in the tributaries to the lake.

Several hundred gulls (Herring Gull 75%, Glaucous-winged Gull 25%) occurred below the falls in the first half of the salmon run and foraged on salmon eggs and carcass remnants that drifted downstream. During the second half of the salmon run, when bear-killed carcasses and senescent carcasses were more common, gulls were observed throughout the length of the stream. These scavengers foraged primarily in the stream channel and to a smaller extent on carcasses from the stream bank.

Northwestern Crows were the most abundant scavenger on fresh carcasses. Several flocks each >100 individuals were present in the habitat throughout the entire observation period but were not present in early November when carcasses were all decayed. They occurred both on the stream channel, banks and well back into the forest where ever fresh bear-killed carcasses were found. Crows commonly congregated near a bear that was feeding on a freshly captured salmon and loud vocalizations developed as numbers of crows increased. As soon as the bear abandoned the carcass, small groups of crows immediately began to feed on the tissues for several minutes before being displaced by other small groups.

Four bald eagles (2 adults, 2 young) usually occurred on several large trees approximately 1 km upstream and close to a large open reach of the stream where salmon were abundant. Over the entire study period, I saw only a single case of an eagle with a freshly captured salmon and infer that much of the foraging activity was directed at the fresh carcasses left by the bear.

Dipper were observed on two occasions feeding on salmon eggs that drifted along the bottom in the current. While Varied-thrush and Winter Wren were common in the riparian habitat at Bag Harbour, I observed only one instance where these birds were associated with a fresh carcass. Ravens were also present daily but in low numbers and scavenged carcasses on the forest floor.

Another major scavenger on carcasses observed in 1993 but which was not seen on any carcasses in 1992 were fly maggots. Within several days after a salmon was transferred to the forest floor, muscoid flies were occasionally observed near the carcasses and fly egg masses were regularly seen. These eggs hatched within two or three days. Eleven percent of the carcasses had maggots after 5 days. The majority (85%) of carcasses were enveloped in maggots by the 7th day. Approximately 20% of the carcasses on gravel bars of the stream were also covered in maggots.

After the tissues were fully consumed, thousands of maggots could be observed moving off of the bony remnants onto the moss substrate and dispersing outwards in all directions. The frontal edge of these maggot migrations were occasionally encountered 3 m from the central carcass remains and as the density of carcasses increased over the salmon run, dispersing maggots were prevalent throughout the entire riparian habitat where carcasses occurred.

Movement of these maggots appeared to have one of three outcomes. For those adjacent to the stream or on gravel bars, this movement often resulted in maggots falling off the banks into the stream. Large number of drowned maggots were present beneath the overhanging banks and were presumably consumed by Dolly Varden, rainbow trout and young of the year coho salmon that are common in this habitat. A second outcome often resulted in colonization of fresh carcasses and in these instances, the new tissues quickly became enveloped in maggots. The noxious odour associated with the high density of maggots on most carcasses appeared to exclude other vertebrate scavengers. While I saw crows and gulls as well as wrens and fox sparrow close to these maggot concentrations, no evidence of foraging was seen. I observed several bear droppings with numerous dead but undigested maggots. The third outcome for this movement of maggots was to locate a suitable substrate for pupation. The pupae overwinter and emerge in spring as adults. The exceptionally high density of maggots on the majority of carcasses suggests a major alternate energy flow to that observed in 1992 when vertebrates dominated the scavenger community.

To obtain a rough measure of tissue consumption by these scavengers, I re-weighed carcasses for 6 days after initial abandonment by the bear. These data (Figure 23) show an average tissue loss of 94 g daily although by the 6th day, the large number of maggots on the carcasses excluded reliable tissue weight measurements. As there are about 80-100 carcasses transferred daily from the stream to the riparian habitat, this indicates that about 9.4 kg of tissue are being cycled daily into these scavengers. I suspect that most of the transfer to vertebrate scavengers occurred when the carcass was fresh, probably within 48 hours of original capture by the bear.

