

Abstract—Streamer tags are commonly used to study the ecology and population biology of the American lobster (*Homarus americanus*). Aquarium observations suggest that streamer tag loss, either through tag-induced mortality or tag shedding, is related to the molt stage of the lobster at the time of tagging, and the molting event itself. Tag-induced mortality, where lobsters did not molt, occurred within eleven and sixteen days following tagging for lobsters tagged in postmolt (4%) and late premolt (10%) stages, respectively; whereas no lobsters tagged in early premolt or intermolt stages died. Tag-induced mortality at time of molting was observed for lobsters tagged in late premolt stage (11%), and tag shedding was observed for lobsters tagged both in early (25%) and late premolt (11%) stages, but was significantly higher ($P=0.014$) for lobsters tagged in early premolt stages. Autopsies revealed that lobsters died mainly of organ perforations (hepato-pancreas and pericardial sac) following the tagging process, and rupture of the dorsal thoraco-abdominal membrane during the molting process. The total tag loss was estimated at 4% for lobsters tagged after molting, and 27% and 31% for lobsters tagged in early and late premolt stages, respectively. There was no tag loss for lobsters tagged in the intermolt stage during four months of laboratory observations (July–October). To minimize streamer tag loss, lobsters should be tagged during the intermolt or postmolt stage. Based on field studies, recapture rates for lobsters tagged in premolt stage are always lower than those of lobsters tagged in postmolt stage. Furthermore, recapture rates during the second year, for lobsters that molt in the year following tagging, were drastically reduced, and no lobster was recaptured after four years at large. Finally, to account for tag loss during the first year at large, a minimal adjustment of 24.9% (SD 2.9%) and 4.4% (SD 1.6%) for the recapture rate of lobsters tagged immediately before and after the molting season, respectively, is recommended. Adjustments beyond one year at large are not recommended for the American lobster at this time.

Manuscript approved for publication 19 February 2003 by Scientific Editor. Manuscript received 4 April 2003 at NMFS Scientific Publications Office. Fish. Bull. 101:476-483 (2003).

The effect of timing of tagging on streamer-tag recapture rates for American lobster (*Homarus americanus*)

Michel Comeau

Manon Mallet

Department of Fisheries and Oceans
343 University Ave
Moncton, New Brunswick, Canada E1C 9B6
E-mail-address (for M. Comeau): comeaum@df-mpo.gc.ca

Tagging methods to study the movement, growth, and exploitation rate for the American lobster (*Homarus americanus*) have improved over the last 70 years. One major improvement in the mid 1960s was the introduction of an insertion tag called the “sphyrion tag” that is anchored to muscle tissue (Scarratt and Elson, 1965), instead of body tags (Templeman, 1935) or carapace-piercing tags (Wilder, 1953) used earlier. By the late 1980s, the sphyrion tag was replaced by another insertion tag called the polyethylene “streamer tag” (Landsburg, 1991; Moriyasu et al., 1995) initially developed for shrimps (*Penaeus* spp.; Marullo et al., 1976). Insertion tags have the advantage of being retained through a series of molts, thus providing information on long-term movement and more accurate data on growth.

Tag loss could greatly bias the estimate of population characteristics and fishery parameters (Ricker, 1975). For obtaining population estimates from mark-recapture data, tag loss generally refers to the reduction of the initial number of tagged animals by means other than fishing. In a series of tagging studies, Comeau et al. (1999) noticed a constant pattern of lower tag recovery rates for lobsters tagged in the premolt stage than for lobsters tagged in the postmolt stage. They indicated that the level of fishermen participation (recovery rate) could be a possible cause of tag loss because they noticed a steady decline of recapture rates where multiyear tagging studies were conducted. However, because the same type of streamer tag was used and each lobster was handled individually, the fishermen

participation could not explain the difference between recapture rates for lobsters tagged in premolt and postmolt stages for a given year; hence possible tag loss at molting was suspected as the cause of the lower recapture rates (Comeau et al., 1999). Furthermore, in an attempt to estimate mortality rates, Comeau and Mallet (2001) used a mark-recapture model and simulations to evaluate the best estimator. They concluded that the level of tag loss is high and could be a serious problem for estimating fishery parameters for the American lobster if information on tag loss is not available.

Moriyasu et al. (1995) showed that sphyrion tag loss for lobsters held in aquaria varies between 3% and 23% depending on the molt stage at tagging. They also mentioned that lobsters tagged with sphyrion tags showed a significantly lower return rate (19%) than lobsters tagged with streamer tags (44%) in a recapture study in the field and suggested a possible lower level of tag loss among lobsters tagged with streamer tags. However, they did not estimate the tag loss for streamer-tagged lobsters. Recently, Rowe and Haedrich (2001) showed that the shedding rate for streamer tags in the field could reach 18% (40% for molted animals and 11% for nonmolting animals) after 8–12 months based on double tagging with a secondary carapace marking. They also found that streamer tag shedding was not related to sex or size, but they did not study the level of tag-induced mortality.

