

Ecosystem-level consequences of movement: seasonal variation in the trophic impact of a top predator

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ABSTRACT: Spatio-temporal patterns of species abundance influence the strength of trophic interactions, while movement of individuals helps determine those patterns of abundance. Thus, understanding movement is a basis for quantifying interactions within a food web. In Puget Sound, Washington, USA, the North Pacific spiny dogfish *Squalus suckleyi* is an abundant top predator with a diverse, generalist diet. Coastal dogfish populations make seasonal north–south migrations, but populations in inland waters are thought to be more resident. In this study, we combined acoustic telemetry and bioenergetics modeling to determine patterns of movement and to quantify seasonal variation in the predatory impact of dogfish in Puget Sound. All tagged dogfish migrated out of Puget Sound in the winter and were absent until the following summer. Individuals that returned to Puget Sound in subsequent years showed consistent timing and duration of residence across years, but these metrics varied across individuals. Incorporating movement data into the bioenergetics model resulted in a 70% decrease in the predatory impact of dogfish in the winter and a 30% decrease in the summer, compared to a year-round resident Puget Sound population. Incorporating metrics of movement into food web or ecosystem models will increase our understanding of species interactions and will improve our ability to predict changes in food web dynamics under various environmental and management scenarios.

KEY WORDS: Acoustic telemetry · Bioenergetics · Migration · Tagging · Movement · *Squalus suckleyi* · *Squalus acanthias*

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INTRODUCTION

Patterns of movement are responsible for many of the spatio-temporal trends of abundance we observe in animal populations (Turchin 1998). This is most evident in species that embark on large-scale seasonal migrations such as African ungulates (Bell 1971), anadromous salmon (Quinn 2005), migratory birds (Winker et al. 1992), and large-bodied fishes such as sharks (Williams et al. 2012) and tunas (Block et al. 2005). Movement of individuals across ecosystem and habitat boundaries is quite frequent and provides connectivity among communities and habi-

tats by linking the structure and function of varied ecosystems (Massol et al. 2011, Semmens et al. 2011). For example, migratory birds regulate insect populations, seed dispersal, and pollination processes as they move across landscapes between breeding and wintering grounds (Whelan et al. 2008, Wenny et al. 2011), while Pacific salmon *Oncorhynchus* spp. redistribute millions of kilograms of biomass and nutrients among marine, freshwater, and terrestrial ecosystems during annual migrations (Gende et al. 2002, Schindler et al. 2003).

These behavioral patterns of movement are fundamentally important to our understanding of food web

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dynamics. As individuals move between adjacent habitats, the amount of time they interact with members of each community varies directly with the amount of time they spend in various habitats. Thus, understanding patterns of movement is necessary for quantifying the strength of intra- and interspecific interactions within a food web (Basille et al. 2012). This is of particular interest for the study of top predators, which may exert control over prey populations and induce cascading effects throughout the food web when they are present (Estes et al. 1998, Pace et al. 1999, Knight et al. 2005). For example, when high abundances of Baltic cod *Gadus morhua* migrated into unoccupied habitats in the Baltic Sea, their predatory impact induced population responses in the forage fish, zooplankton, and phytoplankton communities of the region (Casini et al. 2012). The potential effects caused by the movement of upper trophic level species is why incorporating behavioral movement has been identified as one of the missing pieces in the development of 'end-to-end' ecosystem models for marine systems (Rose et al. 2010).

Quantifying behavioral movement has become more and more practical over the last 2 decades, with advances in satellite and acoustic tracking technologies (e.g. Payne et al. 2010, Block et al. 2011). Large-bodied individuals such as marine mammals and sharks are easily monitored over large spatial scales (Weng et al. 2008, Horton et al. 2011) and across multiple years (Andrews et al. 2010). Monitoring the individual movement patterns of recreationally important marine fishes (Lowe et al. 2003, Topping et al. 2005, Tolimieri et al. 2009) and even invertebrates (Holsman et al. 2006, Withy-Allen 2010, Moriarty et al. 2012) has been successful at smaller spatio-temporal scales. Incorporating behavioral movement of adults has only recently become common practice for modelers investigating the potential effects of marine spatial management tools such as marine protected areas (e.g. Moffitt et al. 2009, Grüss et al. 2011, White et al. 2011), and developers of marine ecosystem models such as Atlantis, Ecospace, GADGET, and SEAPODYM are incorporating movement and migration into model frameworks (Plagányi 2007).

