Migration patterns of spiny dogfish (*Squalus acanthias*) in the North Pacific Ocean

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Abstract—From 1978 to 1988, approximately 71,000 spiny dogfish (*Squalus acanthias*) were tagged off the west coast of Canada. This program is the most extensive tagging study conducted for a shark species. Twelve years after the last year of tagging, recaptured tagged spiny dogfish are still being reported. As of December 2000, 2940 tagged fish (4.1%) have been recaptured. Spiny dogfish were tagged in three major areas: Strait of Georgia, west coast Vancouver Island, and northern British Columbia waters. Generally, spiny dogfish were recaptured close to their release site; however, extensive migrations (up to 7000 km) did occur. Migration rates varied across release areas. Spiny dogfish tagged in the Strait of Georgia underwent the least extensive movement; only 10–14% of the recaptures occurred outside the strait. Spiny dogfish tagged off the west coast of Vancouver Island or in northern British Columbia waters underwent more extensive movement; approximately 49–80% of the tagged spiny dogfish recaptured outside of the release areas. Spiny dogfish from all three release areas were recaptured off the west coast of United States and Alaska. Most impressive are the recaptures of tagged spiny dogfish off the coast of Japan. Over 30 spiny dogfish were recaptured near Japan, most of which originated off the west coast of Vancouver Island or from northern British Columbia waters.

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Interest in sharks, particularly the spiny dogfish (*Squalus acanthias*), is not new. Off the west coast of British Columbia dorsal spines from spiny dogfish have been found in shell midden sites dating as far back as 4000 years (Ketchen, 1986). Aside from a source of food, the skin of the spiny dogfish was used for polishing, the spines as perforation awls, and the liver oil for various domestic purposes. Dogfish even played a role culturally, for native peoples took the dogfish as a symbol of their families. More recently, commercial fisheries for spiny dogfish were dominant from the late-1800s to the mid-1900s as a source of oil for lubrication, lighting, and vitamin A, and as a source of fishmeal, in addition to or in place of fertilizer. In addition, since the mid-1970s spiny dogfish have been used exclusively as a source of food for human consumption.

Spiny dogfish biology is equally as fascinating as their cultural history. They are long lived and slow growing, attaining ages in the North Pacific in excess of 80 years, and sizes in excess of 130 cm (McFarlane and Beamish, 1987). Females in the North Pacific mature at 35 years (Saunders and McFarlane, 1993). One very unique aspect of dogfish biology is their long gestation period (fertilization to birth)—22 months (Holden, 1977)—which is longer than their closest rival for longest gestation, the Asiatic elephant (*Elephas maximus*).

Despite their unique position both economically and culturally, spiny dogfish have been the recipients of considerable disdain, from commercial and sport fishermen alike. The species has been used as a "poster child" for trash fish and has been accused of preying upon other valuable fish such as salmon, herring, and crabs, and of destroying fishing gear. Reports of dogfish being released minus their snouts, fins, and tails; of two fish being tied together (tail to tail), and other ghastly stories are common. Despite all this, spiny dogfish are ubiquitous and abundant throughout the North Pacific Ocean.

Spiny dogfish are distributed from California to Alaska, along the Aleutian chain to the Asian coast, south to Japan. Ketchen (1986) pointed out that knowledge of the movements of spiny dogfish and the interrelationships of spiny dogfish from different areas is at best incomplete. In this report, we present the results of the spiny dogfish tagging program conducted off the west coast of Canada between 1978 and 1988. To date, it is the most comprehensive tagging program for spiny dogfish or for any shark species.

Methods

Tagging occurred in three major areas off the west coast of Canada: Strait of Georgia (SOG) from Johnstone Strait through to, and including, the Juan de Fuca Strait; the west coast of Vancouver Island (WCVI); and northern British Columbia (NBC) from Queen Charlotte Sound through Hecate Strait into Dixon Entrance (Fig. 1).