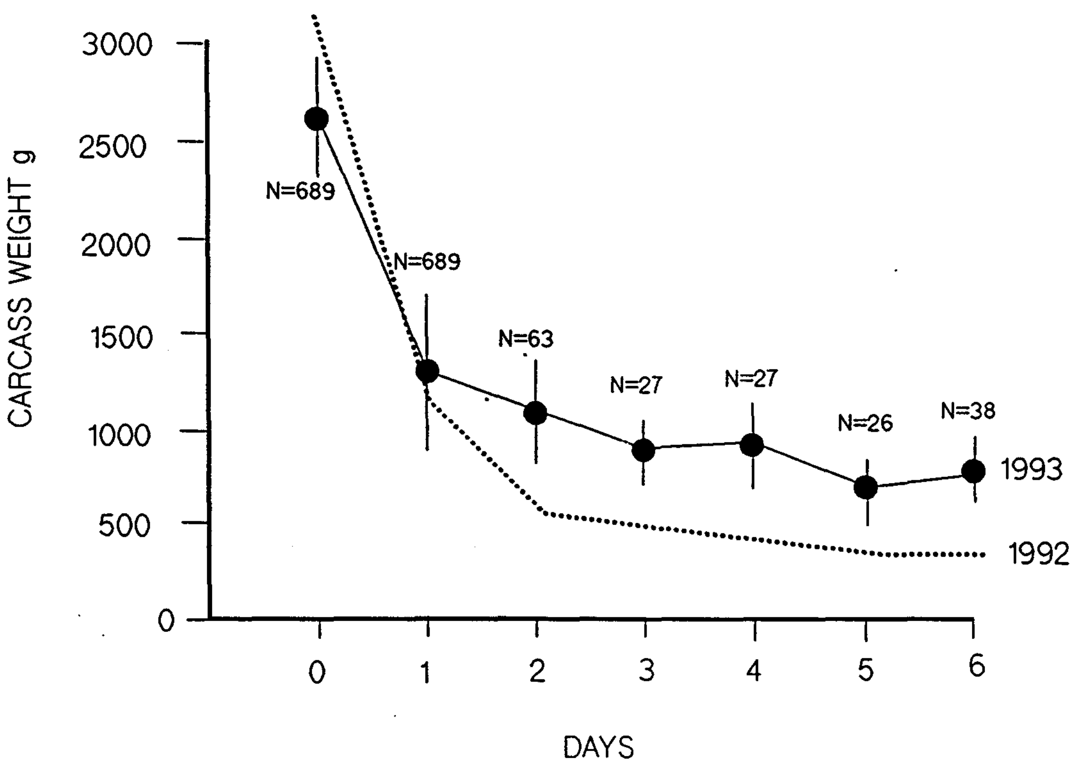


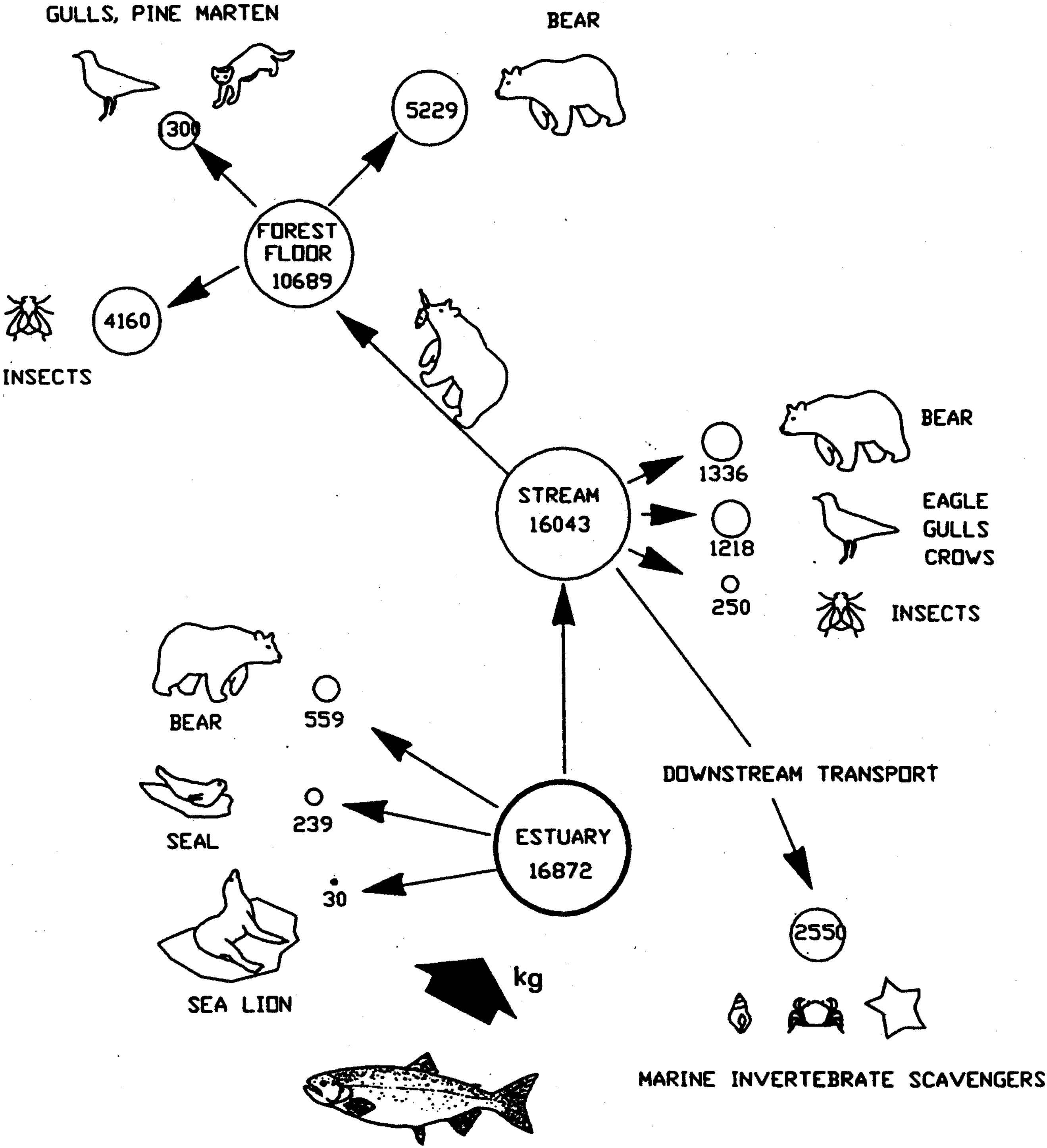
Figure 23. Average daily tissue loss of marked carcasses in the riparian habitat.