Various causes can reduce the initial number of tagged animals, mainly tag shedding, tag-induced mortality, and

death from natural causes (Beverton and Holt, 1957). In the present article, “tag shedding” refers to the physical detachment of the tag from a lobster and “tag-induced mortality” refers to the actual death of a lobster caused by the tagging process.

In the southwestern Gulf of St. Lawrence, lobsters are harvested either in the spring prior to the July–August molting season, or in late summer and early fall (early–August to early October, partially during and shortly after molting) (Comeau and Savoie, 2001). The purpose of our study was to estimate the level of streamer tag loss for the American lobster tagged before and after the summer (July–August) molting season by using aquarium observations. From the results of our aquarium study, we determined adjustments of the recapture rate in relation to the molt stage at the time of tagging.

Materials and methods

Aquarium observations

Two experiments were carried out at the “Aquarium et centre marin” (New Brunswick Department of Agriculture, Fisheries and Aquaculture) in Shippagan, New Brunswick, with lobsters captured in Baie des Chaleurs (47°52'N; 64°52'W). Because the main focus of our study was to investigate tag loss in relation to the molting stage, only males were considered because they have a higher probability of molting annually compared to sexually mature females (Comeau and Savoie, 2001). All lobsters caught were brought to the laboratory where carapace length (CL) and shell rigidity were recorded (the latter with a durometer) (Comeau and Savoie, 2001). In both experiments, lobsters were tagged by the same person to avoid variability in tagging procedure following the technique described by Moriyasu et al. (1995). Streamer tags manufactured by Hallprint Pty. Ltd. (15 Crozier Rd, Victor Harbor, South Australia, 5211 Australia) were used. As is routinely done in our tagging studies in the field (Comeau et al., 1998, 1999), tagged lobsters were kept in a holding tank for a minimum of 30 min following tagging, and dead lobsters were removed from the experiment. Tagged lobsters were then transferred to large tanks partitioned with 25 × 25 cm individual compartments. These tanks were supplied with running seawater at ambient temperature. Lobsters were fed rainbow smelt (*Osmerus mordax*) twice a week. Lobsters were examined three times a day in July and August, and on a daily basis for the rest of the experiment. The date of tag shedding, of molting, or of death was recorded for each lobster.

Limited aquarium space prevented the use of a control group of untagged lobsters. However, autopsies were performed on all lobsters that died in the course of the experiments in order to identify the cause of death. The following tagging traumas, causing death, were identified (Krouse and Nutting, 1990): 1) perforation of vital organs, such as the pericardial sac and the hepato-pancreas; 2) rupture of the thoraco-abdominal membrane; and 3) necrosis or infection of lobster tissue at both the point of entry and exit of the tag.

The first experiment began on 23 June 1998 before the summer molting season with the tagging of 229 hard-shell male lobsters ranging between 66 and 78 mm CL. To avoid unnecessary manipulation of the lobsters, the molt stage at tagging was estimated by the number of days between tagging and molting. Individuals that molted within 30 days of and 30 days after tagging were considered lobsters tagged in late premolt and early premolt stages (Aiken, 1980), respectively. The molt stage of lobsters that died during the experiment was determined by observations of the pleopods (Aiken, 1980). A total of 191 male lobsters were tagged in premolt stage (56 in early and 135 in late premolt stage) and 38 in the intermolt stage (lobsters that did not molt over the entire experiments). Observations of premolt tagged lobsters that molted in June and July ended on 8 September 1998. Observations of the remaining lobsters tagged on 23 June 1998 ended on 30 October 1998. Before releasing the lobsters in the water, their wounds from the tag insertion were examined for infection.

The second experiment began 9 September 1998 with the tagging of 187 soft-shell male lobsters in the postmolt stage based on shell condition criteria (Aiken, 1980; Comeau and Savoie, 2001). They ranged in size between 66 and 83 mm CL. Observations of postmolt tagged lobsters ended on 30 October 1998.

Field studies

Comparison of recapture rates from field studies Six tagging studies were carried out after the fishing season (May–June) in Caraquet, New Brunswick, between 1994 and 1996. Male and female lobsters were captured, tagged, and released on the commercial fishing grounds. For each year, tagging was done before (in early July with hard-shell lobsters) and after (in mid-September with soft-shell lobsters) the molting season. In 1995, the July tagging was delayed one week because the lobster fishing season ended on 7 July instead of 30 June. In 1996, tagging was carried out in early October instead of mid-September because of bad weather. As with the aquarium experiments, the same person performed the tagging procedure. Tagged lobsters were kept in a holding tank for a minimum of 30 min following tagging and any dead lobsters were removed. Finally, an awareness campaign described in Comeau et al. (1998) was conducted to maximize the participation of fishermen in reporting tagged lobsters as tag recovery took place during the fishing seasons following the year of tagging.