One of the impediments to studying spiny dogfish movements has been the availability of a suitable, durable tag. The use of Floy anchor tags was inappropriate because dogfish placoid scales wore through the plastic. Initially (in 1978 and 1979), a Petersen disc tag was used to tag spiny dogfish in the Strait of Georgia. However, based on observed severe wounding caused by the

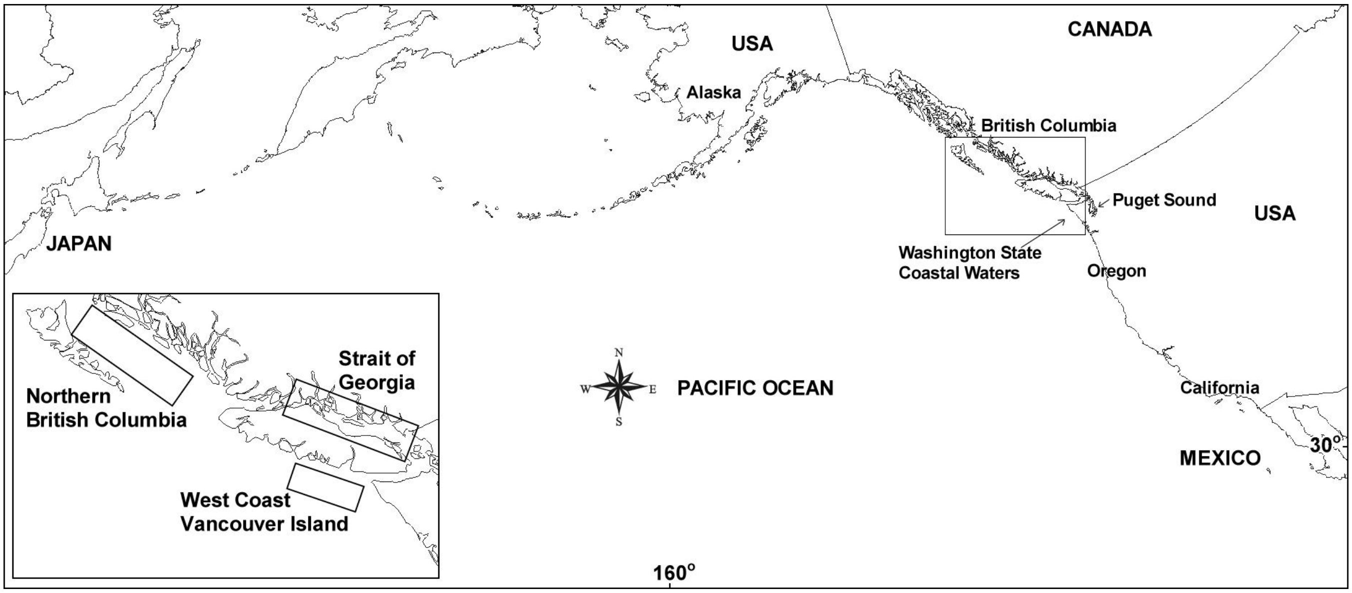

Figure 1

Tagged spiny dogfish were recaptured along the North American coast from Mexico to Alaska through to the eastern Pacific (Japan) and grouped by the areas indicated. The inset shows the west coast of Canada, and release areas for tagged spiny dogfish are denoted by rectangular boxes. Tagging occurred in the Strait of Georgia, northern British Columbia, and the west coast of Vancouver Island.

Petersen disc tag, a modified elongated tag was developed (McFarlane and Beamish, 1986). In 1979, approximately 30% of the tags deployed were modified elongated disc tags. Since then, only the modified elongated tag has been deployed. The tag consists of two elongated plastic discs with rounded ends (Fig. 2A). The application of the tag is similar to that of a Petersen disc tag (Wydoski and Emery, 1983). Each disc is attached to the fish by two pins, which are inserted through holes drilled in each disc 2.5 mm from each end. The disc is fastened to the fin of a dogfish with titanium pins made specifically for this study from grade 4, commercially pure (Ti70A) titanium wire (Fig. 2, A and B). Each pin is 7.6 cm long and 0.99 mm in diameter.

The applicator consists of a pair of hypodermic needles attached to a plexiglas handle (Fig. 2C) in a way that allows for the insertion of the pins with the exact spacing required (McFarlane and Beamish, 1986). The discs, on each side of the fish, are attached just below the anterior base of the first dorsal fin. During the tagging operation, the hypodermic needles are pushed through the base of the fin, the two pins are inserted through one disc and into the hypodermic needles, and the applicator is withdrawn, leaving the pins and disc attached to the fish. The second disc is placed over the pins and secured by bending the end of each pin 180° to form a small circle, with the free end of the pin resting under the bent portion of the pin that projected from the hole in the disc. The discs are loosely affixed and bent outwards to follow the contour of the fish. In 1988, another modification to the tag was initiated in the Strait of Georgia. A more flexible plastic was used as the tag material in one third of the tags used that year.