Biomass transfer and energy flow at Bag Harbour

Summarized data on the movement and transfer of salmon tissue is shown on Figure 24. Based on the cumulative count of carcasses, I will use an estimate of 5700 for the total population entering Bag Harbour. Average weight of all fresh carcasses measured in the estuary was 2.96 kg which converts to a total biomass of 16872 kg. Seals consumed 239 kg (1.4% of total), black bear consumed 593 kg in the estuary (3.5% of total) while Steller's Sea Lion had an estimated consumption of less than 30 kg (<0.2%).

From September 24 to the end of October, 5420 salmon (16043 kg) entered Bag Harbour stream or 95% of the original run. Black bear captured 4641 salmon, consumed 6848 kg and left 5460 kg of tissue in the riparian habitat and 1722 kg in the stream channel. About 1300 kg of tissue was taken by crows and gulls from the forest floor while 2000 to 4000 kg of soft tissues were consumed by maggots. Assuming a standard 10% conversion efficiency between trophic levels, then some 300 kg of maggots or pupae were incorporated into the riparian habitat. Some unknown proportion of these will be consumed by soil arthropods, shrews and probably numerous insectivorous birds when the adult flies emerge in spring.

The stream channel contained 1722 kg of tissues left from bear and 2306 kg of spawned-out carcasses for a total of 4028 kg. Numbers of crows and gulls in the stream and riparian habitat were comparable to 1992 where estimate of total tissues consumed (based on daily caloric requirements) was 1218 kg. Assuming this was comparable in 1993, then the remaining 2550 kg will be swept downstream in the estuary where it was scavenged by marine invertebrates. Gastropods were the major scavengers in shallow water which is where most of the carcasses occurred.


GULLS, PINE MARTEN
BEAR
300
5229
FOREST FLOOR 10689
4160
INSECTS
STREAM 16043
1336
1218
250
BEAR
EAGLE
GULLS
CROWS
INSECTS
BEAR
559
SEAL
239
30
SEA LION
ESTUARY 16872
DOWNSTREAM TRANSPORT
2550
kg
MARINE INVERTEBRATE SCAVENGERS

Discussion

This study has confirmed the principal result obtained during the preliminary study at Bag Harbour in October 1992; black bear transfer a large proportion of the salmon run into the forest habitat and free up large quantities of high quality tissue to a variety of vertebrate and invertebrate scavengers.

In 1992, about ⅓ of the 81 bear-killed carcasses examined were female and most were spawned out contrasting with results in Alaska where black bear targeted gravid female chum salmon (Frame 1974). Results in 1993 which involved a much larger sample size demonstrate that of 3550 carcasses, 33% were female and about 70% appear to spawned-out. Most of the male chum salmon captured had reduced testes weight indicative of prior spawning.

