Reproductive and Natal Homing

of

Marine Threespine Sticklebacks (*Gasterosteus aculeatus*)

by

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ABSTRACT

Natal and reproductive homing were investigated in marine and anadromous populations of threespine sticklebacks (*Gasterosteus aculeatus*). Three breeding sites within 1 km^2 of Pender Harbour, British Columbia, were examined. For the reproductive homing experiment (displacement of adults from a breeding site), female sticklebacks from Oyster Lagoon, Salt Lagoon, and Paq Creek were marked and displaced (.15 - 1.0 km) to three release sites. These displaced females predominately returned to their original breeding sites, although there was some straying. The proportion of marked fish recaptured at their original breeding site ranged from 0.81 to 1.00. The anadromous population (Paq Creek) showed the strongest tendency to return (0.99 - 1.00). Natal homing (return to birth site) was investigated in the Oyster Lagoon population. Young of the year were marked on three different out-migrations (April 1991, August 1991, and April 1992): 0.85 %, 3.5% and 5.2 % respectively, were recaptured as adults during the 1992 breeding season at Oyster Lagoon. Relatively short stays outside the lagoon (2 - 4 months), by juveniles that overwintered in Oyster Lagoon, resulted in strong natal homing and weak straying to adjacent breeding sites; however, straying to Salt Lagoon increased with longer stays outside the lagoon. This suggests an inverse relationship between the length of time spent out of the lagoon and the accuracy of homing. Straying to the anadromous breeding site (Paq Creek) remained low for all lengths of stay in the sea (2 - 16 months). This maintained avoidance of Paq Creek suggests that the marine and anadromous populations may be genetically isolated. The level of straying between Salt and Oyster lagoons probably is sufficient to prevent divergence between these adjacent marine populations. Generally however, this study demonstrates both reproductive and natal homing in threespine sticklebacks and, on a larger geographic scale, this natal

homing may be sufficient to allow the evolution of inter-population heterogeneity among marine and anadromous populations.

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Acknowledgements

This project was conducted in coordination with Regina Saimoto's work on the life history of marine threespine stickleback. It was Regina's useful preliminary evidence of homing that motivated me toward a more complete study of this interesting strategy. Also special thanks to J.D. McPhail for financial support, his introduction to *Gasterosteus aculeatus*, and his editorial comments on my thesis. Max Blouw gave useful suggestions on my initial proposal and field work. Colin Brauner also gave useful comments on the final draft. The people in Pender Harbour were both friendly and helpful; in particular the Patons (Richard, Gail, Julie, Shannon, and Ginger), the Chathams (Roy-boy, Linda, and Boo-Boo), the Phillips (Ray, Doris, Glen and Sandra), Miki and Terry. And in the long tedious days of marking and releasing fish, it was SUPER-DAVE Ghan, and my wife that made the incredible total numbers possible.

GENERAL INTRODUCTION

Earlier studies of the threespine stickleback (*Gasterosteus aculeatus*) document the remarkable array of allopatric, parapatric, and sympatric forms that exist within this species complex (Hagen 1967; McPhail 1969, 1984, 1992, 1993; Moodie & Reimchen 1976; McPhail & Hay 1983; Bentzen & McPhail 1984; Ridgeway & McPhail 1984; Reimchen *et al.* 1985, Blouw & Hagen 1990; Schluter & McPhail 1992; Reimchen 1992). This diversity is especially evident in British Columbia, where research has focused on divergent stream and lake populations. Many of the morphological differences among freshwater populations, and between freshwater and anadromous populations, have a genetic basis and directly influence foraging efficiency or defence from predators (McPhail 1969; Moodie 1970; Wootton 1976; Reimchen 1983, 1988, 1990; Bentzen & McPhail 1984; Taylor & McPhail 1986). Consequently, they are viewed as adaptations to local selection regimes. Typically, there are differences among populations in lateral plates, spine lengths, pectoral fin shape, body shape, mouth width, gill raker number, gill raker lengths, and colouration. In addition, some populations show variability in life history traits such as age at maturity, breeding behaviours, mate choice, breeding site selection, and durations of breeding periods (e.g. McPhail & Hay 1983; Bell 1984; Mori 1984; Saimoto 1993). Also, in B.C., allozyme surveys have revealed genetic differences among freshwater populations, and between freshwater and anadromous populations (Withler & McPhail 1985). Since most of coastal B.C. was glaciated during the last (Fraser) glaciation, most freshwater populations must be post-glacial colonists, and one obvious source of colonists was the sea. Thus, the divergence between freshwater and anadromous, or marine, sticklebacks and the divergences among freshwater populations may be relatively recent. The evolutionary processes involved in these rapid divergences are

poorly understood, but, if marine or anadromous sticklebacks are ancestral to freshwater populations, then an examination of their biology is fundamental to understanding the mechanisms that give rise to the diverse freshwater populations now found in coastal British Columbia.

Generally, anadromous sticklebacks are thought to be the primary ancestor of resident stream and lake populations; however, this hypothesis overlooks the existence of purely marine populations of *G. aculeatus*. Indeed it is possible that marine and estuarine populations, as well as anadromous populations, contributed to the post-glacial recolonization of freshwaters along the B.C. coast (McPhail 1993). This introduces the added complexity of a heterogeneous origin of today's freshwater populations and necessitates a closer examination of both marine and anadromous populations. Questions that need answers are 1) what is the genetic relationship between marine and anadromous sticklebacks, and 2) are these forms genetically homogeneous, or do they exhibit deme structure?

During the last glaciation, most freshwater populations in British Columbia probably were destroyed or forced south into glacial refugia. On the west coast of North America, the primary freshwater refugia of the last glaciation were in Washington, Oregon, California and Alaska (Bell 1976); however, there is growing evidence for central coast refuge that included northern Vancouver Island and Graham Island (McPhail 1993). Certainly some of the morphologically most extreme sticklebacks are found in these areas (Moodie & Reimchen 1976; Lavin & McPhail 1993); however, because of their relatively small populations, freshwater residency, and low dispersal, freshwater populations that survived in isolated refugia, probably did not contribute much to the post-glacial expansion of the species.

Glaciation may not have effected the anadromous populations as drastically as it

effected freshwater populations. They simply may have shifted south to unglaciated streams. If so, whatever pre-glacial diversity that existed among anadromous populations probably was lost to inter-breeding during this shift. Alternatively, they may have fused with marine populations, or simply gone extinct. Some populations south of glaciation may have maintained their distinctive genetic nature and their divergence from marine populations. This would have produced at least two potential post-glacial colonizers. Genetically different anadromous populations may have dispersed up the coastline into newly forming streams and rivers as glaciers retreated. Once established in new streams, natal homing may also have evolved in much the way it is thought to evolve in salmonids (*i.e.* on average, individuals that return to the site where they were successfully reared are more successful reproductively than individuals that stray). Once natal homing evolves, local selection will fine tune the population to local conditions and this should lead to inter-population divergence.

Little attention has been paid to the potential effects of glaciation on marine populations of threespine sticklebacks. Marine breeding sites probably shifted in response to fluctuations in sea level; however, if marine populations show natal homing they are unlikely to be genetically homogeneous. Study of the mechanisms of population isolation will assist in defining the role of ancestry behind the existing diversity of threespine sticklebacks.

Currently, there is no information on relationships among anadromous and marine populations. However, a recent life history study of a marine population along the B.C. coast, suggested natal homing. Saimoto (1993) found that many marked marine sticklebacks returned to their place of birth, but adjacent breeding sites were not monitored for straying. The purpose of my study is to investigate both natal (return to place of birth) and

reproductive (return of displaced adults) homing by threespine sticklebacks. Three adjacent sites (Oyster Lagoon, Salt Lagoon, and Paq Creek) were studied. The two lagoons are marine sites and the creek is a freshwater site used by anadromous sticklebacks. The inclusion of an anadromous breeding site may be questioned because of possible differences in salinity tolerance/preference in marine and anadromous populations; however, Soin *et al.* (1984) and my own preliminary studies showed that both marine and anadromous sticklebacks can spawn in variable salinities (0 - 32 ppt). Thus, the inclusion of a site used by anadromous sticklebacks allows comparisons of the levels of homing in both marine and anadromous populations, and the degrees of straying between the two breeding habitats.

STUDY SITE

Pender Harbour

Pender Harbour (49° 32' N; 124° 02' W) is a small mainland inlet off Malaspina Strait, British Columbia, Canada (Fig. 1). The harbour reaches approximately 4 km inland and two narrow channels link it to the strait. Three small creeks drain into the harbour, but estuarine habitats are limited by daily inflow of high salinity water from the strait. Tide levels in the harbour fluctuate 1 - 4 m bi-daily and maintain a relatively stable marine salinity (28 - 32 ppt). Pender Harbour supports a diverse community made up of marine plant, invertebrate and fish species.

Through early spring into late summer, migrating adult sticklebacks enter Pender Harbour from the strait and select breeding sites. There are three lagoons in the harbour, of which two (Oyster and Salt lagoons) are threespine stickleback breeding sites. The third lagoon is a small, shallow tidal pool that lacks the physical characteristics typical of most stickleback breeding sites: protective cover, nest material, temperature stability, and food availability. This site is not used by sticklebacks. Of the three creeks that drain into Pender Harbour, only Paq Creek appears to support an anadromous population. A fourth breeding site (Gerrans Bay) lies approximately 1 km west of the three study sites, but was not included because it has a short, delayed breeding season, low stickleback density, and less defined boundaries from the open harbour. Oyster Lagoon, Salt Lagoon, and Paq Creek constitute my study sites.