Barbless hooks were used to capture most fish; however, barbed hooks and bottom trawls also were used. In most cases fish were held in tanks on the vessel and only fish that appeared healthy were tagged. Fish were anaesthetized with MS 222 (tricaine methane sulfonate) prior to tagging and were measured for total length (nearest mm) from the tip of the snout to the tip of the upper lobe of the caudal fin when held in a horizontal position. Most tagged fish also were held in shipboard tanks to ensure recovery prior to release. A reward was paid for recaptured fish. Capture locations were recorded for major areas (Fig. 1). All returned fish were measured for length (nearest mm) and their sex was determined.

Movement between major areas was described as the percentage of recaptured fish originating from each release area. Because the number of fish recaptured will decline with time at liberty, we initially assessed the proportion of total fish recaptured (by release area) as a function of time at liberty to select an appropriate timeframe to use as a focus for reporting the percentage of recaptured fish.

It is important to note that these percentages do not reflect differences in fishing effort between major areas. In order to compare long-term movements between areas, it was necessary to standardize tag returns to effort, exploitation rate, or catch. Accurate effort data and estimates of exploitation rates are unavailable for the areas of tag returns. Catch (metric tons [t]) data for spiny dogfish were available for the areas in which the majority ot tagged fish were recaptured (Table 1). The use of catch to standardize recoveries between areas is valid only if population abundances are approximately equal between areas. This is true only for the Strait of Georgia and Puget Sound and west coast of Vancouver Island (Saunders, 1989; Ware and McFarlane, 1995). It is likely that the abundance off the Washington State coast is similar to that off the lower west coast of

Vancouver Island (Ketchen, 1986). For these four areas of tag recapture, annual catch (excluding discards) was used to estimate relative effort. Because catches are reported for the whole year, tag recaptures in the year of release were not standardized. We standardized tag recaptures in each area as the number of recaptured fish per 1000 t.

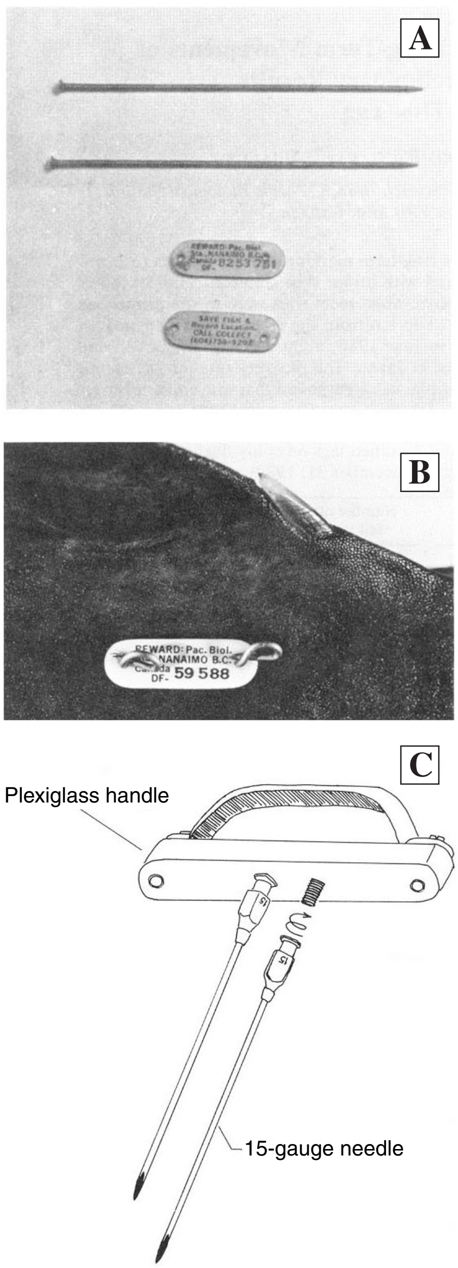

Figure 2
(**A**) Titanium pins and modified elongated disc tags developed for spiny dogfish. (**B**) Modified tag attached to spiny dogfish showing position of attachment, label of tag, and wire pins holding label in position. (**C**) Diagram of plexiglass tag applicator.