Adjustment of the recapture rate Recapture rates observed during the fishing season following tagging were adjusted by using the information from the aquarium observations. In contrast to tag misreporting that biases the estimated number of recaptured lobsters, tag loss affects the number of tagged animals (N) in the population available to the fishery. To account for possible tag loss in our field studies, N was adjusted as follows. Let p represent the tag-retention rate parameter estimate based on aquarium observations with variance $p(1-p)n^{-1}$, where n is the total number of animals observed in each aquarium experiment.

Table 1

Number and rate (in percentage) of tag shedding and tag induced mortality for American lobsters (*Homarus americanus*) tagged in postmolt, intermolt, and premolt stages in the aquarium experiments. Lobsters tagged in the premolt stage have been separated into early and late premolt divisions, and n is the number of lobster used to calculate the adjusted recapture rate.

	Premolt			Intermolt	Postmolt
	Early	Late	Total		
Initial number ¹ (n)	56	135	191	38	183
Tag loss without molting					
Tag-induced mortality	0	13 (10%)	13 (7%)	0	7 (4%)
Shedding	0	0	0	0	1 (<1%)
Total	0	13 (10%)	13 (7%)	0	8 (4%)
Tag loss during or after molting					
Tag-induced mortality	1 (2%)	14 (10%)	15 (8%)		
Shedding	14 (25%)	15 (11%)	29 (15%)		
Total	15 (27%)	29 (21%)	44 (23%)		
Total tag loss	15 (27%)	42 (31%)	57 (30%)	0 (0%)	8 (4%)

¹ Number used in the experiment after accounting for lobsters that died within 30 minutes of tagging.

The adjusted number of tagged animals released during the field studies effectively available to the fishery is equal to

$$N_{adj} = Np, \quad (1)$$

with variance

$$V(N_{adj}) = Np(1 - p). \quad (2)$$

The field study recapture rate (t) is defined as

$$t = m(N_{adj})^{-1}, \quad (3)$$

where m = the number of tags returned.

The variance of t can be calculated by using conditional theory and an approximate variance of $(N_{adj})^{-1}$ (Seber, 1982). In this study, we used Monte-Carlo simulations to obtain the 90% confidence interval (CI) for t . The simulations were carried out in two steps to include variability associated with tag loss from the initial N animals tagged and released, and variability in recapture rate. First, assuming that the number of tags retained (N_{adj}) follows a binomial distribution with parameters N and p , a random number (\tilde{N}_{adj}) was selected from a *Binomial*(N, p), where N was set equal to the number of animal tagged during a particular study, and p equal to the proportion of tag retention estimated from the aquarium study. With this simulated \tilde{N}_{adj} a conditional value of t was derived as

$$t_c = m_o(\tilde{N}_{adj})^{-1}, \quad (4)$$

where “~” = the simulated value; and

m_o = the observed number of recaptures in a field study.

Secondly, a value for \tilde{m} was obtained from a binomial distribution with parameters \tilde{N}_{adj} and a conditional recapture rate t_c . A simulated recapture rate was calculated as

$$\tilde{t} = m(\tilde{N}_{adj})^{-1}. \quad (5)$$

The process was repeated 1000 times and the 90% CI for \tilde{t} was defined as the 5% and 95% quantiles of the resulting 1000 Monte-Carlo values of \tilde{t} .

Results

Aquarium observations

Tag-induced mortality was observed within 30 min of tagging for two lobsters tagged in the late premolt stage (1.5%) and for four in postmolt stage (2.1%) but not for lobsters tagged in early premolt and intermolt stages. The autopsies revealed that all of these lobsters died from perforation of the pericardial sac and these lobsters were not used in our experiments.

Tag loss of premolt lobsters was associated solely with tag-induced mortality and this was restricted to 10% (13) of the late premolt lobsters (Table 1). Autopsies revealed that six lobsters died within three days of tagging from the rupture of the dorsal thoraco-abdominal membrane, one died after one day from the perforation of the pericardial sac, and six died between three to sixteen days after tagging from a perforated hepato-pancreas (Table 2). In contrast, only 4% (7) of postmolt lobsters died from tag-induced mortality (Table 1). Autopsies revealed that all deaths were associated with the rupture of the dorsal thoraco-abdominal membrane. Another death was not related to tagging (Table 2).

Table 2

Number of lobsters (*Homarus americanus*) that died during the aquarium experiments from different traumas identified by autopsies. The number of days between tagging and death, and between molting and death, are indicated in parentheses in the "Before molting" and "During or after molting" categories, respectively.