Paq Creek, Salt Lagoon, and Oyster Lagoon were chosen primarily because of their discrete, confined breeding sites (Fig. 1). The areas between these 3 sites were examined to confirm their complete isolation (*i.e.* no breeding sticklebacks in the intervening areas). The relatively small area containing these three isolated breeding sites (< 1 km^2) permits

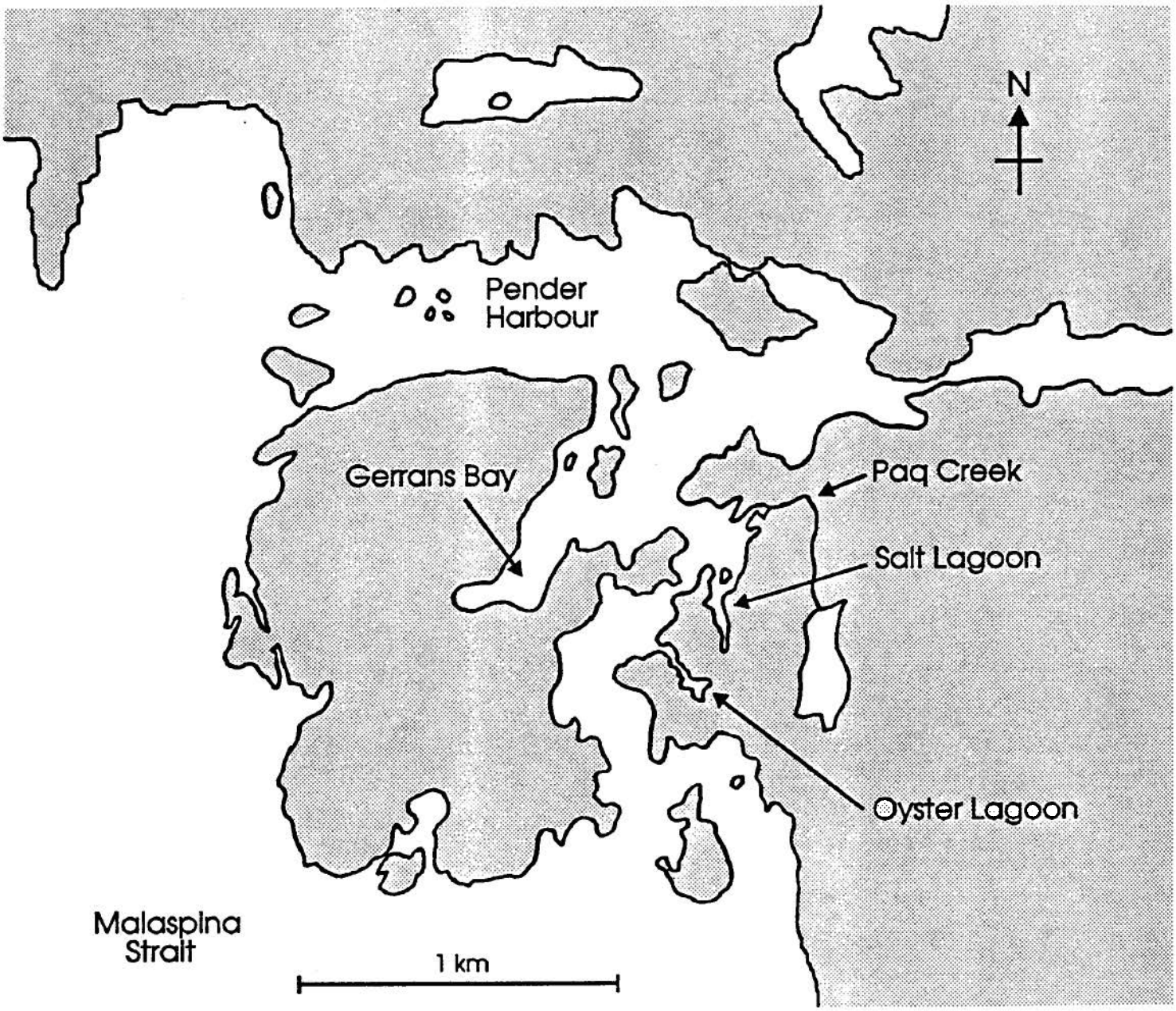


Figure 1. Map of Pender Harbour, British Columbia. Included are the four known breeding sites for marine or anadromous threespine sticklebacks; Paq Creek, Oyster Lagoon, Salt Lagoon, and Gerrans Bay.

evaluation of population dispersal.

Oyster Lagoon

Oyster Lagoon is a small, shallow lagoon. Salinity ranges from 20 ppt in winter to 32 ppt in summer, with rainfall often forming a thin freshwater layer on the surface. The surface area of the lagoon is 1.8 ha and the maximum depth is 3 m. The lagoon is connected to the harbour at 4.0 m tides, and tidal in-flow occurs at tide levels greater than 4.2 m (the highest tide of each day fluctuates from 4.0 - 4.9 m). This limited in-flow allows terrestrial grass to expand to the low tide level of the lagoon and provides protective cover for overwintering young and early nesting adults. At the peak of the 1992 breeding season, half of the lagoon bottom was covered with thick beds of eel grass (*Zostera* sp.) and thick filamentous algal mats. This aquatic vegetation provided seasonal protective cover from birds and perhaps nest protection against attacks by other sticklebacks.

The majority of young that hatched in 1991, left the lagoon that same summer; however, many young also overwintered in the lagoon and did not migrate out until the start of the adult in-migration the following breeding season. In 1992, sticklebacks began entering Oyster Lagoon in late February. The first young of 1992 were observed in late April, and a few males were still nesting in September. The peak of the breeding season was in June and July, and the rapid decrease of nesting males in August appeared to coincide with high water temperatures (> 26 °C) on sunny days prior to flooding (*for details see* Saimoto, 1993).

Salt Lagoon

Salt Lagoon differs from Oyster Lagoon, in that it is slightly larger (surface area ≈ 4 ha) and deeper at low tide (max. depth 6 m). The salinity remains more stable (25 - 32 ppt) because of greater daily flushing at lower tide levels (> 3.0 m). This lagoon's shoreline also

differs from Oyster Lagoon. The bi-daily tidal fluctuations of 1 - 2 m prevents terrestrial grassy shorelines from remaining in contact with the water. This lack of shoreline cover may be what prevents overwintering of young in Salt Lagoon. The two main entrance channels are also wider, and not as long as the one entrance into Oyster Lagoon. In 1992, the breeding season at Salt Lagoon was delayed by 1 - 2 months in comparison to Oyster Lagoon. Perhaps, the delay is because of a slower rise in temperature due to the more frequent and longer periods of flooding, larger area, and greater depth in Salt Lagoon. Apparently, this active tidal flooding also results in more frequent in- and out-migrations of sticklebacks throughout the entire breeding season. Another recognizable, and possibly influential difference between Salt and Oyster lagoons was the higher density of predators (great blue herons, mergansers, kingfishers and cutthroat trouts) at Salt Lagoon.

Paq Creek

Paq Creek is obviously different from the lagoons. The creek is less than 5 m wide with a mean depth of 30 - 50 cm, and only the short, lower stretch (< 100 m) with one small (15 m x 15 m), shallow (< 1 m) pool is suitable for breeding. This stretch of creek is low gradient and is partially clogged and slowed by sedges (*Carex* and *Scirpus* sp.) and cattails (*Typha latifolia*). Up-stream migration is blocked by a culvert with an approximately 60 cm drop to the lower stream. At its mouth, the creek spreads out over gravel and is too shallow to allow in-migration until high tides (> 4.0 m) create access to the first, deepest pool. Although this lowest pool is slightly brackish water for short periods after flooding, salinity tests show the nesting areas to be either always, or predominantly in fresh water. In 1992, in-migration to Paq Creek started earlier and ended earlier (mid July) than at Oyster Lagoon. Other differences between Paq Creek and the lagoons were the presence of predatory crayfish

in the creek and the rarity of the isopod gill parasite (*Rocinella angustata*) that is commonly found in both Oyster and Salt lagoons. Most importantly, the Paq Creek population is anadromous, and thus provides an opportunity for the evaluation of inter-change between marine and anadromous populations of threespine sticklebacks.

REPRODUCTIVE HOMING EXPERIMENT

Introduction

In this study, reproductive homing is defined as the propensity of adults to return to a breeding site after they are displaced from that site. Several authors (Hagen 1967; Kynard 1978; Paepke 1983) have suggested that sticklebacks home, but there is little quantitative evidence to support this suggestion. The primary purpose of my reproductive homing experiment was to determine if both marine and anadromous populations of threespine sticklebacks choose specific breeding sites. The experiment involved displacement of marked sticklebacks from three different initial breeding sites (Oyster Lagoon, Salt Lagoon, and Paq Creek) and release at three locations in Pender Harbour (release sites "A", "B", and "C"; Fig. 2, *page* 14). Returns were then monitored at the three breeding sites for the remainder of the breeding season (14 weeks). If the fish disproportionately return to their initial breeding site, this indicates that they distinguish among breeding sites and have a preference for the site they first chose.

The migratory nature of these populations prevents accurate estimates of population size, and this increases the difficulty of monitoring and comparing total numbers of individuals in each population that home or stray. Consequently, the experiment uses relative numbers of marked individuals from the three displaced populations recaptured at their initial breeding sites as an indication of the strength of the propensity to home. This experiment also gives an estimate of the ratio of homers to strayers for each population. This estimate is important because only the out-migrating young from the Oyster Lagoon population were marked to test natal homing (return to place of birth). For the Oyster Lagoon population, the ratio of "reproductive homers to reproductive strayers" is comparable to recapture ratios of "natal homers to natal strayers" (Natal Homing Exp., *page* 26).

Materials and Methods

Collection for Mark and Release

The experiment began when the in-migration of fish to the three breeding sites produced enough fish for a consistent number of releases over 10 days (May 13th -22nd, 1992). Capture at Oyster Lagoon was by a funnel fence and a large plexiglass minnow trap (100 cm x 90 cm x 60 cm) set in the entrance channel. Salt Lagoon and Paq Creek fish were captured with 20 minnow traps (7 mm mesh) set in the lagoon near its entrance channels and 20 minnow traps set in the lower pool of Paq Creek. To avoid the complications of sampling territorial males, only females were used in the experiment. Fish for mark and release were sorted at the location of capture and males were released; sex was identified by visual recognition of sexual colouration of males (red throat and/or blue eyes), head size (males have longer heads, and larger mouths), and sexual maturity of females (gravid condition).

Each day's collections were stored in 80 litre tanks with no more than 100 fish/tank. Fish from different breeding sites were held in separate tanks. All holding tanks contained water collected from outside the harbour and were maintained at constant salinity (28 ppt) and temperature (8 - 10 °C). Fish used for mark and release were collected two days before release and a portable air compressor was used to aerate water every 2-4 hours in the 24 holding tanks. Fish were marked the day after collection and held overnight to monitor mortality due to stress, dye injection, or anesthesia. At loading for transport to release sites, sex was re-checked, and the exact numbers of different individuals were recorded.

Marking Technique

Three different acrylic dyes (red, orange, and pink) were used to differentiate between the three populations. These concentrated dyes were diluted 1:1 with mammalian Ringer's

solution, and manually injected using 28 gauge needles. Tricainmethansulfonate (MS 222) in sea water was used to anesthetize fish before injections and rapid aeration of 2 litre containers assisted recovery. For an additional distinction between the three release sites, the dyes were injected under different lateral plates in each population. Fish were injected under anterior plates on the right side for release site "A", under posterior plates on the right side for release site "B", and under anterior plates on the left side for release site "C".

Controls

An additional acrylic dye (blue) was used for control releases during the three days following the completion of the displacement releases (May 30th - June 1st). This involved mark and release, but no displacement, of the three populations at their initial breeding sites. For these controls, Oyster Lagoon fish were injected under the right anterior plates, Salt Lagoon fish were dye injected under the right posterior plates, and Paq Creek fish were marked under the left anterior plates. This control was used to estimate the effects of displacement and the efficiency of trapping at the three breeding sites, and it also allowed a rough estimation of the time females stay on a breeding site.