In order to elucidate differences in movement due to size at release or sex, the following categories were used: males ≤70 cm (M1); males >70 cm (M2); females ≤70 cm (F1); females 71–85 cm (F2); females ≥86 cm (F3). Size categories were based on approximate size at maturity and habitat use. Males mature at about 70 cm, which coincides with their movement from a mainly pelagic habitat to a deeper mid-water and demersal habitat. Females undergo a similar habitat change at 70 cm; however, their size at maturity is approximately 85 cm. Recoveries by the categories were then examined by area of recapture.

Results

Suitability of tag

McFarlane and Beamish (1986) reported preliminary results for the modified tag used in the present study compared to Petersen disc tags and Floy anchor tags. In contrast to the Petersen disc tag, the Floy anchor tag was quickly abraded and lost. Of 1688 fish receiving both tags, 49 were recovered from 1978 to 1982. All recovered fish had a Petersen disc tag; however only 11 fish had both tags, and 9 of these were recaptured during the first 18 months. McFarlane and Beamish also compared the modified Petersen disc tag to Petersen disc tags (McFarlane and Beamish, 1986). Petersen discs attached to spiny dogfish in 1978 and 1979 and recaptured from 1978 to 1980 were compared to modified Petersen disc tags applied from 1979 to 1982 and standardized for catch. The standardized recovery percentage (3.9%) for the modified Petersen disc tag compared to the Petersen disc tag (2.4%) was significantly higher (P=0.01).

Because the materials used in the tags were similar and none of the modified tags were returned with one pin missing, the decrease in percentage of recoveries of Petersen tags probably was due to mortality caused by tag wounds and not to disc or pin loss. For a description of the tag wounds see McFarlane and Beamish (1986). Both titanium pins remained in the tag in all recovered fish. A metallurgical stress test indicated that the pins were durable in salt water and might be expected to last more than 20 years (McFarlane and Beamish, 1986). In the present study we report that fish with the modified Petersen disc tag were recaptured with tags intact 20 years after release. After correcting for differences between years in catch (t) for tagged fish recaptured in the Strait of Georgia in 1988–90, a chi-square test on the ratios of the numbers released to the numbers returned indicated no significant level of difference in return percentages between the standard hard plastic tag and the more flexible plastic tag used in 1988 (P=0.304).

Tag return rates

Within the Strait of Georgia, tagging took place every year from 1978 to 1988 with the exception of 1986 (Table 2). Off the west coast of Vancouver Island, tagging was conducted in 1984, 1985, and 1987 (Table 2). Tagging was conducted in northern British Columbia waters in 1980, 1982, and 1987 (Table 2). In total, 70,770 fish were tagged throughout all

Table 1

Catch (in metric tons) from 1978 to 2000 of spiny dogfish (*Squalus acanthias*) for areas in which targeted fisheries operate.

Year	Strait of Georgia	West coast of Vancouver Island	Puget Sound	Washington State coastal waters
1978	2366	271	2647	42
1979	4469	303	3882	129
1980	2133	1874	3004	57
1981	781	312	1808	79
1982	1297	973	1944	38
1983	1281	596	1291	26
1984	1991	460	1445	318
1985	962	1499	971	274
1986	610	1935	746	113
1987	1247	2110	1429	984
1988	1200	3724	1396	200
1989	852	1847	1098	319
1990	820	2353	904	488
1991	667	1958	1303	853
1992	575	1426	931	1044
1993	135	111	758	1245
1994	941	876	958	1392
1995	1494	1076	929	367
1996	3019	938	818	251
1997	1584	531	214	425
1998	1831	953	115	462
1999	1062	1787	111	515
2000	610	2951	62	627

areas: 51,063 fish tagged in the Strait of Georgia, 10,087 fish tagged off the west coast of Vancouver Island, and 9620 fish tagged in northern British Columbia waters (Table 2). As of 31 December 2000, the total number of tagged fish recaptured were 2454 (4.8%) for Strait of Georgia released fish; 297 (2.9%) for the west coast of Vancouver Island fish; and 190 (2.0%) for fish in northern British Columbia waters (Table 2).

Recoveries over time

Approximately 93%, 96%, and 93% of the fish released in the Strait of Georgia, west coast of Vancouver Island, and northern British Columbia waters, respectively, were recaptured in the first 10 years at liberty (Fig. 3). Most recoveries (>70%) were made within ≤5 years after release (Fig. 3). In the Strait of Georgia, 81% were recovered ≤5 years; for the west coast of Vancouver Island 88% were recovered ≤4 years; and for northern British Columbia waters 71% were recovered ≤5 years. The maximum time at liberty was 19, 15, and 20 years for the Strait of Georgia, west coast of Vancouver Island, and northern British Columbia waters, respectively (Table 2).