	Premolt stage		Postmolt stage
	Early	Late	
Total number of lobster in the experiments	56	133	183
Before molting			
Perforation of the pericardial sac	0	1 (1)	0
Rupture of the dorsal thoraco-abdominal membrane	0	6 (1–3)	7 (1–11) ¹
Perforation of the hepato-pancreas	0	6 (3–16)	0
No sign of trauma (death not related to tagging)	0	0	1 (5)
During or after molting			
Rupture of the dorsal thoraco-abdominal membrane	0	11 (<1–1)	—
Poor healing of the entry and exit wounds revealing a punctured dorsal thoraco-abdominal membrane	1 (1)	3 (5–57) ²	—
No sign of trauma (death not related to tagging)	0	1 (<1)	—

¹ Five lobsters died within four days, and two more died after nine and eleven days.

² Two lobsters died five and ten days after molting, and one lobster died 57 days after molting from severe infections at the tag-insertions sites.

A total of 70% (134) of the lobsters tagged in the premolt stage molted between 30 June and 8 September (between 7 and 77 days after tagging) without any tag loss (Table 1). Tag-induced mortality represented 8% (15) of the tag loss (Table 1). Autopsies revealed that the majority (11) of the lobsters tagged in late premolt stage died from the rupture of the dorsal thoraco-abdominal membrane (Table 2); the tag was still attached to the old membrane and had caused the rupture of the new one. The four remaining lobsters died from poor healing of the tissue at the point of entry and exit of the tag, revealing a punctured dorsal thoraco-abdominal membrane (Table 2). For all lobsters that healed poorly and later died, one side of the tag had been pulled inside the body cavity during molting. One death was not related to tagging but was caused by the crusher claw becoming wedged within the old carapace, thus preventing the animal from successfully completing the molting process. Furthermore, the autopsy for this lobster did not reveal any sign of tagging trauma.

Tag shedding was observed during molting for 21% (29) of the lobsters tagged in the premolt stage (Table 1). Tag shedding was observed for lobsters tagged in both early and late premolt stages (Table 1) but was significantly higher ($\chi^2=5.9$; $P=0.014$) for lobsters tagged in the early premolt stage. Twenty-one percent (28) of lobsters tagged in the premolt stage that molted had a misaligned tag (pulled to one side).

Only 4% (8) of the lobsters tagged in the postmolt stage died during the second experiment, and only one individual (<1%) shed a tag (Table 1). The autopsies revealed that tags were not well embedded in the muscle tissue and large scars were observed on the dorsal thoraco-abdominal membrane of seven individuals (Table 2). These lobsters died

within 11 days of tagging. The death of the other individual was not related to tagging for there was no sign of tagging trauma. Three percent (5) of the lobsters had a misaligned tag at the end of the experiment.

From a total of 229 lobsters initially tagged for the first experiment, 17% (38) were in the intermolt stage. Although the sample number was small, none of these lobsters shed their tag, died from the tagging procedure, or molted. This finding indicates that these small male lobsters (67–78 mm CL) skipped an entire molting season (July–August) in 1998 and retained their tags without risk. Only one (3%) lobster had a misaligned tag at the end of the experiment. No lobster that was returned to the sea after the experiments had infected wounds from the tag insertion procedure.

Field studies

Tag-induced mortality was observed within 30 min in every tagging study conducted between 1994 and 1996, varying in rate between 0.4% to 3.5%. The majority of the lobsters tagged in early July 1994, 1995, and 1996 were in the premolt stage because 94% to 99% had molted before being recaptured the following fishing season. Except for two lobsters (1.1%) tagged in 1994 that were recaptured the following fishing season with a size increase, all of lobsters tagged in September–October were in the postmolt stage. Recapture rates based on the first recapture period for lobsters tagged in early July (premolting) were significantly lower than the recapture rates for lobsters tagged in September–October (postmolt) for the 1994 ($\chi^2=10.6$; $P=0.001$) and 1995 ($\chi^2=11.4$; $P=0.0007$) tagging, but not for the 1996 ($\chi^2=2.0$; $P=0.156$) tagging (Table 3). Although

Table 3

Numbers and percentage (in parentheses) of lobsters (*Homarus americanus*) tagged and recaptured during the field tagging studies. Lobsters were tagged before (July) and after (September–October) the molting season between 1994 and 1996, and recaptured the following fishing seasons (May–June). The recapture rates during the first fishing season were adjusted on the basis of the tag loss observed in aquarium observations, and Monte-Carlo simulations were used to calculate the confidence interval. The recapture is based only on the number of legal-size (LS=66.7 mm) lobsters released for the experiment (n). No lobster was recaptured during its fourth year at liberty.