Many of the peripheral results were also comparable between the years. Numbers of predators, scavengers and species assemblage in the estuary were similar other than for Steller's sea lion which was uncommon in 1993.

Several substantive differences occurred between the years one of which was the flow of energy through the forest habitat. In 1992, of the 2229 kg of tissue left by the bear, most appeared to be cycled to vertebrates, primarily crows, gulls, eagles and pine marten. A comparable amount was used by these scavengers in 1993 but there was an additional 3000 kg of tissue cycled into invertebrate scavengers. Fly maggots colonized 85% of the carcasses in 1993 compared to 0% in 1992 and were certainly the major scavengers of the decaying tissues. The pungent odour associated with these maggots largely excluded all other scavengers. There may be a diversity of physical and biological variables associated with this yearly difference in fly abundance. One of the obvious factors that might reduce flight and scavenging activity of flies is low ambient temperatures. I calculated average temperatures for October during the two years. Daytime temperatures were similar (Oct 1 - 15, 1992 = 11°C, 1993 = 12.1°C; Oct 16 - 31, 1992 = 10.3°C, 1993 = 12.2°C). However, nighttime temperatures were substantially cooler in 1992 than in 1993 at least in the early part of October (Oct 1-15 1992 = 4.0°C, 1993 = 8.1°C; Oct 16-31 1992 = 6.5°C, 1993 = 7.6°C). Although speculative, temperature may represent an important variable in understanding direction of energy flow through the riparian habitats.

There were a number new findings in the 1993 study. Carcasses which are swept downstream into the estuary are extensively scavenged by gastropods in shallow water and secondarily crabs and starfish in deeper water. Generally tissues decayed rapidly in the water and within 5-6 days were very soft and appeared to flow into solution when moved. These nutrients, possibly more than 2000 kg, will be cycled into both primary producers and primary consumers.

During darkness on the estuary, a great deal of activity is usually evident, including loud splashes and other surface turbulence. In 1992, I suspected that this was primarily associated with seal pursuits on salmon which formed tight schools close to shore. Use of the night-viewing devices in 1993 demonstrated that the majority of this activity was not due to seals but rather to black bear plunging in the estuary for salmon. Bear reached their highest numbers on the estuary some 4 - 6 hours after dusk and were active throughout the night. During daylight, bears use visual cues to avoid interactions with other bears but at night, visual cues are lost and bears frequently interact at close range to each other using primarily auditory and olfactory cues. This observation represents a potentially important and valuable contribution for understanding the biology of black bear.

The highly distinctive foraging behaviour in which the bear made 'belly flops' into the shallow water has not been seen during daylight. The behaviour probably depends on auditory cues in initially locating the salmon school and then tactile cues as salmon move past their legs. Capture success of bear during nocturnal foraging (24%) was very similar to dusk and dawn foraging success of black bear in Alaska (26%, Frame 1974).

There were a maximum of three bears on the stream during daylight and six bears on the estuary during darkness. Of the bears arriving on the estuary after dusk, only one approached from the direction of the stream and may have shared both habitats. In southern regions of Gwaii Haanas, Bag Harbour was the only major salmon producing stream in 1993 (K. Rowsell, personal communication) and it seems probable that bear from adjacent watersheds would have congregated in the harbour. If so, the eight or nine bear seen in Bag Harbour may comprise most or all of the bear bear in the region.

Over the entire salmon run (45 days), bear consume 7451 kg of salmon. Assuming that 8 bear were present throughout the run, then daily salmon consumption averages 20.7 kg per bear. Extracting data from Frame (1974) on black bear consumption of chum and pink salmon in Alaska suggests an approximate daily consumption of eight chum and 1 pink salmon per bear. Although weights of carcass remnants were not available, on the assumption that the Alaskan black bear consume 50% of each carcass, as at Bag Harbour, then daily ingestion would range from 8 - 16 kg.

There were more than twice as many salmon that returned to Bag Harbour in 1993 compared with 1992 (5700 vs 2300). Although the number of bear appeared to be comparable between the years, they transferred over the same time period almost twice as many salmon to the forest floor. Average weights of carcasses after abandonment were comparable between the years and it is reasonable to suspect that bear have put on substantially more weight during the 1993 salmon season than during autumn of 1992. The absence of cubs among the six adult bear at Bag Harbour (at least two females) suggests some limitation, possibly poor physiological condition of the female during the previous winter. In the survey for salmon carcasses in October 1993, 3 black bear cub skeletons were found. Two of these occurred together and the skeletons were intact and undisturbed, suggesting death possibly from abandonment and starvation.