Movement of tagged fish outside of release areas

Tagged spiny dogfish were recaptured throughout the North Pacific, from Japan, through Alaska, south to Mexico (Fig. 4). A large number of recaptured fish were reported from Puget Sound and Washington State coast (Table 3). For fish released in the Strait of Georgia, only three fish were recaptured outside of Canadian or Washington State waters (Table 3). For fish released in coastal waters (west coast of Vancouver Island and northern British Columbia), a large number of fish were recaptured in Japan (n=18+11) and United States waters, excluding Washington State (n=17+5). Two fish tagged off the west coast of Vancouver Island were recaptured in Mexico (Table 3).

Movement between release areas

Approximately 98% of the total number of recaptured fish were recaptured in Canadian waters or Washington State waters (coastal and Puget Sound). Because at least 70% of the recoveries occurred within the first 5 years at liberty (Fig. 3), we compared movement between release areas by examining the proportion of recaptured fish (percentage) at liberty for 5 years or less. For fish released in the Strait of Georgia, the majority (91%) were recaptured in the Strait of Georgia and another 5% off the west coast of Vancouver Island (Table 4). Only 2% were recaptured in northern British Columbia waters and 1% were recaptured in Puget Sound or in Washington State coastal waters (Table 4). For fish released off the west coast of Vancouver Island, again the majority of recaptures (62%) were in the area of release. A large percentage were recaptured in the

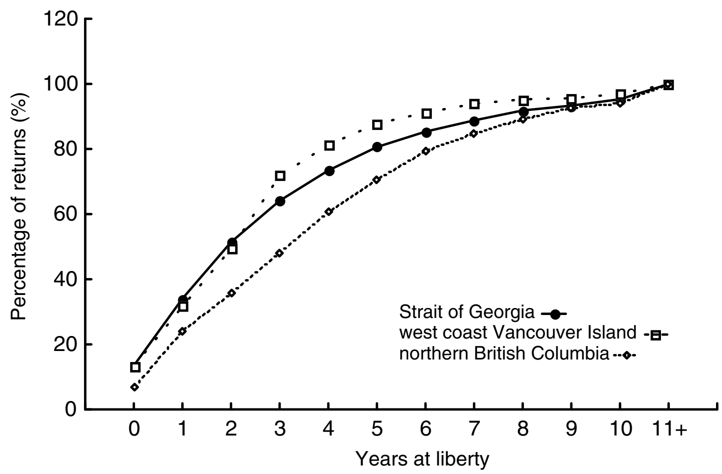

Figure 3
The cumulative percentage of recoveries standardized to catch by release area and years at liberty.

Table 2
Summary of the number of released and recaptured spiny dogfish by release year and release area.

Year of release	Released	Recaptured	Max. years at liberty
Strait of Georgia			
1978	1692	56	12
1979	4563	320	17
1980	7522	478	19
1981	7054	426	17
1982	10646	569	18
1983	1630	61	16
1984	7333	332	17
1985	4124	108	14
1987	3124	39	11
1988	3375	65	12
Total	51063	2454	
West coast of Vancouver Island			
1984	2066	77	14
1985	7124	198	15
1987	897	22	11
Total	10087	297	
Northern British Columbia			
1980	1075	34	20
1982	4873	120	16
1987	3672	36	11
Total	9620	190	

Strait of Georgia (13%) and in other areas (11%) including Japan, Alaska, Oregon, California, and Mexico (Fig. 4B). Only half of the recaptured fish from northern Bristish Columbia releases were recaptured in northern British Columbia (Table 4). Approximately 13% were recaptured in the Strait of Georgia, and another 28% off the west coast of Vancouver Island. As with west coast Vancouver Island releases, a large proportion (7%) of recaptured fish were found in other areas, namely in waters off Japan, Alaska, Oregon, and California (Fig. 4C).