In Puget Sound, Washington, USA, the North Pacific spiny dogfish *Squalus suckleyi* is an abundant upper trophic level predator (Palsson et al. 2003, Harvey et al. 2010). Mark-recapture studies have suggested that spiny dogfish along the outer coasts of the Northeast Pacific (McFarlane & King 2003, Taylor et al. 2009) and Atlantic (Rulifson et al. 2002, Stehlik 2007) oceans are highly migratory, with fish moving

north in the spring/summer and south in the autumn/winter. Inshore/offshore seasonal migrations in response to water temperature have also been observed off the US Atlantic coast (Garrison 2000). Mark-recapture studies in inland waters of Puget Sound showed that 87 and 96 % of individuals tagged in Puget Sound in the 1940s and 1970s, respectively, were recaptured in Puget Sound (Taylor et al. 2009), suggesting that this inland population is more resident than coastal populations (Holland 1957). However, recent bottom trawl sampling in Puget Sound showed that dogfish are nearly absent in the winter, while they are one of 2 dominant species in summer and autumn surveys (Reum & Essington 2011). Understanding the timing and duration of residence of a top predator population will certainly increase our understanding of interactions within the Puget Sound food web.

In this study, we integrated data on spiny dogfish movement and bioenergetics to determine how the predatory impact of spiny dogfish varied throughout the year in Puget Sound. Specifically, we used 4 yr of re-location data from acoustically tagged spiny dogfish to determine movement and residence patterns in and out of Puget Sound, including variation among and within individuals. We then used a bioenergetics model to calculate prey consumption requirements of the central Puget Sound spiny dogfish population throughout the year, comparing a null model, where spiny dogfish were year-round residents, to a model that included patterns of individual-based movement.

MATERIALS AND METHODS

Study location

Puget Sound is a fjord-like inland estuary of the eastern North Pacific Ocean in Washington State, USA (Fig. 1). Relatively shallow sills isolate the main central basin from the other sub-basins within Puget Sound, which can potentially restrict ocean circulation and the movement of organisms, sediments, and contaminants (NMFS 2007). Tides, gravitational forces, and seasonal freshwater input drive estuarine circulation in Puget Sound. Within the highly urbanized central basin, Elliott and Commencement Bays, associated with the cities of Seattle and Tacoma, respectively, have depths in excess of 100 m. The average depth of greater Puget Sound is 62.5 m at mean low tide, while the main channel is ~250 m at its greatest depth. Temperatures at depths fre-