Dates of tagging	Number of LS lobsters released (n)	Number recaptured (1 st fishing season)	Number recaptured (2 nd fishing season)	Number recaptured (3 rd fishing season)	Adjusted recapture rate (1 st fishing season)	90% confidence interval
6–7 Jul 1994	476	153 (32.1%)	8 (1.6%)	0 (0.0%)	42.7%	(39.0, 48.0)
14–15 Sep 1994	427	182 (42.6%)	10 (2.3%)	4 (0.9%)	44.6%	(40.7, 48.9)
11–13 Jul 1995	320	79 (24.7%)	5 (1.6%)	2 (0.6%)	32.9%	(28.0, 38.7)
19–20 Sep 1995	442	160 (36.2%)	15 (3.4%)	3 (0.7%)	37.9%	(34.3, 42.1)
3–5 Jul 1996	111	31 (27.9%)	3 (2.7%)	0 (0.0%)	37.2%	(28.7, 48.1)
2–3 Oct 1996	355	125 (35.2%)	22 (6.2%)	3 (0.8%)	36.8%	(32.5, 41.6)

lobsters were recaptured for up to three years following their tagging, the recapture rate was drastically reduced between the first and second recapture period (Table 3). No lobsters were recaptured after four years.

Based on the information from our aquarium observations, the adjusted recapture rates of the field tagging studies showed no difference between lobsters tagged in the premolt and postmolt stages (Table 3). Because the 1995 July tagging was carried out one week later and the molting season was early that year (Comeau and Savoie, 2001), the adjusted recapture rate, based only on late premolt lobsters, was 35.2% (CI 30.8, 42.1). The confidence intervals calculated from Monte-Carlo simulations were always wider for lobsters tagged in the premolt stage (Table 3).

Discussion

Our results suggest that streamer tag loss for the American lobster depended upon the molt stage of the lobster at the time of tagging. Tag-induced mortality without molting was observed mainly within four days of tagging for lobsters tagged in late premolt and postmolt stages; whereas lobsters tagged in early premolt and intermolt stages seemed to be less affected by tagging trauma because none died following the tagging process. Autopsies revealed that the length of time between tagging and death was related to a specific tagging trauma and depended upon the molt stage. Perforation of the pericardial sac caused massive bleeding and resulted in death within 30 min of tagging. The rupture of the dorsal thoraco-abdominal membrane, which also caused bleeding, killed the lobsters within days. Perforation of the hepato-pancreas killed the lobsters within weeks. These types of tagging trauma that caused death were reported by Krouse and Nutting (1990) for American lobsters tagged with Australian western rock lobster (*Panulirus longipes cygnus*) insertion tags. With more careful tagging manipulations, these types of trauma could possibly be reduced. However, even with extreme care during

tagging manipulations, the rupture of the dorsal thoraco-abdominal membrane for lobsters tagged in the postmolt stage might be difficult to avoid. Tagging postmolt lobsters was sometimes difficult because the abdominal muscles of some lobsters were thin, and insuring the insertion of the tag through these muscles was a delicate operation. Thus, streamer tags not completely embedded into well-developed abdominal muscles could be a serious problem for tag retention. Tag shedding without molting was observed only for one lobster tagged in the postmolt stage. In general, lobsters tagged with streamer tags during intermolt and postmolt stages had a lower level of tag loss than lobsters tagged in the premolt stage. The level of streamer tag loss was the highest for lobsters tagged in the late premolt stage.

Tag-induced mortality observed during or shortly after molting was almost exclusively observed for lobsters tagged in the late premolt stage. Although lobsters tagged in the early premolt stage did not die from tagging trauma, they shed proportionately more tags during molting than lobsters tagged in the late premolt stage. Unlike tag loss for lobsters that did not molt, tag loss at molting was not the result of the perforation of internal organs or a questionable tag insertion during tagging but was caused by the tag being firmly attached to the old thoraco-abdominal membrane and being shed, still attached to the exuvia. For tagged lobsters that died during molting, which were almost exclusively lobsters tagged in the late premolt stage, tag loss was caused by massive bleeding resulting from the rupture of the entire new thoraco-abdominal membrane by the tag that was still firmly attached to the old thoraco-abdominal membrane. In addition, we observed a high level (21%) of tag misalignment due to the partial attachment of the tag to the old carapace for lobsters that did not have tag loss during molting. For these lobsters, incorrect insertion of the streamer tag was not an issue. Hence, firm tag attachment of the tag to the dorsal thoraco-abdominal membrane of the old carapace (which causes tag-induced mortality or tag shedding) is a serious problem.

The level of streamer tag shedding in nature seems to be higher than that observed in our aquarium observations and could provide additional information for adjusting streamer-tag recapture rates. From a field study, Rowe and Haedrich (2001) observed that 11% of nonmolted lobsters shed their tags in a one-year period. If we assumed that these lobsters were tagged in the intermolt and postmolt stages, their estimate for streamer-tag shedding is higher than our estimate of less than 1%. Different tagging techniques could explain this difference because Rowe and Haedrich (2001) tagged larger lobsters (>100 mm) differently (with the tag inserted in only one abdominal muscle) than did Moriyasu et al. (1995) for smaller lobsters. The difference could also be explained by the artificial conditions of our aquarium experiment. Under natural conditions tagged lobsters could shed their tags through interspecific interactions (Rowe and Haedrich, 2001), intraspecific interactions, and by being dislodged by obstacles in their habitat (Ennis, 1986; Krouse and Nutting, 1990). Streamer tag loss related to inter- and intraspecific interactions and the habitat has already been reported for the brown shrimp (Howe and Hoyt, 1982; *P. aztecus*) and the tiger prawn (Hill and Wassenberg, 1985; *P. esculentus*). However, more research would be needed to identify the cause of tag shedding in nature and assess its variability in relation to different lobster habitat before the recapture rate could be adjusted based on inter- and intraspecific interactions and the habitat.