The effects on survival of different colour dyes and different locations of injection were monitored for seven days after marking. Separate tanks with ten female fish for each of the four different colour dyes and three different places of injection were monitored. This represented three replicates of tests for mortalities due to different coloured dyes, and four replicates of tests for mortalities due to different locations of injection.

Release Sites

The displacement experiment included three release sites ("A", "B", and "C"). Release site "A" was within 150 m of the entrance to Oyster Lagoon; release site "B" was positioned

between the entrances to Salt Lagoon and Paq Creek (approximately 150 m from both breeding sites); while release site "C" was a control release site at an equal distance (500 m) from site "A" as site "B" but in the opposite shoreline direction (Fig. 2). Site "C" was included to test the effects of the relative positioning of sites "A" and "B", since there is a narrow, shallow pass between sites "A" and "B" but no constriction between sites "A" and "C" (Fig. 2).

Release Procedure

During afternoon high tides, the three populations were released concurrently on ten consecutive days (May 13th - 22nd, 1992). Individuals from the three populations were released at the same site but, to help avoid inter-population schooling, the releases of different populations were separated by 5 minute intervals. For both Oyster Lagoon and Salt Lagoon populations, I attempted to include 100 females each day at each site. Since fewer fish were available from Paq Creek, approximately 50 females were released each day at each site (Appendix I).

Monitoring of Returns

Sampling for reproductive homers and strayers was done at the Oyster Lagoon, Salt Lagoon, and Paq Creek breeding sites. The goal was to recapture at least 100 marked fish from each population. This would allow reasonable comparisons of recaptures of homers to strayers. Because of geographic differences between release sites, and habitat differences and differential access among breeding sites, different (most efficient) methods of trapping were used at each site. Initially, recaptures were preserved in 10 % formalin, but later, new recaptures were recorded, re-marked with different spine clips, and re-released. Re-recaptures of fish with both dye marks and clipped spines were recorded separately and were not

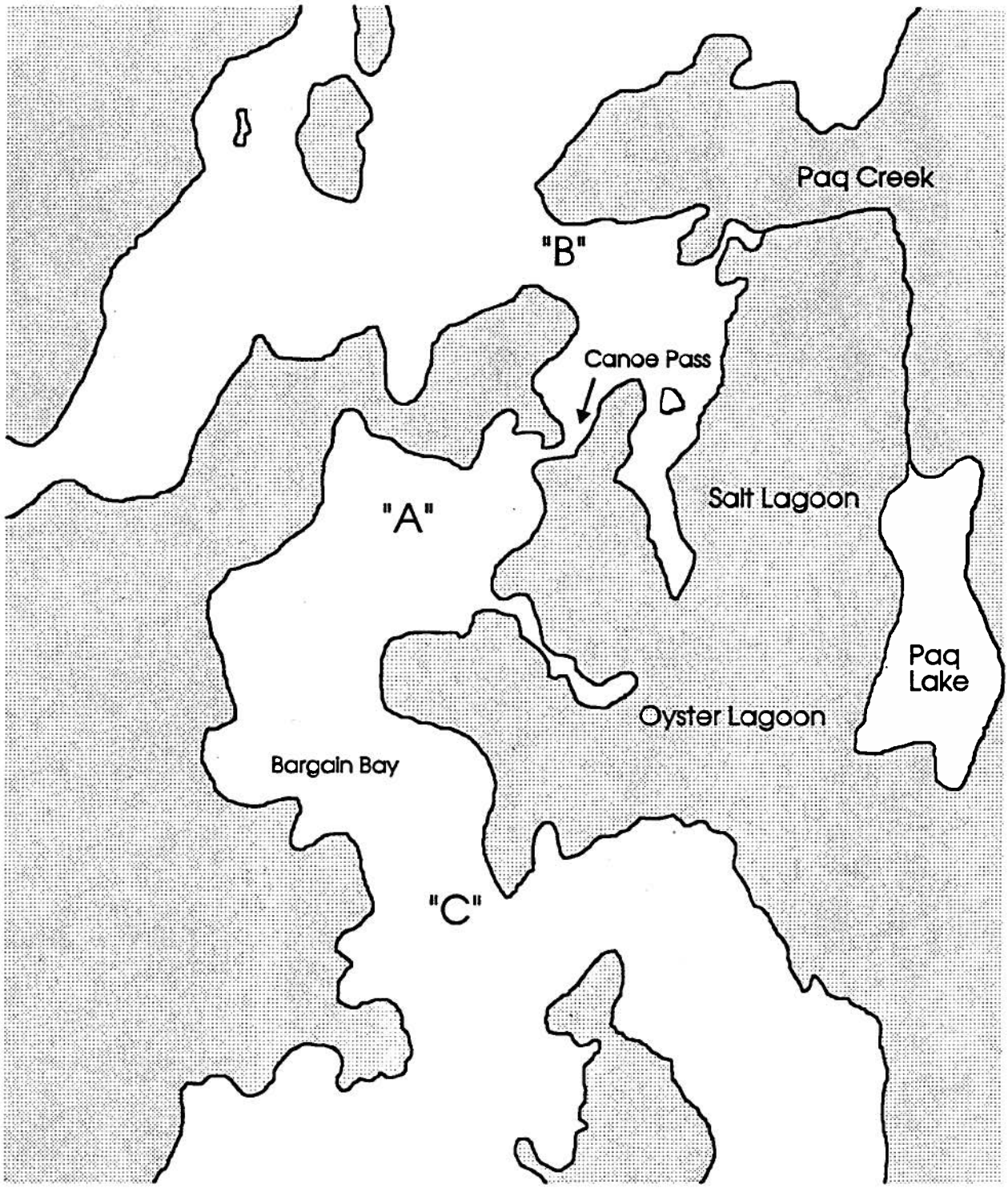


Figure 2. Release sites "A", "B", and "C" used for displacements during the reproductive homing experiment.

included in total recapture counts.

Sampling at Oyster Lagoon

A funnel fence with a large plexiglass minnow trap (100 cm x 90 cm x 60 cm) set in the entrance channel was used to collect fish during, and after, marking in Oyster Lagoon. The trap was emptied daily and fish were sexed, counted and checked for dye markings (Appendix II). This trap was used rather than setting minnow traps because it caught a higher proportion of new in-migrating fish, and allowed for less time consuming collection and sorting. The mark for re-release after recapture was the clipping of both the first dorsal and right pelvic spines.

Sampling at Salt Lagoon

During the 10 days of marking, and for the following two weeks, 20 standard mesh minnow traps were set in Salt Lagoon near the entrance channels. The traps were checked each day for marked fish. Later, to increase the sample sizes of collections, 20 additional minnow traps were distributed along the lagoon shoreline. Daily sampling continued to the end of June and then was reduced to alternate days until completion of this experiment (Appendix III). The fish were sexed, counted and released, except for a small number of recaptures that were preserved. Re-released recaptures were marked with the spine clips of both right and left pelvic spines.

Sampling at Paq Creek

Twenty minnow traps were used for all collections at Paq Creek. All fish were sexed, counted, and checked for dye markings (Appendix IV). Recaptures were preserved until > 100 fish had been obtained from each of the 3 release sites. Recaptures were then re-marked by spine clip of the first dorsal spine and re-released. Paq Creek was sampled daily from

May 14th to June 7th, and then less frequently because of efficient trapping and an early end to the breeding season (Appendix IV).

Data Analysis

Analysis required accounting for different numbers of fish that were marked and displaced from different sites and to different release sites. Since the numbers of fish released from each site were different, the number of recaptures were corrected as follows:

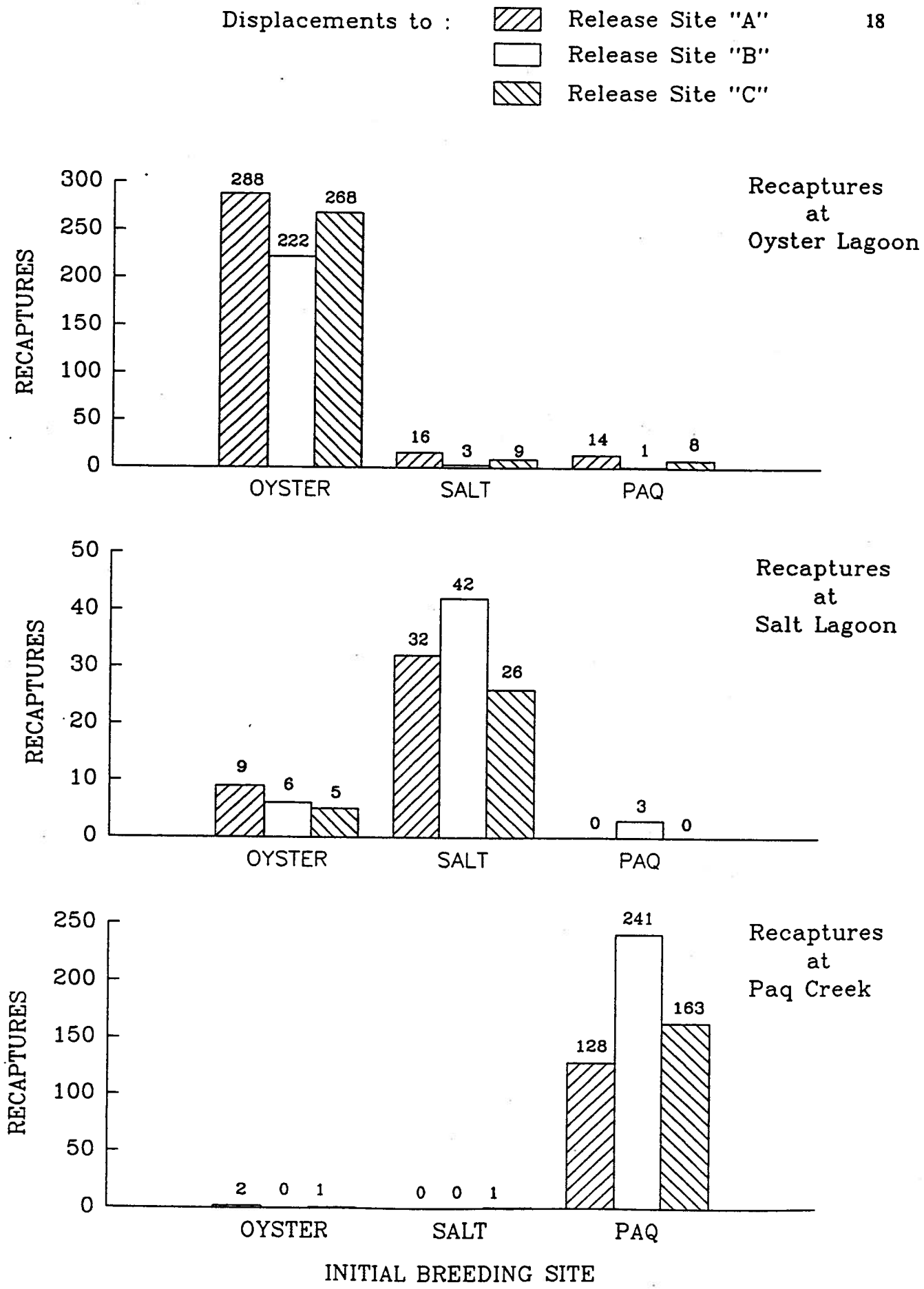
$$\text{Corrected Values} = (511/\#\ \text{released}) \times \#\ \text{of recaptures},$$

where 511 is the lowest number of a particular population released from any site. Thus, these corrected values (CV) provide a conservative, relative comparison of recaptures of displaced fish from each breeding site. Log likelihood ratio analysis (G test) was used to test for equal returns of all populations. Yates correction (G_c test) was used for the more specific comparisons of two populations.