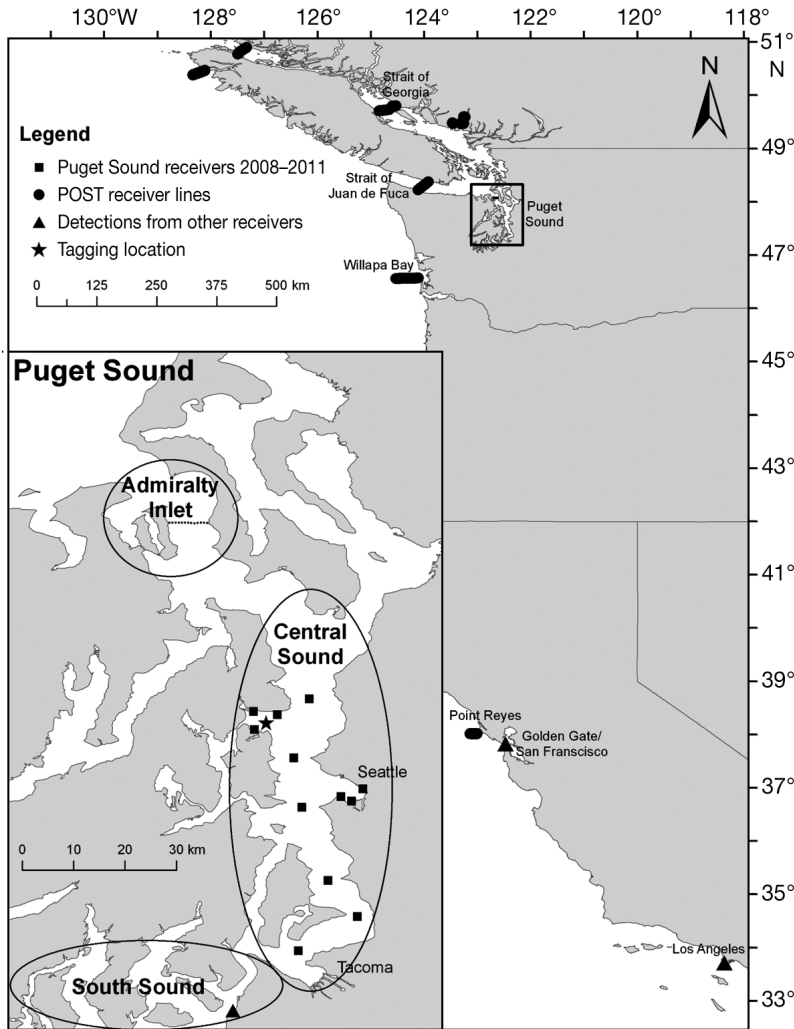


Fig. 1. Collection site in Port Madison Bay, Washington, and the location of acoustic receivers in Puget Sound and along the West Coast of the United States. POST: Pacific Ocean Shelf Tracking project

quented by spiny dogfish *Squalus suckleyi* range between 8 and 9°C in the winter and spring and between 10 and 12°C in the summer and autumn. The central basin is generally stratified in the summer, because of river discharge and solar heating, and is often well-mixed in the winter (NMFS 2007). This seasonal pattern is responsible for a peak in production of phytoplankton and macroalgae during the summer (Winter et al. 1975), which influences the abundance of consumers and predators in the pelagic and benthic communities (Strickland 1983).

Study species

Taxonomists have recently separated the North Pacific spiny dogfish *Squalus suckleyi* from the rest

of the world's spiny dogfish *S. acanthias* based on morphological, meristic, and molecular data (Ebert et al. 2010, Veríssimo et al. 2010). The North Pacific spiny dogfish ('dogfish' hereafter) is a relatively small, semi-pelagic elasmobranch inhabiting the Asian and North American rim of the North Pacific (Ebert et al. 2010). It prefers water temperatures between 7 and 15°C, making longitudinal and depth migrations to follow this temperature preference (Ebert 2003, Brodeur et al. 2009). Along the North American Pacific Coast, dogfish have a long history of exploitation (Beamish et al. 2009), and populations are hindered by slow growth, low fecundity, and late age of maturity (McFarlane & King 2003).

The benthic fish assemblage in Puget Sound is dominated by dogfish and ratfish (Palsson et al. 2003). The dogfish is the most abundant demersal piscivore in Puget Sound (Reum & Essington 2008); it represents ~5.4% of the total fish biomass and ~87% of the total biomass of consumers with a trophic level >4.0 in the central Puget Sound basin (Harvey et al. 2012). Biomass estimates of dogfish in Puget Sound have shown a decline of 82% over the past 3 decades (Palsson 2009). Dogfish are opportunistic predators on pelagic and benthic prey in Puget Sound, suggesting that they

may play an important role in the connectivity between these 2 habitats (Jones & Geen 1977a, Reum & Essington 2008). In the central Puget Sound food web, dogfish have the second-greatest keystone index, which is an estimate of their total direct and indirect trophic impacts, weighted according to their abundance (Harvey et al. 2012).

Dogfish have internal fertilization and ovoviviparous development, with gestation periods of 22 to 24 mo (Holden 1977, Jones & Geen 1977b). In Puget Sound, parturition peaks in October through November, and the average litter size is 6.9 pups (Tribuzio 2004). Dogfish have the latest known age-at-maturity (50% maturity for females at 35.5 yr) and are the longest lived of all sharks (Saunders & McFarlane 1993, Smith et al. 1998, Taylor 2008).