The overall level of streamer tag loss compared to sphyrion tag loss seems to be lower, but also depends upon the molt stage of the lobster at tagging and molting. In their study, Moriyasu et al. (1995), suggested that sphyrion tag loss mainly occurs within days after tagging or during molting and is related to the lobster molt stage at tagging. We observed lower levels of tag loss compared to those of Moriyasu et al. (1995), except for the tag shedding during molting for early premolt lobsters and tag-induced mortality for lobsters tagged in late premolt. They observed 3% and 11% of tag shedding without molting for lobsters tagged in early and late premolt stages, respectively, compared to none in our study. Furthermore, the most striking difference is the level of tag loss that reached 10% and 30% for lobsters tagged in intermolt and postmolt stages compared to 0% and <1%, respectively, in our study. The difference in tag loss for lobsters tagged in the postmolt stage could be explained by the physical nature of the tags themselves and the tagging techniques. Compared to the streamer tag that is threaded through two abdominal muscles, the sphyrion tag is anchored to only one muscle by means of a hypodermic needle (Moriyasu et al., 1995). Because the muscles of postmolt lobsters (in the early stages) are not well formed, it is difficult to firmly embed an object, such as a tag, and the probability of tag loss for a tag embedded into only one thin muscle is greater than that for a tag treaded through two muscles. Hence, it seems that streamer tags are more effective in terms of tag retention compared to sphyrion tags for lobsters tagged in intermolt and postmolt stages, but equally so for lobsters tagged in the premolt stage.

In field tagging studies, streamer tags yielded a good recapture rate within the first year following tagging for lob-

sters tagged immediately before or after the molting season. The efficiency of streamer tags compared to sphyrion tags had already been established (Moriyasu et al., 1995; Comeau et al., 1999). Moriyasu et al. (1995) reported that there was a significantly greater recapture rate for lobsters tagged with streamer tags (44%) compared to those tagged with sphyrion tags (19%). Based on the results of Comeau et al. (1999), the recapture rate of lobsters tagged with sphyrion tags is 22% and 16% for lobsters tagged in premolt and postmolt stages, respectively, compared to 33% and 45% for lobsters tagged with streamer tags. These recapture rates corroborate aquarium observations by Moriyasu et al. (1995) on the tag retention of sphyrion tags and ours on the tag retention of streamer tags for lobster tagged at various molt stages.

Knowledge of the level of tag loss is paramount for adjusting the recovery rate to estimate population characteristics and fishery parameters for the American lobster. We observed that the recapture rate dropped significantly in the second and third years at large; this finding suggests a high level of tag loss. A similar multiple-years recapture rate pattern was observed for six other sites within the southwestern Gulf of St. Lawrence (Comeau and Savoie, 2002). Rowe and Haedrich (2001) indicated that the streamer tag shedding level for lobsters that molted almost a year later reached 40%. This high level of tag shedding, probably related to the streamer tag remaining firmly attached to the old dorsal thoraco-abdominal membrane during molting, might explain the drastic decrease of tag recaptures observed between the first and the second tag-recapture periods in our field study. We believe that the adjustment of the recapture rate due to tag loss should be limited to lobsters recaptured within the first year at large and prior to the molting season for lobsters tagged in intermolt and postmolt stages.

The multiple-years recapture pattern of a high recapture rate within the first year at large followed by low recapture rates in subsequent years could have a significant impact on multiyear tagging models. These models that were proposed by Seber (1970) could be used to estimate population characteristics and fishery parameters if underlying assumptions are followed. Based on these multiyear models originally developed for birds (Seber, 1970; Brownie et al., 1985), a suite of models adapted for fishery data and adjustments, mainly by reparameterization, were proposed to address underlying assumption violations (Pollock et al., 1991, 2001; Hearn et al., 1998, 1999; Hoenig et al., 1998a, 1998b; Frusher and Hoenig, 2001; Latour et al., 2001a, 2001b). Some of these models were developed to take into account fishing effort, incomplete mixing, and tag recovery rate. The latter is a composite parameter involving tag retention and tag-induced mortality (tag loss), exploitation rate, and tag reporting rate. There is no argument that the participation of fishermen in returning tags (tag reporting rate) is very important; however, for crustacean fisheries, underlying assumptions dealing with tag loss (see assumptions 2 and 3 in Pollock, 1991, 2001) are equally important and have to be addressed. In general, Pollock et al. (2001) indicated that the assumptions of no tag loss could be violated in two ways: by tag loss in the first