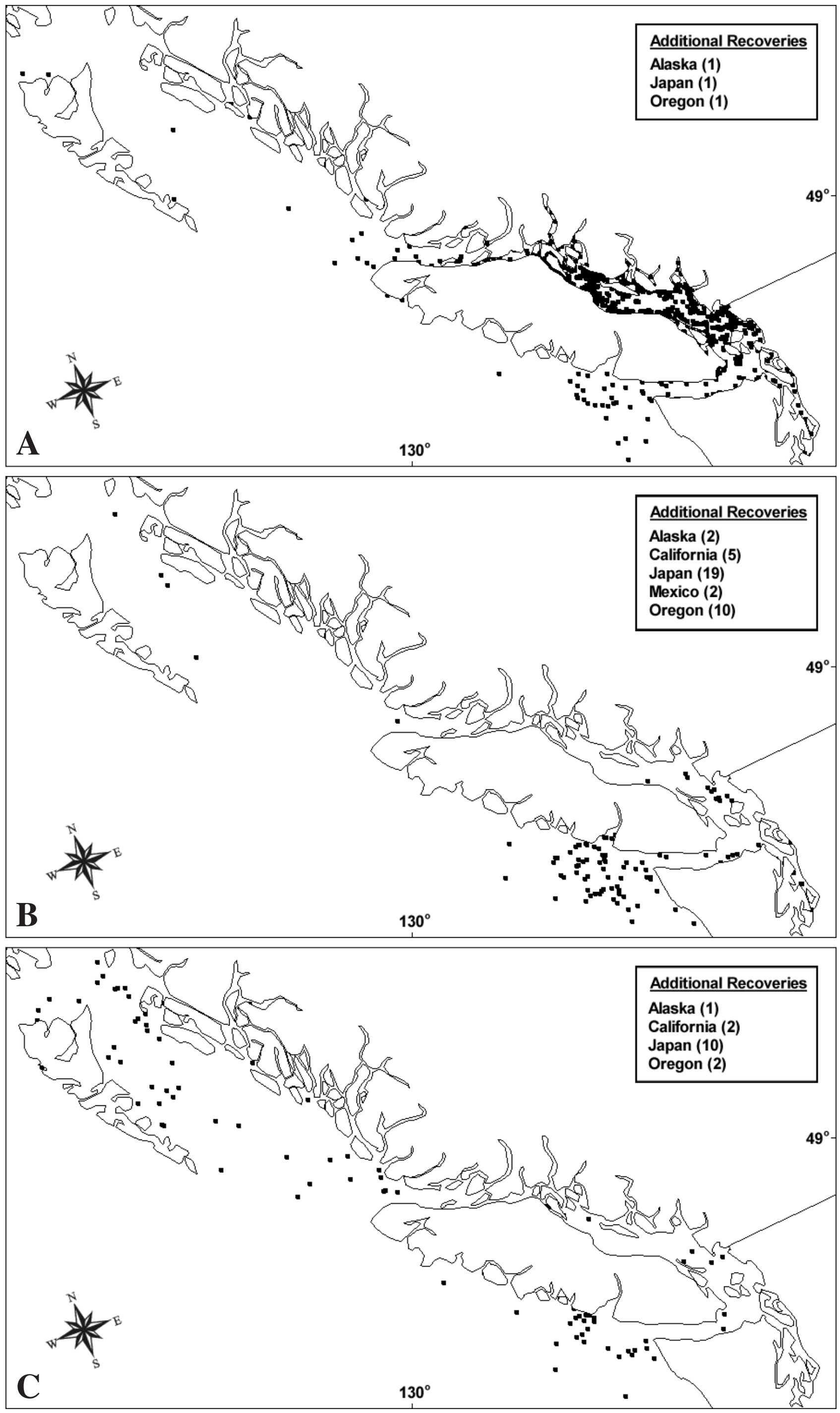

Figure 4

Recapture locations of tagged spiny dogfish released in (**A**) the Strait of Georgia; (**B**) west coast of Vancouver Island; and (**C**) northern British Columbia. The number of additional recoveries of spiny dogfish (by recapture area) that are not plotted on each figure are listed in the upper right key.

Table 3

The number of tagged dogfish recaptured from outside Canadian waters. SOG = Strait of Georgia; WCVI = west coast of Vancouver Island: NBC = northern British Columbia.

Area of release	Area of recapture							
	Japan	Alaska	Puget Sound	Washington	Oregon	California	Mexico	Total
SOG	1	1	28	18	1	0	0	49
WCVI	18	2	11	13	10	5	2	61
NBC	11	1	0	2	2	2	0	18
Total	30	4	39	33	13	7	2	128

Similar to the results for nonstandardized recoveries, the standardized recaptures for Strait of Georgia, Puget Sound, west coast of Vancouver Island, and Washington State coastal waters were based on recaptured fish at liberty for 5 years or less. For fish released in the Strait of Georgia, the majority (86%) were recaptured in the Strait of Georgia (Table 4). A further 7% were recaptured off the west coast of Vancouver Island, 6% in Washington State coastal waters, and only 1% in Puget Sound (Table 4). For fish released off the west coast of Vancouver Island, the majority of standardized recoveries (73%) occurred in Washington State coastal waters (Table 4). Only 20% were recaptured in the area of release.