Collection and tagging

On September 30 and October 1, 2008, we used NOAA's 13.7 m research vessel 'Harold Streeter' to make a total of 6 standard demersal longline fishing sets (Williams et al. 2010) at depths between 60 and 80 m. We used frozen herring to bait each of 30 hooks set⁻¹, and each longline was set for approximately 2 h before retrieval. Sharks were brought onboard and placed upside down on a V-shaped, closed-cell foam surgical table with their gills irrigated with running seawater. We measured (total length with tail extended), sexed, and placed an external Floy® tag through the dorsal fin of each dogfish collected. In order to get a range of sizes and equal numbers of each sex for tracking, select individuals had a Vemco® V16P coded acoustic transmitter with pressure sensor (16 mm diameter, 98 mm length, 36 g weight in air, and 160 dB) implanted into the peritoneal cavity via a 3 cm incision made anterior of the pelvic fins along the midline. Incisions were closed with surgical staples, and sharks were returned immediately to the water (time out of water averaged 5 min). At random intervals of 40 to 114 s, each transmitter emitted a train of 'pings' at 69 kHz that contained a specific ID code allowing us to identify individuals. Data on the depth of the transmitter were contained in the train of pings every other transmission. The expected battery life of transmitters was 1429 d.

Arrays of acoustic receivers

We deployed an array of fixed automated acoustic receivers (Vemco® VR2 and VR2W) on navigational buoys or markers at 12 sites within the central basin of Puget Sound from 2008 to 2011 (Fig. 1). These receivers continuously 'listened' for and recorded the date, time, ID, and depth of acoustic transmitters throughout the duration of this study. Many other researchers use the same types of receivers; thus,

tagged dogfish were also detected by other receivers in Puget Sound and arrays of receivers along the coast of North America. Of particular note is the array of acoustic lines deployed by the Pacific Ocean Shelf Tracking project (POST; see Fig. 1). POST has deployed several lines of receivers in which the receivers are spaced approximately 800 m apart to form a 'curtain' across constriction points (e.g. Straits of Juan de Fuca and Georgia) or along the coast from ~20 m depth to the edge of the continental shelf (e.g. Willapa Bay, Washington, and Point Reyes, California). These lines of receivers allowed for nearly 100% detection probability of our transmitters as individuals moved through the straits or within range of receivers along the continental shelf. Data from acoustic receivers were used to characterize the movement patterns of dogfish in and out of Puget Sound over the 4 yr of the study.

Consumption model for spiny dogfish population

A bioenergetics simulation was run using model equations and parameter values described by Harvey (2009) in order to calculate monthly estimates of prey consumption by individual dogfish in Puget Sound. Briefly, the model followed the general form of the fish bioenergetics model, which uses a core thermodynamic equation:

$$C = R + S + F + U + \Delta B$$

where the rate of consumption (C , in units of mass or energy) is equal to the sum of the rates of respiration (R), specific dynamic action (S), egestion (F), excretion (U), and somatic growth (ΔB); the equations underlying each term are described by Kitchell et al. (1977). The model was based on a population of sharks, ages 0 to 75. We revised von Bertalanffy growth parameters and maturation schedules in Harvey (2009) to values consistent with dogfish sampled in Puget Sound in the 2000s (Table 1; Taylor &

Table 1. *Squalus suckleyi*. Demographic parameters used in the bioenergetics modeling to calculate monthly consumption of spiny dogfish in Puget Sound. For all other parameters in the bioenergetics equations, we used those stated in Harvey (2009). Sources are in respective order for information on females and males. VBGF: von Bertalanffy growth function; a: Taylor & Galucci (2009); b: Gertseva & Taylor (2011); c: Tribuzio (2004)

Parameter	Description	Females	Males	Source
L_{∞}	VBGF theoretical maximum length (cm)	109	86	a,b
k	VBGF growth parameter (yr ⁻¹)	0.0481	0.052	a,b
a	Condition parameter of length–weight relationship (g)	2.3065×10^{-3}	3.4911×10^{-3}	b
b	Curvature of length–weight relationship (g)	3.1526	3.0349	b
$L_{50\%}$	Length at 50% maturity (cm)	88.2	74.1	a,c