While the salmon run at Bag Harbour was substantially larger in 1993 than in 1992, the numbers of returning salmon are about 16% of the maximum (35000) recorded in 1947 (Figure 25). Consequently, it is probable that the carrying capacity of the estuary and riparian habitat remains well below historical levels.

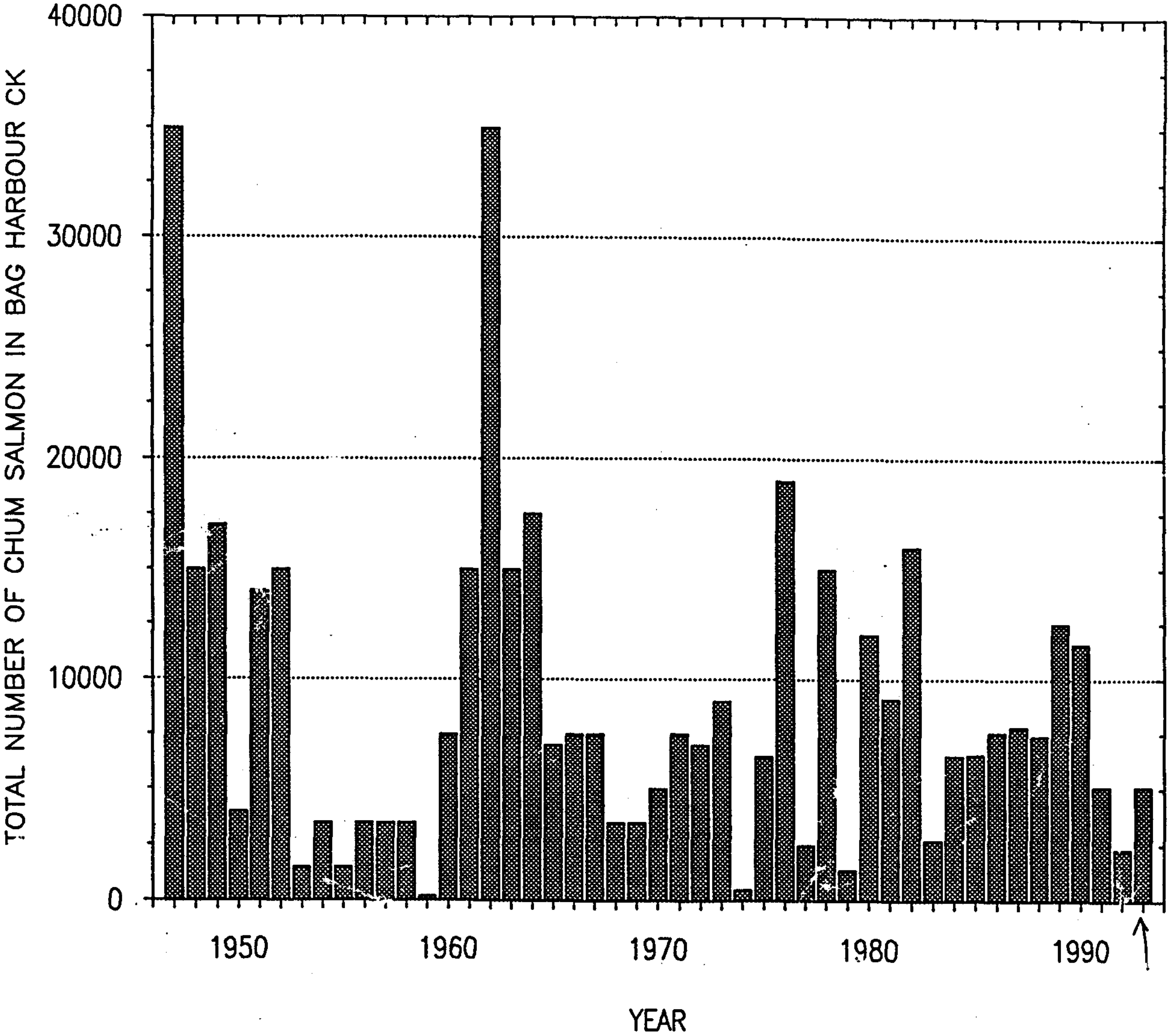


Figure 25. Yearly chum salmon abundance at Bag Harbour 1947-1993.