Table 4

Mean percentage (%) of recaptured fish (at liberty ≤5 years) by area of release and known area of recapture including Puget Sound (PS), Washington State coastal waters (WS), and other areas. Standardized percentages could be calculated for only Strait of Georgia (SOG), west coast Vancouver Island (WCVI), Puget Sound, and Washington State coastal waters and are based on total standardized recaptures for these areas only. Standardized percentages could not be calculated for northern British Columbia (NBC).

Release area	Recapture area	Percentage of recaptures	
		Non-standardized	Standardized
SOG	SOG	91	86
	WCVI	5	7
	NBC	2	
	PS	1	1
	WS	1	6
	Other	0	
WCVI	WCVI	62	20
	SOG	13	5
	NBC	4	
	PS	5	2
	WS	5	73
	Other	11	
NBC	NBC	51	
	SOG	13	
	WCVI	28	
	PS	0	
	WS	1	
	Other	7	

Movement by sex and size

In general, small-size females (<70 cm) released in the Strait of Georgia and northern British Columbia were of the sex-size category (F1) of spiny dogfish that were recaptured in the highest proportion in other areas (Table 5). All sex-size categories of spiny dogfish (except M1, small males <70 cm) released off the west coast of Vancouver Island were recaptured in other areas in high proportions (Table 5).

Discussion

The low recovery percentage in this study is probably related to a low reporting rate. Until recently spiny dogfish catches in Canadian waters were discarded without being examined. However, this low recovery percentage also reflects the high abundance of spiny dogfish off the west coast of North America. Ketchen (1986) reported abundance estimates of 300 000 t for the whole North American coast and Saunders (1989) estimated 210,000–260,000 t in Canadian waters. It is clear that spiny dogfish are common and relatively abundant from northern Oregon to southeastern Alaska. Knowledge of the movements of spiny dogfish within eastern waters and between eastern and western waters is still limited but indicates that this shark is a key species in these coastal ecosystems. The use of the more durable modified Petersen tag in other areas would add to our knowledge of dogfish movement between these ecosystems.

Holland (1957), reporting on tagging studies conducted in the 1940s, concluded that Puget Sound and the Strait of Georgia supported indigenous populations. However, Ketchen (1986) reviewing studies by Foerster (1942), Fujioka et al. (1974), and McFarlane et al. (1982) suggested more movement between the inside populations than reported in

Table 5

Percentage (%) of tagged dogfish by size at release and sex-size category across recapture areas. (M1=males ≤70 cm; M2=males >70 cm. F1=females ≤70 cm; F2=females 71–85 cm; F3=females ≥86 cm.)

		Recapture area		
Release area	Sex-size category	Strait of Georgia	West coast Vancouver Island	Northern British Columbia
Strait of Georgia	M1	90	6	4
	M2	85	6	9
	F1	53	2	45
	F2	94	6	0
	F3	86	8	6
West coast of Vancouver Island	M1	0	100	0
	M2	37	63	0
	F1	17	61	22
	F2	0	23	77
	F3	39	50	11
Northern British Columbia	M1	0	0	100
	M2	9	9	82
	F1	9	21	70
	F2	0	6	94
	F3	6	8	86

earlier studies. Ketchen (1986) concluded that populations in inside waters (i.e. Strait of Georgia and Puget Sound) are largely independent of those off the open coast. Our study supports the idea that the majority of spiny dogfish in the Strait of Georgia remain in the Strait of Georgia. However, the low proportion of standardized recoveries in Puget Sound suggests very little movement between these two areas. In fact, a higher proportion of standardized recoveries of spiny dogfish from the Strait of Georgia were reported for coastal waters of Washington State than for Puget Sound.