Gallucci 2009, Gertseva & Taylor 2011). The model used a monthly time step with monthly mean water temperatures (averaged across years 2008 to 2011; see Appendix 1) at the northern end of the central basin of Puget Sound (WDE 2011). We averaged temperatures across depths that were frequently occupied by dogfish each month in Puget Sound (K. S. Andrews unpubl. data). Size-dependent diet information from coastal populations (Jones & Geen 1977a) was used to characterize differences in prey energy density consumed by different size classes. We iteratively adjusted the feeding rate (the proportion of maximum consumption) for each size class (see P values in Harvey 2009) in order to fit the model's size-at-age estimates to those of the von Bertalanffy growth functions.

To scale these individual estimates of consumption to the population level and to calculate monthly estimates of total prey biomass consumed by the dogfish population in the central basin of Puget Sound, we used the following equation:

$$C_m = \sum_{a=0}^{75} (P_{sa} \times B \times C_{msa})$$

where P_{sa} is the proportion of individuals in each sex (s) and age class (a) based on length-frequency and sex-ratio data collected from bottom trawl surveys in the central basin of Puget Sound during 2007 (Fig. 2; Reum & Essington 2013); B is a biomass estimate of

the overall population size of dogfish in the central basin of Puget Sound ($5.254 \text{ mt km}^{-2} \times 757.08 \text{ km}^2 = 3977 \text{ mt}$ of dogfish; Reum 2006, Harvey et al. 2010); and C_{msa} is the monthly (m) consumption estimate for each sex and age class from the bioenergetics model.

Applying movement data to monthly consumption estimates

We calculated the proportion of tagged individuals detected in Puget Sound waters each month each year as:

$$P_m = \frac{D_m}{A_y}$$

where D_m is the number of individuals detected (or known to be present) in Puget Sound each month and A_y is the number of individuals detected anywhere during the year using June to May as our calendar year. For example, 10 individuals were detected from June 2009 to May 2010 (see Table 2) and 5 of those 10 were detected in Puget Sound in September 2009; thus, 50% of the population was considered present in Puget Sound in September 2009. We then calculated the mean and SD for each month across all years. This estimation assumed that the detection probability for any individual is similar across the various regions of the study. This is most important for determining whether individuals were present or absent in Puget Sound (moved across the Admiralty Inlet line) or had migrated to the outer coast (moved across the Strait of Juan de Fuca line). Because these 2 lines of receivers span the entire waterway and provided nearly 100% detection probability for the transmitters used in this study, detection of movement across these regions was most likely similar among all individuals.

We used these monthly proportions (mean and mean \pm 1 SD) to produce a model of consumption where we accounted for variation in movement patterns. First, we limited the application of the movement data to age classes (>18 for females, >28 for males) that corresponded to individuals >70 cm because we only tagged individuals ≥ 70 cm. Individuals <70 cm were assumed to remain in Puget Sound for the entire year. We then calculated the movement-adjusted