Results

Returns to the breeding sites were monitored through the entire 1992 breeding season. After displacement, most sticklebacks returned to their initial breeding site within four weeks; however, small numbers continued to return throughout the entire breeding season (Appendices II,III,IV). The data (Fig. 3) show a marked tendancy for displaced sticklebacks to return to their initial breeding sites. This implies that both marine and anadromous sticklebacks can distinguish among breeding sites and, once they have chosen a site, they show a strong preference for this initial site. The following sections present a detailed analysis of these recaptures and compares the numbers of homers and strayers relative to both release sites and breeding sites.

Figure 3. Numbers of marked fish released at sites "A", "B", and "C" recaptured in Oyster Lagoon, Salt Lagoon and Paq Creek. The numbers graphed are not corrected.


Displacements to :
Release Site "A"
Release Site "B"
Release Site "C"
Recaptures at Oyster Lagoon
RECAPTURES
300
250
200
150
100
50
0
288
222
268
16
3
9
14
1
8
OYSTER
SALT
PAQ
Recaptures at Salt Lagoon
RECAPTURES
50
40
30
20
10
0
9
6
5
32
42
26
0
3
0
OYSTER
SALT
PAQ
Recaptures at Paq Creek
RECAPTURES
250
200
150
100
50
0
2
0
1
0
0
1
128
241
163
OYSTER
SALT
PAQ
INITIAL BREEDING SITE

Controls

Effects of Dye Injection

Comparisons of mortalities due to injection indicated no significant differences among either colors or locations of injection. Mortality was low in all 12 control tanks: five deaths in the 120 marked fish after one week.

Non-Displacement

RECAPTURES AT OYSTER LAGOON

Over three days, 1 013 Oyster Lagoon females were caught, marked (blue, right anterior lateral plate) and released back into the lagoon. The day after the total release (June 2nd), 10 minnow traps in Oyster Lagoon caught 376 female sticklebacks, of which 37 were non-displaced recaptures. In addition, six reproductive homers from displacements were recaptured and preserved. These reproductive homers were missed in my in-migration monitoring, and suggest that a significant number of reproductive homers may have by-past the in-migration funnel fence trap. Consequently, the numbers of recaptures at the Oyster Lagoon funnel fence are a conservative estimate of total returns. Further trapping in the lagoon showed a daily decline in the number of non-displaced recaptures. Following this release, recaptures at the funnel fence showed a slow but steady in-migration of non-displaced fish for 3 - 4 weeks. This return suggests that many of the marked and non-displaced fish initially may have left the lagoon but then returned after only a short absence.

Non-displacement controls also were run at Salt Lagoon and Paq Creek. Over the entire breeding season only one Salt Lagoon, and no Paq Creek, non-displaced strayers were recaptured at the Oyster Lagoon in-migration fence. This low straying indicates that once an initial breeding site choice is made, it is maintained for the entire breeding season.

RECAPTURES AT SALT LAGOON

Over three days, 1 277 Salt Lagoon females were caught, marked (blue, right posterior lateral plate) and released back into the lagoon. The day after the complete release (June 2nd), minnow traps caught 607 females, of which two were non-displaced recaptures (released) and one was a reproductive homer (preserved). On the next day (June 3rd), 570 females were sampled of which none were marked non-displaced individuals, and two were marked displaced homers (preserved). Again on June 4th, 431 females were sampled, three of which were marked non-displaced fish (released) and none were displaced homers. These results emphasize the difficulty of trapping in Salt Lagoon, and account for the low number of recaptures in the reproductive homing experiment from this lagoon. After 10 days (June 2nd - 11th), the total recaptures consisted of 15 non-displaced controls (CV = 8) and 20 reproductive homers from the three displacements (CV's : "A" = 6, "B" = 7, and "C" = 3). The four of these corrected values are not significantly different ($G = 5.131$, $p > 0.10$). This suggests that trapping difficulties rather than high dispersal after displacement caused the low numbers of recaptures at Salt Lagoon.

RECAPTURES AT PAQ CREEK

Over two days, 401 Paq Creek females were caught, marked (blue, left anterior lateral plate) and released back into the creek. On the first day after releases (June 1st), 156 females were caught, 85 of which were non-displaced recaptures (released), and 18 were reproductive homers (preserved). The next day's sample (June 2nd) consisted of 292 females, 35 of which were non-displaced recaptures (released) and 35 were reproductive homers (preserved). On June 3rd, 310 females were sampled, 20 of which were non-displaced recaptures (released), and 42 were reproductive homers (preserved). The recapture rates indicate trapping in Paq

Creek is an efficient collecting technique, but the rapid decline in recaptures of the non-displaced fish suggest either a relatively rapid turnover of the creek's spawners or that marked fish leave the system. Thus, the actual numbers of reproductive homers recaptured at Paq Creek represent conservative estimates of total returns.

Monitoring of Displacements

Monitoring returns to the three breeding sites suggest that more fish home than stray; regardless to which of the three release sites they were displaced. Corrected values of recaptures from the different populations and different release sites are summarized in Table 1. This section presents detailed comparisons of results, with tests for differences between displacements, and for differences in the proportions of homers or strayers.

Recaptures in Oyster Lagoon

Of the fish originating in Oyster Lagoon, 26.1 % were recaptured at Oyster Lagoon (release sites : "A" = 27.8 %, "B" = 22.5 %, and "C" = 27.3 %). Strays from the other displaced populations (Salt Lagoon and Paq Creek) represented only 1.3 % and 1.5 %, respectively, of their total numbers marked and released. For all three populations, release site "B" produces fewer returns to Oyster Lagoon than release sites "A" and "C". For Paq Creek strayers there is a significant difference of returns from different release sites ("A" = 14, "B" = 1, and "C" = 8; $G = 13.508$, $p < 0.005$). Curiously, however, recaptures of Oyster Lagoon homers (CVs : "A" = 142, "B" = 115, and "C" = 140) and Salt Lagoon strayers to Oyster Lagoon (CVs : "A" = 10, "B" = 2, and "C" = 7) were not significantly different among different release sites ($G = 3.522$, $p > 0.10$, and $G = 5.946$, $p > 0.05$). Despite this lack of statistical significance, the corrected values were in the direction of lower returns from release site "B". Perhaps, reproductive homing to Oyster Lagoon from release site "B"

Displacement to **RELEASE SITE "A"**

Recaptured at :	Initial Breeding Site : Oyster Lagoon	Salt Lagoon	Paq Creek	Proportion of Homers
Oyster Lagoon	142	10	14	0.86
Salt Lagoon	5	21	0	0.81
Paq Creek	1	0	128	0.99

Displacement to **RELEASE SITE "B"**

Recaptured at :	Initial Breeding Site : Oyster Lagoon	Salt Lagoon	Paq Creek	Proportion of Homers
Oyster Lagoon	115	2	1	0.97
Salt Lagoon	3	29	3	0.83
Paq Creek	0	0	232	1.00

Displacement to **RELEASE SITE "C"**

Recaptured at :	Initial Breeding Site : Oyster Lagoon	Salt Lagoon	Paq Creek	Proportion of Homers
Oyster Lagoon	140	7	8	0.90
Salt Lagoon	3	19	0	0.86
Paq Creek	1	1	163	0.99

Table 1. Recaptures (corrected for different numbers released) and "Proportion of homers" (the ratio of homers to combined strayers) at each breeding site.

was partially influenced by the narrow channel at Canoe Pass and easier access to an alternate breeding site (eg. Salt Lagoon, Gerrans Bay, or Paq Creek).

The few recaptures of strayers into Oyster Lagoon makes a statistical comparison of the propensity of marine and anadromous populations to stray difficult. There is no clear difference between the number of recaptures of Salt Lagoon and Paq Creek strayers in Oyster Lagoon. This implies that straying rates of nearby anadromous and marine populations (ie. Salt Lagoon and Paq Creek) to this marine breeding site are not different. Still, the predominance of homers over strayers from all three release sites clearly demonstrates reproductive homing by the Oyster Lagoon population.

Recaptures in Salt Lagoon

Of the fish originating in Salt Lagoon, 4.5 % were recaptured in Salt Lagoon (release sites : "A" = 4.1 %. "B" = 5.6 %, and "C" = 3.8 %). Strays from the other displaced populations (Oyster Lagoon and Paq Creek) represented only 0.7 % and 0.2 %, respectively, of their total numbers marked and released. Potentially, either Canoe Pass or proximity to Oyster Lagoon could inhibit the return of Salt Lagoon homers from release sites "A" and "C" (CVs : "A" = 21, "B" = 29, and "C" = 19); however, the small numbers recaptured requires that such comparisons be treated with caution ($G = 2.364$, $p > 0.25$).

For the same reason (small sample size), straying rates of the marine (Oyster Lagoon) and anadromous (Paq Creek) populations were difficult to compare. As in Oyster Lagoon, there are no obvious differences between the numbers of recaptures of Oyster Lagoon and Paq Creek fish in Salt Lagoon. Although the numbers are small, it is clear for all three release sites that more displaced Salt Lagoon fish return to Salt Lagoon than do strayers from the Oyster Lagoon and Paq Creek populations.

Recaptures in Paq Creek

Of the displaced fish originating in Paq Creek, 34.3 % were recaptured in Paq Creek (release site : "A" = 25.0 %, "B" = 45.5 %, and "C" = 31.9 %). Strays from the other displaced populations (Oyster Lagoon and Salt Lagoon) represented only 0.1 % and 0.05 %, respectively, of their total numbers marked and released. Again, either Canoe Pass or proximity to Oyster Lagoon could inhibit returns to Paq Creek from release sites "A" and "C". Comparison of homers from the different displacement sites (CVs : "A" = 128, "B" = 232, and "C" = 184) indicate a significant difference among sites ($G = 30.56$, $p < 0.001$). Recaptures from release site "B" were higher than from release sites "A" and "C". Release site "A" also produced fewer returns than release site "C". This suggests that a release site's proximity to an alternate breeding site may influence the number of fish that home.