few days after tagging or by chronic tag loss spread over an extended period of time, the latter being more difficult to model. Furthermore, Seber (1970) mentioned that the usefulness of the multiyear models depends not only on the validity of the underlying assumptions but also on the number of recaptures (i.e. parameter estimates based on a small number of tag recaptures would be biased). From our aquarium observations and field studies that show a small number of lobsters caught during the second and third recapture periods, we conclude that a significant chronic tag loss does occur for the American lobster due to molting (i.e. the molt stage of the lobster at tagging and molting itself). Chronic tag loss impedes the effectiveness of multiyear recapture models currently used (Hearn et al., 1998; Hoenig et al., 1998a; Frusher and Hoenig, 2001) because it is not taken into account. We believe that assuming only a constant short-term tag loss for lobsters tagged with streamer tags is inadequate and can only bias estimates of survival and exploitation rate. Correcting for chronic tag loss after the first year at large for the American lobster, however, requires further knowledge, and more studies would be required to fully understand long-term tag loss.

In conclusion, a high level of streamer tag loss is a major obstacle for using tagging studies to estimate natural mortality or to apply multiyear models for the American lobster. Because streamer tag loss is related to molting, adjustment is difficult because the molting frequency is size, sex, and environment dependent (Comeau and Savoie, 2001). In our attempt to estimate mortality at molt, it was found that differences in recapture rates of lobsters tagged in premolt and postmolt stages for a given molting period were not statistically significant, thus suggesting a low level of natural mortality during the molt. The recapture rate for the 1996 tagging, for instance, was even higher for lobsters tagged in the premolt stage. Hence, tagging with streamer tags to establish the level of natural mortality during the molt, or any other mortality that could be low, for the American lobster is not recommended. The alternative would be to develop another insertion tag with better retention through the molting process. Nevertheless, the streamer tag remains an adequate choice for studying lobster ecology and population biology. Streamer tags could be used to tag intermolt and postmolt lobsters during single recapture tagging studies to estimate the exploitation rate (Xiao et al., 1999). Based on our observations, a minimum adjustment of 24.9% (SD 2.9%) and 4.4% (SD 1.6%) is suggested for lobsters tagged in premolt and inter- or postmolt stages, respectively, and recaptured during the first recovery period.

Acknowledgments

The authors wish to thank all fishermen from Caraquet and the adjacent wharves that returned lobster tags and T. Brideau, B. Comeau, J. Roussel, and F. Savoie for their technical assistance in the field and during the tag collection. We especially thank A. Godin and his staff at the Aquarium et centre marin in Shippagan, New Brunswick, for their professional help during the aquarium experiment. We also want to thank J. M. Hanson and M. Moriyasu for critically

reviewing the manuscript, and three anonymous reviews for thoughtful suggestions that improved the quality of this manuscript.

Literature cited

- Aiken, D. E.
1980. Molting and growth. *In* The biology and management of lobsters. Vol. I: Physiology and behavior (J. S. Cobb and B. F. Phillips, eds.), p. 91–163. Academic Press, New York, NY.
- Beverton, R. J. H., and S. H. Holt.
1957. On the dynamics of exploited fish populations. U.K. Minist. Agric. Fish., Fish. Invest. 19:1–533.
- Brownie, C., D. R. Anderson, K. P. Burnham, and D. S. Robson.
1985. Statistical inference from band recovery data: a handbook, 2nd ed. U.S. Fish Wildl. Serv. Resour. Publ. 156, 305 p.
- Comeau, M., W. Landsburg, M. Lanteigne, M. Mallet, P. Mallet, G. Robichaud, and F. Savoie.
1998. Lobster (*Homarus americanus*) tagging project in Caraquet (1993)—tag return from 1994 to 1997. Can. Tech. Rep. Fish. Aquat. Sci. 2216, 35 p.
- Comeau, M., M. Lanteigne, G. Robichaud, and F. Savoie.
1999. Lobster (*Homarus americanus*) movement in the southern Gulf of St. Lawrence—summary sheets of tagging projects conducted between 1980 and 1997. Can. Ind. Rep. Fish. Aquat. Sci. 249, 111 p.
- Comeau, M., and M. Mallet.
2001. Estimating mortality rates by capture-recapture, catch-effort and change-in-ratio models for a spring American lobster (*Homarus americanus*) fishery (LFA 23). Can. Tech. Rep. Fish. Aquat. Sci. 2373, 20 p.
- Comeau, M., and F. Savoie.
2001. Growth increment and molt frequency of the American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. J. Crust. Biol. 21:923–936.
2002. Movement of American lobster (*Homarus americanus*) in the southwestern Gulf of St. Lawrence. Fish. Bull. 100: 181–192.
- Ennis, G. P.
1986. Sphyrion tag loss from the American lobster *Homarus americanus*. Trans. Am. Fish. Soc. 115:914–917.
- Frusher, S. D., and J. M. Hoenig.
2001. Estimating natural and fishing mortality and tag reporting rate of southern rock lobster (*Jasus edwardsii*) from a multiyear tagging model. Can. J. Fish. Aquat. Sci. 58:2490–2501.
- Hearn, W. S., K. M. Pollock, and E. N. Brooks.
1998. Pre- and post-season tagging models: estimation of reporting rate and fishing and natural mortality rates. Can. J. Fish. Aquat. Sci. 55:199–205.
- Hearn, W. S., T. Polacheck, K. H. Pollock, and W. Whitelaw.
1999. Estimation of tag reporting rates in age-structured multicomponent fisheries where one component has observers. Can. J. Fish. Aquat. Sci. 56:1255–1265.
- Hoenig, J. M., N. J. Barrowman, W. S. Hearn, and K. H. Pollock.
1998a. Multiyear tagging studies incorporating fishing effort data. Can. J. Fish. Aquat. Sci. 55:1466–1476.
- Hoenig, J. M., N. J. Barrowman, K. H. Pollock, E. N. Brooks, and W. S. Hearn.
1998b. Models for tagging data that allow for incomplete mixing of newly tagged animals. Can. J. Fish. Aquat. Sci. 55:1477–1483.