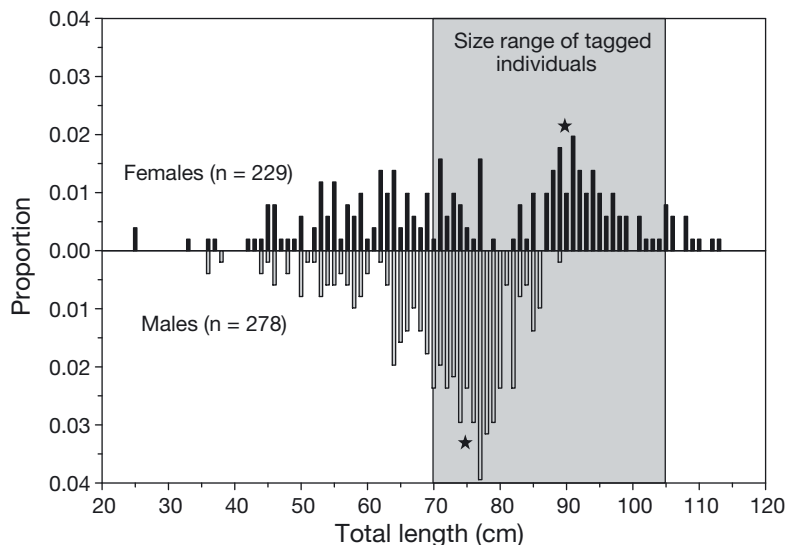


Fig. 2. *Squalus suckleyi*. Length-frequency data for females (black bars) and males (gray bars) collected in bottom trawl surveys in Puget Sound in 2007 (data from Reum & Essington 2013). Shading shows range of sizes tagged with acoustic transmitters. Stars show size at 50% maturity for each sex in Puget Sound (Tribuzio 2004)

monthly consumption for the dogfish population in the central basin of Puget Sound as:

$$C_m = \sum_{a=0}^{75} (P_{sa} \times P_m \times B \times C_{msa})$$

where P_m equals the mean (or mean \pm 1 SD) proportion of the population in Puget Sound each month for age classes ≥ 70 cm (P_m equals 1 for age classes < 70 cm). We used the same proportion (P_m) for both sexes and across all age classes ≥ 70 cm within a month.

RESULTS

Movement

We detected 14 of 17 tagged dogfish *Squalus suckleyi* at locations inside and outside Puget Sound over a 4 yr period. The 3 individuals undetected were assumed to have died shortly after tagging. Dogfish showed distinct seasonal patterns of movement into and out of Puget Sound each year (Table 2, Fig. 3). After tagging, all 14 individuals left Puget Sound and

Table 2. *Squalus suckleyi*. Biological information and monthly regional detections of acoustically tagged spiny dogfish (TL: total length, cm; M: male; F: female). Shading represents months that individuals were in Puget Sound. Letters denote geographical regions of detection (S: South Puget Sound; C: Central Puget Sound; A: Admiralty Inlet; J: Strait of Juan de Fuca; W: Willapa Bay, WA; F: San Francisco; L: Los Angeles). Months shaded without letters are those where individuals were not detected but had to be in Puget Sound. The order of regions listed within a month represents the order in which individuals moved between regions

ID	Sex	TL	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
136	M	78	2008										C	CAJ	
137	M	81	2008										C	C	J
			2009		J	J			A						
139	F	94	2008										C	A	J
			2009				W		JA	CS		S	SCA	J	
			2010						JAC	C		C	C	C	AJ
			2011	J			J		JAC				CA		
140	F	74	2008										CAJ	J	
			2009							JA	ACAJ	AJ	J		
			2010						JA	A	AC	CAJ	J		
			2011						JA	A	ACA	AJ			
141	F	96	2008										C	CAJ	
142	F	105	2008										C	SC	CAJ
			2009						F						
			2010						L						
144	F	70	2008										CAJ		
			2009				W				J	J			
145	F	83	2008										C	CAJ	
			2009						JAC			C		CAJ	
			2010						JA					CAJ	
146	F	97	2008										C	C	CAJ
147	F	87	2008										C	AJ	
151	M	82	2008										CAC	C	
			2009	C	CAJ				J	A	C		C	C	
			2010	A	J										
152	M	82	2008										C	CAC	CJ
			2009	J					JAC	C	C	C	C	C	CAJ
			2010						JAC		C	C	C	C	CAJ
			2011		J	J			JAC		C	C	C	C	CA
154	M	82	2008										CAJ		
			2009						JAC	CA		J			
			2010					J		J	J				
			2011							J	J				
155	M	79	2008										CAC	C	CAJ
			2009	W							J				