Despite the efficient recapture in Paq Creek, there were low numbers of strayers recaptured (3 from Oyster Lagoon, 1 from Salt Lagoon). Apparently straying to this anadromous (freshwater) breeding site is lower than straying to lagoons.

Summary

The primary goal of this experiment was to examine reproductive homing by threespine sticklebacks. Since the relationship between straying and gene flow is unknown, the actual number of strays is not critical for this study. The null hypothesis was that the number of recaptures for each population would be equal at each breeding site. This would indicate an equal distribution of returns regardless of initial breeding site. The null hypothesis was rejected at all breeding sites. The predominance of homers among recaptures at each breeding site indicates the presence of reproductive homing in all three populations

used in this study. Clearly, sticklebacks show a strong propensity to return to an initial breeding site even after displacements of up to 1 km. Some individuals did not return for up to three months after release, and this is comparable to the duration of natal migration times (*see* Natal Homing, *page* 26). This prolonged delay in reproductive homing suggests that threespine sticklebacks can retain a "memory" of their breeding site for at least three months.

There was some variation in proportion of homers at different breeding sites and the propensity to home from different release sites. Proportions of homers ranged from 0.81 at Salt Lagoon from release site "A", to 1.00 at Paq Creek from release site "B" (Table 1, *page* 22). Possible influences on returns from different release sites involve variation in geography, intensity of predation through different migratory routes, degree of disorientation, presence of alternative breeding sites, and habitat identification. Apparently, these factors do significantly influence both homing success and straying; nevertheless, sticklebacks clearly show reproductive homing. The results from this experiment raise the possibility that they may also show natal homing. If so, this could have profound effects on levels of gene flow and deme structure in marine and anadromous sticklebacks.

NATAL HOMING EXPERIMENT

Introduction

This section investigates natal homing in the Oyster Lagoon population of threespine sticklebacks (*Gasterosteus aculeatus*). Natal homing refers to the return of sexually mature adults from the ocean to their site of birth. There is no direct evidence for natal homing by threespine sticklebacks; however, the evidence for reproductive homing given in the preceding chapter suggests the possibility of natal homing. If natal homing occurs in this species it could result in genetic differences among populations from different breeding sites. The following experiment attempts to determine whether natal homing occurs in marine sticklebacks and, if so, to estimate the precision of natal homing. The latter goal involves estimating the amount of straying. Presumably, there is some relationship between the amount of straying and the probability that a population will diverge.

Coincident with the reproductive homing experiment (Reproductive Homing, *page* 10), the Oyster Lagoon population was monitored for natal returns into the Oyster Lagoon, and straying into the Salt Lagoon and Paq Creek breeding sites. In the 1992 breeding season, I monitored returns of fish that were marked at 3 different times (April 1991, August 1991, and April 1992) during their migration out of Oyster Lagoon. The April and August markings were necessary because some young of the year leave in their first summer (summer migrators) while other individuals overwinter in the lagoon and leave the next spring (overwinterers). Apparently, overwintering at a breeding site before migration is not common among marine or anadromous populations (pers. obs.) and, even in Oyster Lagoon, most of the young leave the lagoon during the summer or early fall of their birth year. In Oyster Lagoon, these overwintering migrators allowed a partial replication of natal homing.

Materials and Methods

Mark and Release

As they migrated out of Oyster Lagoon, young of the year were collected at the entrance channel to Oyster Lagoon. This was accomplished by partially blocking the migration channel with a large funnel fence (10 mm mesh) and trapping out-migrators with 2 small plexiglass minnow traps (30 cm x 30 cm x 60 cm). Daily catches were marked with spine clips and released on the other side of the fence. Different spines were clipped at different release times (April 1991, August 1991 and April 1992). April 1991 migrators were clipped on the second dorsal spine and August 1991 migrators were clipped on the right pelvic spine. These out-migrators (April 1991 and August 1991) ranged in length from 20 - 35 mm. Out-migrators in April 1992 ranged in standard length from 25 mm to 35 mm and were clipped on the first dorsal spine. During the out-migrations, 100 - 1500 fish were released per day but were divided into groups of 50 - 100 fish; small groups were used to reduce the likelihood of individuals migrating back into the lagoon.

Spine Clipping Controls

The effect of spine clipping on survival of juvenile sticklebacks was tested, and the recognition of spine clips after winter growth was evaluated. A grab sample (variable sizes) of 61 migrating young were taken from Oyster Lagoon on August 31st, 1991 and raised in the laboratory over the 1991/92 winter. All fish were measured and their left pelvic spines clipped on September 14th. They were fed *Tubifex* and *Artemia* and their survival monitored until March 18th, 1992. At this time, several individuals of both sexes began showing signs of sexual maturation. Standard lengths at times of death and at the end of monitoring were recorded.

Monitoring of Returns

Returns to Oyster Lagoon and the two nearest alternative breeding sites (Salt Lagoon and Paq Creek; Fig. 1, *page* 6) were monitored at the same time as the reproductive homing experiment. There was an additional sampling earlier in the season (April and May; Appendices V, VI, and VII) that used the same trapping techniques (Monitoring of Returns, *page* 13). All recaptured fish were preserved. Occasionally there were fish with broken spines, apparently due to bird predation, but these were easily identified and not included in recapture data.

Data Analysis

The comparison of homers and strayers is complicated by several factors : the marking of only one population but the monitoring of three breeding sites, my inability to estimate population sizes, and the use of different trapping techniques at each breeding site (*see* Monitoring of Returns, *page* 13). Therefore, ratios of natal homers to natal strayers were compared to ratios of returns by displaced adults from the reproductive homing experiment. For these comparisons, data from release site "A" (288 reproductive homers to 9 strayers at Salt Lagoon and 2 strayers at Paq Creek; reproductive homing, Fig. 3, *page* 17) were used because "A" was in a similar location to where the young of the year were released for the monitor of natal homing. When increases of straying were suspected, log likelihood ratio analysis of contingency tables were used to test for significant differences. These statistical comparisons tested whether natal homing was similar to reproductive homing. If necessary, tables were subdivided and William's adjusted log likelihood ratio analysis (G_{adj} test) independently compared proportions of natal strayers, to reproductive strayers for both Salt Lagoon and Paq Creek. These comparisons allowed for better definitions of how, and to

which sites, natal straying was different from the low levels of reproductive straying. Where the numbers of natal strayers were found to be significantly higher than reproductive strayers, log likelihood with Yates correction (G_c test) also compared numbers of natal strayers to the reproductive homers of that site; corrected values (CV) were calculated to adjust numbers of natal strayers for relative comparisons to the reproductive homers :

Corrected Values = # natal strayers x (288/# natal homers),

where 288 is the number of reproductive homers from release site "A". No significant difference between natal strayers and reproductive homers indirectly implied equal natal returns to the two different breeding sites (i.e. natal homers equal natal strayers).

Results

Returns were monitored through the entire 1992 breeding season (March - August) at Oyster Lagoon, Salt Lagoon, and Paq Creek (Appendices V, VI, and VII). Clearly, fish born in Oyster Lagoon show a strong tendency to return to Oyster Lagoon and exhibit relatively low straying rates to Paq Creek (Table 2). Interestingly, straying to Salt Lagoon was low for overwinterers, but higher for summer migrants. This suggests that there may be an inverse relationship between time since migration and the precision of homing.

Effects of Spine Clipping

At marking, the mean standard length of the 61 control fish was 25.8 mm. All recorded deaths (35) occurred within two weeks of marking (32 after only one day) and fell disproportionately on smaller fish (mean standard length of those that died = 22.3 mm). The largest fish that died was 28 mm. Some fungus appeared on spines that were clipped too short, but no deaths occurred from October to March. This experiment shows that spine

			BREEDING SITES MONITORED				
			Oyster Lagoon	Salt Lagoon		Paq Creek	
			Oyster homers	Oyster strayers	Salt homers	Oyster strayers	Paq homers
Reproductive Homing from RELEASE SITE "A"							
date released	# released	length of migration					
MAY 1992	1009	0 - 3 months	288	9	32	2	128
Natal Homing							
APR 1992	10025	2 - 4 months	520	7		0	
AUG 1991	7476	5 - 11 months	260	59		11	
APR 1991	11000	8 - 16 months	94	11		0	

Table 2. Number of marked Oyster Lagoon fish recaptured in Oyster Lagoon, Salt Lagoon, and Paq Creek during spring/summer 1992 (*for detail see* Appendices V, VI, and VII). Recaptures from release site "A" of the Reproductive Homing Experiment (*see* Reproductive Homing, *page* 14) are included as comparaive ratios of recapture.

clipping has a fast and relatively large effect on small fish (S.L. < 25 mm). The surviving fish increased in standard length (mean = 40.7 mm on March 18th) from September to March. Although these fish grew, the clipped pelvic spines were still easily recognized in March.

Comparisons to Reproductive Homing

Of the 10 025 young of 1991 that were marked as they migrated out of Oyster Lagoon in April 1992 (overwinterers), 520 were recaptured 2 - 4 months later as they re-entered the lagoon. In addition, seven individuals were recaptured in Salt Lagoon but, despite efficient trapping, no fish were recaptured in Paq Creek (Table 2). By comparison to recaptures of

displaced adults (288 homers, 9 strayers to Salt Lagoon, and 2 strayers to Paq Creek), it is clear that natal straying by fish that overwintered in Oyster Lagoon, and thus spent relatively short time (2 - 4 months) out of the lagoon, return to the lagoon with the same fidelity as displaced adults.

Of the 7 476 young of 1991 that were marked as they left Oyster Lagoon in August 1991 (summer migrators), 260 were recaptured 7 to 12 months later as they re-entered the lagoon. In contrast to overwinterers, 59 summer migrators were recaptured in Salt Lagoon and 11 in Paq Creek (Table 2). Statistical comparison of this ratio of summer migrator returns, to the returns of displaced adults, shows a significant difference ($G = 47.88$, $p < 0.001$). In more detail, the proportion that strayed to Paq Creek (260 : 11) was significantly different from the proportion of displaced adults that strayed to the creek (288 : 0) ($G_c = 15.459$, $p < 0.001$) indicating more natal straying than reproductive straying; however, 11 natal strayers (CV = 12) was considerably less than the 128 reproductive homers to Paq Creek which implies that fewer summer migrators returned to Paq Creek than to Oyster Lagoon. Also, the proportion of summer migrators that strayed to Salt Lagoon (260 : 59) was compared to the proportion of displaced adults that strayed (288 : 6) and there was a significant difference ($G_c = 50.109$, $p < 0.001$). Interestingly, further comparison of the 59 strayers (CV = 53) to the 32 Salt Lagoon homers (displaced adults), indicates that natal straying by summer migrators was significantly higher than reproductive homing to Salt Lagoon ($G_c = 4.750$, $p < 0.05$); this implies that there were more Oyster Lagoon summer migrators returning to Salt Lagoon than to Oyster Lagoon.