- Hill, B. J., and T. J. Wassenberg.
1985. A laboratory study of the effect of streamer tags on mortality, growth, moulting and duration of nocturnal emergence of the tiger prawn *Penaeus esculentus* (Haswell). *Fish. Res.* 3:223–235.
- Howe, N. R., and P. R. Hoyt.
1982. Mortality of juvenile brown shrimp *Penaeus aztecus* associated with streamer tags. *Trans. Am. Fish. Soc.* 111: 317–325.
- Krouse, J. S., and G. E. Nutting.
1990. Effectiveness of the Australian western rock lobster tag for marking juvenile American lobsters along the Maine coast. *Am. Fish. Soc. Symp.* 7:94–100.
- Landsburg, A. W.
1991. A field comparison of recapture rates of polyethylene streamer and modified sphyrion tags through molting of lobster (*Homarus americanus*). *J. Shellfish. Res.* 10, 225 p.
- Latour, R. J., J. M. Hoenig, J. E. Olney, and K. H. Pollock.
2001a. Diagnostics for multiyear tagging models with application to Atlantic striped bass (*Morone saxatilis*). *Can. J. Fish. Aquat. Sci.* 58:1716–1726.
2001b. A simple test for nonmixing in multi-year tagging studies: application to striped bass tagged in the Rappahannock River. *Trans. Am. Fish. Soc.* 130:848–856.
- Marullo, F., D. A. Emiani, C. W. Caillouet, and S. H. Clark.
1976. A vinyl tag for shrimp (*Panaeus* spp.). *Trans. Am. Fish. Soc.* 105:658–663.
- Moriyasu M., W. Landsburg, and G. Y. Conan.
1995. Sphyrion tag shedding and tag induced mortality of the American lobster, *Homarus americanus* H. Milne Edwards, 1837 (Decapoda, Nephropidae). *Crustaceana* 68:184–192.
- Pollock, K. H., J. M. Hoenig, W. S. Hearn, and B. Calingaert.
2001. Tag reporting estimation: an evaluation of the reward tagging method. *N. Am. J. Fish. Manage.* 21:521–532.
- Pollock, K. H., J. M. Hoenig, and C. M. Jones.
1991. Estimating of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. *Am. Fish. Soc. Symp.* 12:423–434.
- Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. *Bull. Res. Board Can.* 191, 382 p.
- Rowe, S., and R. L. Haedrich.
2001. Streamer tag loss from American lobsters. *Trans. Am. Fish. Soc.* 130:516–518.
- Scarratt, D. J., and P. F. Elson.
1965. Preliminary trials of a tag for salmon and lobsters. *J. Fish. Res. Board Can.* 22:421–423.
- Seber, G. A. F.
1970. Estimating time-specific survival and reporting rates for adult birds from band returns. *Biometrika* 57: 313–318
1982. The estimation of animal abundance and related parameters, 2nd ed., 654 p. Griffin, London.
- Templeman, W.
1935. Lobster tagging in the Gulf of St. Lawrence. *J. Biol. Board Can.* 1:269–278.
- Wilder, D. G.
1953. The growth of the American lobster (*Homarus americanus*). *J. Fish. Res. Board Can.* 10:371–403.
- Xiao, Y., J. D. Stevens, and G. J. West.
1999. Estimation of fishing and natural mortalities from tag experiments with exact or grouped times at liberty. *Can. J. Fish. Aquat. Sci.* 56:868–874.