Until this present study, little tagging had been conducted in open waters off the west coast of North America (Bonham et al., 1949; Holland, 1957; Ketchen, 1986). Holland (1957) observed a tendency for fish tagged off Washington and Vancouver Island to move south in the fall and winter, and north in spring and summer. The distance travelled (with a few exceptions) was generally small. Ketchen (1986) reported a similar pattern (based on seasonal fishery catches during the liver fishery of the 1940s) but noted that fishing did occur year round from northern British Columbia to Oregon. He concluded that some individuals may traverse the full commercial range of the species (Oregon to northern British Columbia) between summer and winter, but these instances are more the exception than the rule.

Seasonal movement aside, it is clear from our study that male and female spiny dogfish of all size categories in open coastal areas migrate considerably farther than previous studies suggest. For example, in the recapture areas where abundance estimates are similar and standardization to catch is possible (Strait of Georgia, Puget Sound, west coast Vancouver Island, Washington State coastal waters), the percentage of recaptures for west coast Vancouver Island releases indicates substantial movement south to Washington State coastal waters. This movement is greatly underestimated with nonstandardized data. Unfortunately it is not possible to standardize recapture data for all releases because of the paucity of fishing data or abundance estimates. Outside of Canadian waters, excluding Washington State (Puget Sound and coastal waters), there are no targeted spiny dogfish fisheries (i.e. landings are typically less than 10 t) and therefore the proportion of recaptured spiny dogfish in these areas would be expected to be small. However, it is possible to comment on the long-range movements (up to 7000 km) of these open coastal dogfish.

Tagged spiny dogfish released between 1980 and 1987 in open coastal waters (west coast of Vancouver Island and northern British Columbia) underwent extensive migrations and approximately 16% of recaptured fish came from outside Canada waters. From earlier studies, a few recaptured fish indicated that some spiny dogfish at least are highly mobile. In the early 1940s a large male dogfish tagged in northern British Columbia waters was recovered off California 171 days later (Manzer, 1946). Holland (1957) reported that a fish tagged off the west coast of Vancouver Island was recaptured off Baja California. One trans-Pacific migration (Washington State to Japan) was reported by Kauffman (1955). In our study, the 30 fish captured off Japan were all (with one exception) tagged in outside waters. These recaptures represented 6% of the recaptures from these release areas. Similarly, nine fish were captured off

California and Mexico, all from outside tag release areas. These rather remarkable recaptures do provide evidence for the trans-Pacific connection of spiny dogfish stocks but pose the question of the significance of such east to west exchanges. One possible significance would be the transfer of genetic material. The fact that these recaptures occurred regularly from 1982 to 2001 suggests ongoing migration between areas. Two recent recoveries off Japan support this hypothesis. One fish, a 69-cm female was released off the west coast of Vancouver Island in 1984, and the other, also a female (72-cm) was released in the Strait of Georgia in 1988. Both fish were recovered in May 2001 off Hokkaido. Although the evidence is limited, and the magnitude of the exchange between eastern and western Pacific stock, and indeed northern Canadian fish and those off southern California and Mexico, is small, it is clear that the interrelationships between these areas needs to be examined if ecosystem management incorporating these apex predators is to be developed.

In the eastern North Pacific, the management of spiny dogfish was recently identified as a priority by the American Fisheries Society (Musick et al., 2000). In addition, the global decline in many shark populations, and in particular spiny dogfish in the Atlantic ocean (Stevens et al., 2000), raises the question: What are the effects of the removal of large numbers of sharks (spiny dogfish) on marine ecosystems? A recent attempt (Stevens et al., 2000) to examine this question (albeit a somewhat simplistic one) identified a number of significant ecological and economic impacts. The study illustrated that under differing conditions, the consequences of depleting sharks in certain ecosystems are complex and could lead to unforeseen consequences that extend beyond the fished ecosystem. The highly migratory nature of many shark species complicates management efforts (Musick et al., 2000), and adding to the complexity are relationships between distribution, migration, and environmental conditions, such as those documented for blue, salmon, and thresher sharks in the northern Pacific (Holts, 1988; McKinnell and Seki, 1998; Bigelow et al., 1999). The development of effective ecosystem-based management hinges on understanding the implications of indirect and direct impacts on ecosystem structure and function (Fogarty and Murawski, 1998) and will require improved understanding of 1) species interactions, i.e. what, when, and where dogfish eat, and what eats dogfish, 2) migration patterns (both seasonal and long term) from and between all ecosystems within the range for dogfish (identified in this report), and 3) changes in migration and distribution in relation to changing climate and ocean conditions. To date, the effects of the removal of large numbers of spiny dogfish remain essentially unexamined, in part because of the limited information in each of these three areas.

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