For Oyster Lagoon sticklebacks, the longer times spent out of the lagoon appear to range from 8 - 16 months. Of the 11 000 overwintering young of 1990 that were marked as

they left Oyster Lagoon in April 1991, 94 were recaptured returning to Oyster Lagoon in the spring and summer of 1992 (8 -16 months after marking). In addition, 11 strayers to Salt Lagoon, and none to Paq Creek were recaptured (Table 2). Comparison of this ratio of two year old returns, to returns of displaced adults found a significant difference ($G = 9.124$, $p < 0.025$). Interestingly, with no recaptures of these overwinterers at Paq Creek, there is no recognizable difference between natal straying, and straying by displaced adults to Paq Creek. However, recaptures of these overwinterers were comparatively high at Salt Lagoon (11 strayers; CV = 34); comparison of proportion of natal strayers (94 :11) to displaced Oyster Lagoon adults shows a significant difference ($G_{adj} = 7.65$, $p < 0.01$). In fact, the number of two year old strayers to Salt Lagoon was not significantly different from the 32 displaced adults that homed to Salt Lagoon ($G_c = 0.015$, $p > 0.90$); this relative similarity implies that the Oyster Lagoon fish that overwintered, and left the lagoon for 8 - 16 months, returned in similar numbers to both Oyster and Salt lagoons.

These results suggest that the precision of homing in marine threespine sticklebacks is an inverse function of the length of time the fish are away from the breeding site. Interestingly, in the 1992 breeding season, no overwinterers from either year (April 1991 or April 1992 markings) strayed to Paq Creek; however, summer migrators did stray to the creek. Why there is this difference in propensity to stray to Paq Creek between summer migrators and overwinterers is still not resolved.

Summary

My study suggests that marine sticklebacks born in Oyster Lagoon return to the lagoon to breed as adults. The percent return is similar to that found in salmonids : 0.85 %

to 5.2 % for Oyster Lagoon sticklebacks and 1 % to 20 % for salmonids (Groot & Margolis 1992). The level of straying to nearby Paq Creek and Salt Lagoon is generally low but variable. The level of straying seems to be related to season and lengths of time away from the lagoon. Also, this marine population strays less to Paq Creek (a freshwater breeding site) than to the Salt Lagoon marine breeding site. Summer migrators stray more than overwintering fish, and the level of straying between the two marine populations probably is sufficient to prevent divergence. Overwintering juveniles that spent only 2 to 4 months outside of the lagoon, returned more successfully than summer migrators which were absent for 7 to 12 months. Although they are not common in the lagoon, two year old fish had the lowest returns (0.85 % of those marked). The total returns of the summer migrators (3.5 % of those marked) is most representative of the role of natal homing at Oyster Lagoon.

The low numbers of strayers to Paq Creek suggest little or no gene flow from marine to anadromous populations of sticklebacks. The salinity differences between freshwater and marine breeding sites may contribute to the apparent ease with which Oyster Lagoon fish distinguish between these sites. However, there may be isolation between marine and freshwater breeding habitats without effective isolation among anadromous populations, although geographic distance may provide some reduction in inter-population gene flow. The results from Paq Creek indicate the possibility of genetic isolation between marine and anadromous populations, and this introduces the possibility of two sources of post-glacial colonists to fresh water.

The high number of Oyster Lagoon summer migrators recaptured at Salt Lagoon (August 1991 release) bring into question the strength of this population's natal homing. Because more marked fish returned to Salt Lagoon than Oyster Lagoon, in reality, these two

marine breeding sites may be one site; however, the straying by overwinterers (April release) to Salt Lagoon was as low as reproductive straying and this suggests some degree of isolation between the two.

The most important outcome from this experiment is the confirmation of natal homing by threespine sticklebacks. It is this knowledge that opens the way to more detailed studies. There is now a need to better measure the levels of gene flow between, and among, anadromous and marine populations.

GENERAL DISCUSSION

This study examines the propensity of both marine and anadromous threespine sticklebacks (*Gasterosteus aculeatus*) to return to their place of birth to breed (natal homing), and of breeders to return to their breeding site if displaced (reproductive homing). All three populations (Oyster Lagoon, Salt Lagoon, and Paq Creek) exhibited strong reproductive homing but only the Oyster Lagoon population was tested for natal homing. Young of the year that were marked as they left the lagoon returned to the lagoon as mature adults. Overwinterers showed remarkable fidelity to Oyster Lagoon with only a relatively small number of individuals returning to nearby Salt Lagoon and no strayers were recovered at the anadromous spawning site (Paq Creek). This level of homing with little or no straying to alternative breeding sites that are within a kilometer of Oyster Lagoon, suggests the possibility that these populations are genetically isolated from one another. The level of straying between the two marine populations (Oyster and Salt lagoons) may be sufficient to prevent divergence but, for natal homing, the anadromous population (Paq Creek) appears to be completely isolated. Consequently, given enough time and strong enough selection, the marine and anadromous populations could diverge. Clearly, information, especially on homing and straying, is needed before the evolution of post-glacial diversity in this species can be understood.

Ortí *et al.* (1992) suggests at least three ancestral clades (of northern, eastern and western Pacific origins) were involved in the post-glacial invasion of British Columbia. Their suggestion is based on mtDNA sequence analysis of the cytochrome B gene, and the differences among the three clades imply pre-glacial divergence. Much of the divergence in freshwater, however, clearly is post-glacial (Bell 1976; Withler & McPhail 1985). Most

freshwater populations are thought to be derived from anadromous or marine populations, and these founding populations generally are viewed as homogeneous (Bell 1976; Withler & McPhail 1985). The discovery of natal homing in threespine sticklebacks provides a mechanism that could generate heterogeneity in marine sticklebacks, and between marine and anadromous populations. Certainly, divergence among marine populations of *Gasterosteus* has been demonstrated on the east coast of North America. The recently discovered white stickleback is reproductively isolated from *G. aculeatus* and has distinctly different breeding colouration, nest site selection, and parental care (Blouw & Hagen 1990). Since the diversity among freshwater populations of *Gasterosteus* is greater on the west coast than on the east coast of North America, it is possible that there is more diversity among marine and anadromous populations in this area than has previously been supposed. For example, sexually mature sticklebacks occur at least 150 km offshore on the west coast (Quinn & Light 1989), and would have to make prodigious migrations to reach shore in time to spawn. Perhaps there is some unique, pelagic stickleback out in the North Pacific. Also, there are hints in the literature of morphological and electrophoretic divergences among anadromous populations (Withler 1980), and if anadromous populations home as accurately as marine populations, they may have a deme structure comparable to anadromous salmonids.

Sticklebacks could also be useful models for the study of mechanisms of homing in anadromous species. At present, nothing is known about the sensory mechanisms that sticklebacks use to return to their place of birth, or whether this propensity is inherited. Certainly, there is evidence of a genetic component in the homing and migrations of salmonids (Brannon, 1972; Kelso *et al.*, 1981; Taylor, 1988). Salmonids have also demonstrated abilities such as sun compass, or celestial orientation, and experiments have

shown that both vision and olfaction play a role in natal homing (*for examples see* Quinn and Dittman, 1992). The major advantage that sticklebacks have over salmonids for studying homing is their short life cycle (one year to maturity). Indeed, some marine sticklebacks return to their breeding site within two months. Also, the species is abundant and easy to work with.

This study of homing was designed to investigate a possible mechanism that contributes to the evolution of post-glacial diversity among sticklebacks along the northwest coast of North America. The data clearly demonstrate natal homing, but it remains to be demonstrated that homing, in conjunction with local selection, has produced significant heterogeneity among marine and anadromous populations of this fascinating species.

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Appendix I. Numbers of female sticklebacks that were collected at Oyster Lagoon, Salt Lagoon, and Paq Creek breeding sites for displacements to release sites "A", "B", and "C". Fish were dye injected under anterior lateral plates on the right side for release site "A", under posterior right lateral plates for release site "B", and under left anterior lateral plates for release site "C". Fish with different initial breeding site choices were marked with different colour dyes : orange for Oyster Lagoon (Appendix Ia), pink for Salt Lagoon (Appendix Ib), and red for Paq Creek (Appendix Ic).

Appendix Ia. Numbers of female sticklebacks from the Oyster Lagoon that were marked and released for the Reproductive Homing Experiment.

	DATE	# OF FISH RELEASED at RELEASE SITES			TOTAL # of FISH DISPLACED
		"A"	"B"	"C"	
1	MAY 13th	84	88	87	259
2	MAY 14th	85	85	100	270
3	MAY 15th	100	96	86	282
4	MAY 16th	95	90	96	281
5	MAY 17th	95	96	94	285
6	MAY 18th	120	108	110	338
7	MAY 19th	93	87	94	274
8	MAY 20th	120	120	110	350
9	MAY 21st	110	116	100	326
10	MAY 22nd	105	101	104	310
	TOTAL NUMBERS RELEASED	1009	987	981	2987

Appendix Ib. Numbers of female sticklebacks from Salt Lagoon that were marked and released for the Reproductive Homing Experiment.

	DATE	# OF FISH RELEASED at RELEASE SITES			TOTAL # of FISH DISPLACED
		"A"	"B"	"C"	
1	MAY 13th	80	79	71	230
2	MAY 14th	76	65	28	169
3	MAY 15th	78	71	70	219
4	MAY 16th	49	48	32	129
5	MAY 17th	40	51	38	129
6	MAY 18th	91	83	77	251
7	MAY 19th	84	82	91	257
8	MAY 20th	109	109	111	329
9	MAY 21st	95	94	95	284
10	MAY 22nd	79	79	77	235
	TOTAL NUMBERS RELEASED	781	750	690	2221

Appendix Ic. Numbers of female sticklebacks from Paq Creek that were marked and released for the Reproductive Homing Experiment.

	DATE	# OF FISH RELEASED at RELEASE SITES			TOTAL # of FISH DISPLACED
		"A"	"B"	"C"	
1	MAY 13th	55	50	60	165
2	MAY 14th	44	50	31	125
3	MAY 15th	88	98	96	272
4	MAY 16th	35	36	40	111
5	MAY 17th	44	42	35	121
6	MAY 18th	40	40	45	125
7	MAY 19th	42	43	44	129
8	MAY 20th	42	45	44	131
9	MAY 21st	56	57	58	171
10	MAY 22nd	65	69	58	192
	TOTAL NUMBERS RELEASED	511	530	511	1552

Appendix II. Summary of recaptures in Oyster Lagoon for the Reproductive Homing Experiment from May to August, 1992. For daily record of returns, see Appendices IIa - IIf.

	HOMERS			STRAYERS					
	OYSTER LAGOON POPULATION FROM RELEASE SITES			SALT LAGOON POPULATION FROM RELEASE SITES			PAQ CREEK POPULATION FROM RELEASE SITES		
	A	B	C	A	B	C	A	B	C
May 14 - 31	133	52	138	13	0	7	11	0	7
June 1 - 15	121	125	87	1	2	0	2	0	1
June 16 - 30	17	26	22	2	1	0	0	0	0
July 1 - 15	15	16	17	0	0	2	1	0	0
July 16 - 31	2	1	4	0	0	0	0	1	0
Aug. 1 - 15	0	2	0	0	0	0	0	0	0
TOTAL RECAPTURES	288	222	268	16	3	9	14	1	8

Appendix IIa. Daily record of recaptures in Oyster Lagoon for the Reproductive Homing Experiment from May 14th - 31st, 1992.

MAY	SAMPLE SIZE of Females	HOMERS OYSTER LAGOON POPULATION FROM RELEASE SITES			STRAYERS SALT LAGOON POPULATION FROM RELEASE SITES			STRAYERS PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
14	234	5	0	4	0	0	1	0	0	0
15	643	20	2	19	5	0	0	1	0	0
16	90	7	1	7	1	0	0	1	0	0
17	387	11	4	12	1	0	2	2	0	1
18	444	25	4	25	1	0	1	0	0	0
19	285	3	4	8	0	0	0	0	0	3
20	388	11	3	10	2	0	2	3	0	1
21	406	15	2	17	1	0	1	1	0	1
22	73	5	7	12	1	0	0	1	0	1
23	28	3	0	2	0	0	0	1	0	0
24	97	6	1	4	0	0	0	0	0	0
25	91	3	6	4	0	0	0	1	0	0
26	102	3	0	7	0	0	0	0	0	0
27	45	1	0	1	0	0	0	0	0	0
28	39	1	2	1	0	0	0	0	0	0
29	77	3	2	1	0	0	0	0	0	0
30	22	0	0	2	0	0	0	0	0	0
31	397	12	14	6	1	0	0	0	0	0
TOTAL RECAPTURES MAY 14 - 31		133	52	138	13	0	7	11	0	7

Appendix IIb. Daily record of recaptures in Oyster Lagoon for the Reproductive Homing Experiment from June 1st - 15th, 1992.

JUNE	SAMPLE SIZE of Females	HOMERS			STRAYERS					
		OYSTER LAGOON POPULATION FROM RELEASE SITES			SALT LAGOON POPULATION FROM RELEASE SITES			PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
1	443	19	12	7	0	0	0	0	0	0
2	779	11	18	13	0	1	0	0	0	0
3	1219	20	23	14	0	0	0	0	0	1
4	992	15	24	14	0	0	0	0	0	0
5	922	19	10	7	0	0	0	2	0	0
6	726	12	7	5	1	0	0	0	0	0
7	119	1	3	3	0	0	0	0	0	0
8	42	1	0	0	0	0	0	0	0	0
9	91	0	0	2	0	0	0	0	0	0
10	73	3	1	0	0	0	0	0	0	0
11	184	3	3	2	0	0	0	0	0	0
12	419	4	5	6	0	0	0	0	0	0
13	714	2	8	3	0	0	0	0	0	0
14	744	3	5	7	0	1	0	0	0	0
15	696	8	6	4	0	0	0	0	0	0
TOTAL RECAPTURES JUNE 1 - 15		121	125	87	1	2	0	2	0	1

Appendix IIc. Daily record of recaptures in Oyster Lagoon for the Reproductive Homing Experiment from June 16th - 31st, 1992.

JUNE	SAMPLE SIZE of Females	HOMERS			STRAYERS					
		OYSTER LAGOON POPULATION FROM RELEASE SITES			SALT LAGOON POPULATION FROM RELEASE SITES			PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
16	1037	3	7	6	1	1	0	0	0	0
17	860	1	4	3	0	0	0	0	0	0
18	527	3	2	1	0	0	0	0	0	0
19	1330	6	7	3	1	0	0	0	0	0
20	769	2	1	3	0	0	0	0	0	0
21	629	0	2	2	0	0	0	0	0	0
22	125	0	0	0	0	0	0	0	0	0
23	50	1	1	0	0	0	0	0	0	0
24	32	0	0	0	0	0	0	0	0	0
25	17	0	0	0	0	0	0	0	0	0
26	20	0	0	1	0	0	0	0	0	0
27	31	0	0	1	0	0	0	0	0	0
28	340	0	1	1	0	0	0	0	0	0
29	764	1	0	0	0	0	0	0	0	0
30	768	0	1	1	0	0	0	0	0	0
TOTAL RECAPTURES JUNE 16 - 30		17	26	22	2	1	0	0	0	0

Appendix IId. Daily record of recaptures in Oyster Lagoon for the Reproductive Homing Experiment from July 1st - 15th, 1992.

JULY	SAMPLE SIZE of Females	HOMERS OYSTER LAGOON POPULATION FROM RELEASE SITES			STRAYERS SALT LAGOON POPULATION FROM RELEASE SITES			STRAYERS PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
1	533	0	1	1	0	0	0	0	0	0
2	784	2	3	0	0	0	1	0	0	0
3	385	0	3	0	0	0	0	0	0	0
4	736	3	1	4	0	0	0	0	0	0
5	1223	1	0	1	0	0	0	0	0	0
6	105	1	0	1	0	0	0	1	0	0
7	388	0	1	1	0	0	0	0	0	0
8	69	0	1	0	0	0	0	0	0	0
9	218	0	0	0	0	0	0	0	0	0
10	142	1	1	0	0	0	0	0	0	0
11	87	1	1	2	0	0	0	0	0	0
12	1052	0	2	1	0	0	0	0	0	0
13	798	0	1	3	0	0	0	0	0	0
14	595	3	0	2	0	0	0	0	0	0
15	1204	2	1	1	0	0	1	0	0	0
TOTAL RECAPTURES JULY 1 - 15		15	16	17	0	0	2	1	0	0

Appendix IIe. Daily record of recaptures in Oyster Lagoon for the Reproductive Homing Experiment from July 16th - 31st, 1992.

JULY	SAMPLE SIZE of Females	HOMERS			STRAYERS					
		OYSTER LAGOON POPULATION FROM RELEASE SITES			SALT LAGOON POPULATION FROM RELEASE SITES			PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
16	865	0	0	1	0	0	0	0	0	0
17	1201	0	0	1	0	0	0	0	0	0
18	1194	1	0	1	0	0	0	0	0	0
19	873	0	1	0	0	0	0	0	0	0
20	568	0	0	0	0	0	0	0	0	0
21	578	0	0	0	0	0	0	0	0	0
22	87	0	0	1	0	0	0	0	0	0
23	100	0	0	0	0	0	0	0	0	0
24	140	0	0	0	0	0	0	0	1	0
25	45	0	0	0	0	0	0	0	0	0
26	-	-	-	-	-	-	-	-	-	-
27	-	-	-	-	-	-	-	-	-	-
28	397	0	0	0	0	0	0	0	0	0
29	1564	1	0	0	0	0	0	0	0	0
30	528	0	0	0	0	0	0	0	0	0
31	942	0	0	0	0	0	0	0	0	0
TOTAL RECAPTURES JULY 16 - 31		2	1	4	0	0	0	0	1	0

Appendix IIf. Daily record of recaptures in Oyster Lagoon for the Reproductive Homing Experiment from August 1st - 15th, 1992.

AUG.	SAMPLE SIZE of Females	HOMERS OYSTER LAGOON POPULATION FROM RELEASE SITES			STRAYERS SALT LAGOON POPULATION FROM RELEASE SITES			STRAYERS PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
1	666	0	0	0	0	0	0	0	0	0
2	764	0	0	0	0	0	0	0	0	0
3	288	0	1	0	0	0	0	0	0	0
4	612	0	0	0	0	0	0	0	0	0
5	578	0	0	0	0	0	0	0	0	0
6	245	0	1	0	0	0	0	0	0	0
7	498	0	0	0	0	0	0	0	0	0
8	-	-	-	-	-	-	-	-	-	-
9	83	0	0	0	0	0	0	0	0	0
10	431	0	0	0	0	0	0	0	0	0
11	306	0	0	0	0	0	0	0	0	0
12	154	0	0	0	0	0	0	0	0	0
13	1077	0	0	0	0	0	0	0	0	0
14	1641	0	0	0	0	0	0	0	0	0
15	608	0	0	0	0	0	0	0	0	0
TOTAL RECAPTURES AUG. 1 - 15		0	2	0	0	0	0	0	0	0

Appendix III. Summary of recaptures in Salt Lagoon for the Reproductive Homing Experiment from May - August, 1992. For daily record of returns, see Appendices IIIa - IIIe.

	HOMERS			STRAYERS					
	SALT LAGOON POPULATION FROM RELEASE SITES			OYSTER POPULATION FROM RELEASE SITES			PAQ CREEK POPULATION FROM RELEASE SITES		
	A	B	C	A	B	C	A	B	C
May 14 - 31	6	9	6	4	4	3	0	2	0
June 1 - 15	10	10	3	1	2	0	0	1	0
June 16 - 30	8	11	10	1	0	1	0	0	0
July	6	7	5	3	0	0	0	0	0
August	2	5	2	0	0	1	0	0	0
TOTAL RECAPTURES	32	42	26	9	6	5	0	3	0

Appendix IIIa. Record of recaptures in Salt Lagoon for the Reproductive Homing Experiment from May 14th - 31st, 1992.

MAY	SAMPLE SIZE of Females	HOMERS SALT LAGOON POPULATION FROM RELEASE SITES			STRAYERS OYSTER POPULATION FROM RELEASE SITES			STRAYERS PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
14	210	0	0	4	0	0	0	0	0	0
15	130	0	0	0	0	0	0	0	0	0
16	129	0	0	0	0	1	0	0	1	0
17	251	0	0	0	0	0	0	0	0	0
18	257	0	1	0	0	0	0	0	0	0
19	329	0	0	0	0	0	0	0	0	0
20	284	1	0	0	0	0	0	0	0	0
21	235	2	0	1	0	1	1	0	0	0
22	295	1	0	1	0	0	1	0	0	0
23	324	0	1	0	0	0	0	0	0	0
24	498	0	2	0	0	1	0	0	0	0
25	565	2	1	1	1	0	1	0	0	0
26	519	0	2	0	0	0	0	0	0	0
27	368	0	1	1	3	0	0	0	0	0
28	231	0	1	0	0	1	0	0	0	0
29	310	0	0	1	0	0	0	0	1	0
30	275	0	0	1	0	0	0	0	0	0
31	360	0	0	0	0	0	0	0	0	0
TOTAL RECAPTURES MAY 14 - 31		6	9	6	4	4	3	0	2	0

Appendix IIIb. Record of recaptures in Salt Lagoon for the Reproductive Homing Experiment from June 1st - 15th, 1992.

JUNE	SAMPLE SIZE of Females	HOMERS SALT LAGOON POPULATION FROM RELEASE SITES			STRAYERS OYSTER POPULATION FROM RELEASE SITES			STRAYERS PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
1	382	1	0	0	1	0	0	0	0	0
2	610	0	1	0	0	0	0	0	0	0
3	572	1	1	0	0	0	0	0	0	0
4	435	0	0	0	0	1	0	0	0	0
5	504	0	0	1	0	0	0	0	0	0
6	595	2	1	0	0	0	0	0	0	0
7	830	2	4	0	1	0	0	0	0	0
8	724	1	1	0	0	0	0	0	1	0
9	747	1	0	1	0	0	0	0	0	0
10	596	0	0	1	0	0	0	0	0	0
11	577	1	1	0	1	0	0	0	0	0
12	422	0	1	0	0	0	0	0	0	0
13	289	1	0	0	1	0	0	0	0	0
14	470	0	0	1	0	0	0	0	0	0
15	394	0	0	0	0	0	0	0	0	0
TOTAL RECAPTURES JUNE 1 - 15		10	10	3	1	2	0	0	1	0

Appendix IIIc. Record of recaptures in Salt Lagoon for the Reproductive Homing Experiment from June 16th - 31st, 1992.

JUNE	SAMPLE SIZE of Females	HOMERS SALT LAGOON POPULATION FROM RELEASE SITES			STRAYERS OYSTER POPULATION FROM RELEASE SITES			STRAYERS PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
16	579	0	1	0	0	0	0	0	0	0
17	744	0	2	1	0	0	0	0	0	0
18	975	0	0	0	0	0	0	0	0	0
19	905	1	0	0	0	0	0	0	0	0
20	891	0	1	2	0	0	1	0	0	0
21	1026	1	2	0	1	0	0	0	0	0
22	1251	1	1	0	0	0	0	0	0	0
23	-	-	-	-	-	-	-	-	-	-
24	806	1	0	4	0	0	0	0	0	0
25	726	1	1	0	0	0	0	0	0	0
26	1011	2	1	0	0	0	0	0	0	0
27	701	1	2	1	0	0	0	0	0	0
28	765	0	0	1	0	0	0	0	0	0
29	-	-	-	-	-	-	-	-	-	-
30	338	0	0	1	0	0	0	0	0	0
TOTAL RECAPTURES JUNE 16 - 30		8	11	10	1	0	1	0	0	0

Appendix IIId. Record of recaptures in Salt Lagoon for the Reproductive Homing Experiment during July, 1992.

JULY	SAMPLE SIZE of Females	HOMERS SALT LAGOON POPULATION FROM RELEASE SITES			STRAYERS OYSTER POPULATION FROM RELEASE SITES			STRAYERS PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
2	533	1	0	1	0	0	0	0	0	0
4	784	1	0	0	0	0	0	0	0	0
6	385	0	1	0	0	0	0	0	0	0
8	736	1	2	1	0	0	0	0	0	0
10	1223	0	2	1	0	0	0	0	0	0
12	105	2	0	1	1	0	0	0	0	0
14	388	0	1	0	1	0	0	0	0	0
16	69	0	0	0	0	0	0	0	0	0
18	218	0	1	0	0	0	0	0	0	0
20	142	1	0	0	1	0	0	0	0	0
22	87	0	0	0	0	0	0	0	0	0
24	1052	0	0	0	0	0	0	0	0	0
26	798	0	0	0	0	0	0	0	0	0
28	595	0	0	0	0	0	0	0	0	0
30	1204	0	0	1	0	0	0	0	0	0
TOTAL RECAPTURES JULY 1 - 30		6	7	5	3	0	0	0	0	0

Appendix IIIe. Record of recaptures in Salt Lagoon for the Reproductive Homing Experiment during August, 1992.

AUG.	SAMPLE SIZE of Females	HOMERS SALT LAGOON POPULATION FROM RELEASE SITES			STRAYERS OYSTER POPULATION FROM RELEASE SITES			STRAYERS PAQ CREEK POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
1	492	0	1	0	0	0	0	0	0	0
3	424	0	2	1	0	0	0	0	0	0
5	500	0	0	0	0	0	0	0	0	0
7	-	-	-	-	-	-	-	-	-	-
9	571	0	2	0	0	0	1	0	0	0
11	605	0	0	0	0	0	0	0	0	0
13	468	1	0	0	0	0	0	0	0	0
15	544	0	0	1	0	0	0	0	0	0
17	387	1	0	0	0	0	0	0	0	0
TOTAL RECAPTURES AUG. 1 - 15		2	5	2	0	0	1	0	0	0

Appendix IV. Summary of recaptures in Paq Creek for the Reproductive Homing Experiment from May - August, 1992. For daily record of returns, see Appendices IVa - IVc.

	HOMERS			STRAYERS					
	PAQ CREEK POPULATION FROM RELEASE SITES			OYSTER POPULATION FROM RELEASE SITES			SALT LAGOON POPULATION FROM RELEASE SITES		
	A	B	C	A	B	C	A	B	C
May 14 - 31	55	126	56	2	0	0	0	0	0
June 1 - 7	47	77	70	0	0	1	0	0	0
June 19 & 20	19	26	26	0	0	0	0	0	1
July 15 & 16	5	8	6	0	0	0	0	0	0
July 29 & 30	1	2	1	0	0	0	0	0	0
Aug. 1 - 15	1	2	4	0	0	0	0	0	0
TOTAL RECAPTURES	128	241	163	2	0	1	0	0	1

Appendix IVa. Record of recaptures in Paq Creek for the Reproductive Homing Experiment from May 14th - 31st, 1992.

MAY	SAMPLE SIZE of Females	HOMERS PAQ CREEK POPULATION FROM RELEASE SITES			STRAYERS OYSTER LAGOON POPULATION FROM RELEASE SITES			STRAYERS SALT LAGOON POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
14	139	0	4	0	0	0	0	0	0	0
15	116	2	4	0	0	0	0	0	0	0
16	105	2	18	1	0	0	0	0	0	0
17	121	3	7	2	0	0	0	0	0	0
18	226	3	9	4	0	0	0	0	0	0
19	205	2	5	3	0	0	0	0	0	0
20	180	3	5	5	1	0	0	0	0	0
21	147	2	6	3	0	0	0	0	0	0
22	115	0	8	4	0	0	0	0	0	0
23	120	7	5	4	0	0	0	0	0	0
24	197	6	7	4	0	0	0	0	0	0
25	360	3	11	5	0	0	0	0	0	0
26	231	2	8	4	0	0	0	0	0	0
27	302	6	5	5	0	0	0	0	0	0
28	219	0	3	2	0	0	0	0	0	0
29	195	8	3	3	0	0	0	0	0	0
30	123	1	4	2	0	0	0	0	0	0
31	167	5	14	5	1	0	0	0	0	0
TOTAL RECAPTURES MAY 14 - 31		55	126	56	2	0	0	0	0	0

Appendix IVb. Record of recaptures in Paq Creek for the Reproductive Homing Experiment during June and July, 1992.

JUNE	SAMPLE SIZE of Females	HOMERS PAQ CREEK POPULATION FROM RELEASE SITES			STRAYERS OYSTER LAGOON POPULATION FROM RELEASE SITES			STRAYERS SALT LAGOON POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
1	259	2	5	11	0	0	0	0	0	0
2	362	6	18	11	0	0	0	0	0	0
3	372	10	13	19	0	0	0	0	0	0
4	414	11	11	11	0	0	0	0	0	0
5	321	7	9	8	0	0	0	0	0	0
6	226	6	6	5	0	0	0	0	0	0
7	181	5	6	5	0	0	1	0	0	0
19	289	10	11	10	0	0	0	0	0	1
20	279	9	15	16	0	0	0	0	0	0
JULY										
15	190	4	5	4	0	0	0	0	0	0
16	137	1	3	2	0	0	0	0	0	0
29	50	1	1	0	0	0	0	0	0	0
30	61	0	1	1	0	0	0	0	0	0
TOTAL RECAPTURES MAY 14 - 31		72	104	103	0	0	1	0	0	1

Appendix IVc. Record of recaptures in Paq Creek for the Reproductive Homing Experiment during August, 1992.

AUG.	SAMPLE SIZE of Females	HOMERS PAQ CREEK POPULATION FROM RELEASE SITES			STRAYERS OYSTER LAGOON POPULATION FROM RELEASE SITES			STRAYERS SALT LAGOON POPULATION FROM RELEASE SITES		
		A	B	C	A	B	C	A	B	C
2	44	0	1	3	0	0	0	0	0	0
3	39	0	0	0	0	0	0	0	0	0
5	45	0	1	1	0	0	0	0	0	0
7	25	0	1	0	0	0	0	0	0	0
9	23	0	0	0	0	0	0	0	0	0
11	24	0	0	0	0	0	0	0	0	0
13	23	1	0	0	0	0	0	0	0	0
TOTAL RECAPTURES AUGUST		1	3	4	0	0	0	0	0	0

Appendix V. Number of Oyster Lagoon fish recaptured at Oyster Lagoon (natal homers) during spring/summer 1992.

	SAMPLE SIZE	RECAPTURED # OF OYSTER LAGOON NATAL HOMERS released in		
		APR. 1991 (11000)*	AUG. 1991 (7476)*	APR. 1992 (10025)*
MARCH, 1992	1 822	1	9	-
APRIL, 1992	11 323	11	114	-
MAY, 1992	13 638	9	79	0
JUNE, 1992	23 419	34	47	61
JULY, 1992	21 852	35	10	319
AUGUST, 1992	10 679	4	1	140
TOTAL #	82 733	94	260	520

NOTE : ( )* = Total number of fish marked and released at given dates.

Appendix VI. Number of Oyster Lagoon fish recaptured at Salt Lagoon (natal strayers) during spring/summer 1992.

	SAMPLE SIZE	RECAPTURED # OF OYSTER LAGOON NATAL STRAYERS released in		
		APR. 1991 (11000)*	AUG. 1991 (7476)*	APR. 1992 (10025)*
APRIL 12th, 1992	40	0	0	0
MAY, 1992	26 889	2	19	0
JUNE, 1992	57 353	5	25	0
JULY, 1992	30 950	3	14	5
AUGUST, 1992	8 429	1	1	2
TOTAL	123 661	11	59	7

NOTE : ( )* = Total number of fish marked and released at given dates.

Appendix VII. Number of Oyster Lagoon fish recaptured at Paq Creek (natal strayers) during spring/summer 1992.

	SAMPLE SIZE	RECAPTURED # OF OYSTER LAGOON NATAL STRAYERS released in		
		APR. 1991 (11000)*	AUG. 1991 (7476)*	APR. 1992 (10025)*
APRIL 27-28, 1992	481	1	2	0
MAY, 1992	9 884	0	6	0
JUNE, 1992	4 984	0	2	0
JULY, 1992	634	0	1	0
AUGUST, 1992	268	0	0	0
TOTAL	16 221	1	11	0

NOTE : ( )* = Total number of fish marked and released at given dates.