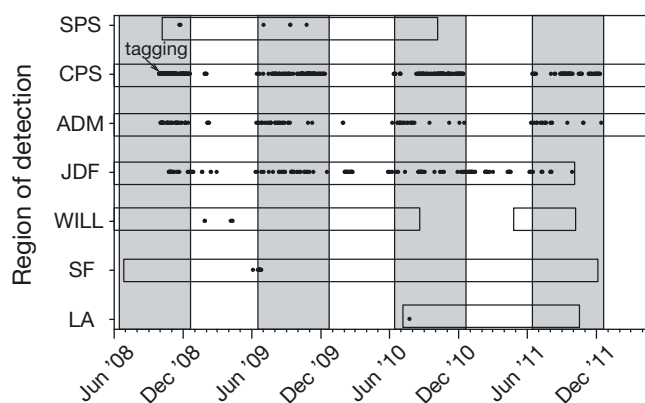


Fig. 3. *Squalus suckleyi*. Detections of all acoustically tagged spiny dogfish along the West Coast of North America. Each dot represents multiple detections of various numbers of individuals. Rectangles represent the dates receivers in each region were deployed and data uploaded during the study period. Shading approximates summer and autumn months in Puget Sound, Washington, USA. SPS: south Puget Sound; CPS: central Puget Sound; ADM: Admiralty inlet; JDF: Strait of Juan de Fuca; WILL: Willapa Bay; SF: San Francisco/Pt. Reyes; LA: Los Angeles (see Fig. 1 for geographic locations of regions)

migrated through the Strait of Juan de Fuca (JDF; Table 2). This occurred primarily in November and December, but 1 individual (No. 151) remained in Puget Sound until February before migrating through JDF. Three of the 14 were detected moving along the continental shelf at Willapa Bay, Washington (Fig. 1, Table 2): 1 in January (likely moving south) and 2 in April (likely moving north).

In 2009, 10 of the 14 individuals were detected; 9 of the 10 migrated back into inland waters through JDF beginning in June, and 7 of those 9 moved into Puget Sound (Table 2). Similar to 2008, all individuals that were detected in Puget Sound in 2009 eventually left and migrated through JDF, generally in November and December, although 1 individual (the same as in 2008) migrated through JDF in February. This pattern of distinct seasonal movement was repeated in 2010 and 2011, with fewer individuals returning each year (Table 2).

We observed individual variation in the timing and duration of months spent in Puget Sound (Table 2), but we also observed consistency in the timing and duration of residence within individuals across years. For example, No. 152 migrated through JDF, Admiralty Inlet, and into central Puget Sound in June of all 3 yr that it returned; it spent July to November in the central basin; and it then migrated out of the system and through JDF in December (Table 2)—residing approximately 7 mo in Puget Sound each year. Dogfish 140 showed similar consistency in timing of resi-

dence across years, but resided in Puget Sound for only 4 mo each year. Other dogfish (Nos. 139 & 145) were not detected as frequently inside Puget Sound, but still showed consistency in overall timing of entering and leaving Puget Sound each year.

Within Puget Sound, we observed variation in the spatial extent of movement among individuals, but within individuals, we observed consistent movement patterns across years (Fig. 4). Some individuals took very direct routes to south Puget Sound and stayed there for most of their time in Puget Sound (Fig. 4a), while others remained near the entrance to Puget Sound and made 1 relatively quick foray to the tagging location in central Puget Sound (Fig. 4b). Even the most frequently detected individual visited the same locations in Puget Sound during the same months each year (Fig. 4d). Many of the southernmost locations did not show detections after 2009 due to loss of receivers by other research groups.

The proportion of tagged individuals in Puget Sound each month varied slightly across years (Fig. 5). In general, ~60% of tagged individuals were present in Puget Sound during each month in the summer. We then observed a decline throughout the fall and winter until no individuals remained in Puget Sound after February.

Consumption by spiny dogfish population in Puget Sound

The mean temperature of Puget Sound at the mean depth of dogfish detections varied seasonally between 8 and 12°C (Table A1 in Appendix 1). We found good agreement between the age-weight relationship as determined by the bioenergetics model and the expectation based on the von Bertalanffy growth function for both sexes (Fig. A1 in Appendix 1). The feeding rates (P values; proportion of maximum consumption) across size classes of Puget Sound individuals ranged between 0.308 and 0.355 for females and 0.225 and 0.343 for males. These feeding rates were lower than those found for individuals in the California Current (Harvey 2009; range: 0.351 to 0.407). The baseline consumption model calculated the total consumption of the Puget Sound central basin population of dogfish assuming they were resident all year (Fig. 6). When we accounted for the proportion of the population actually residing in Puget Sound, based on the migrations of tagged individuals, we found that consumption rates were lower throughout the year, but especially during the winter when all tagged individuals were

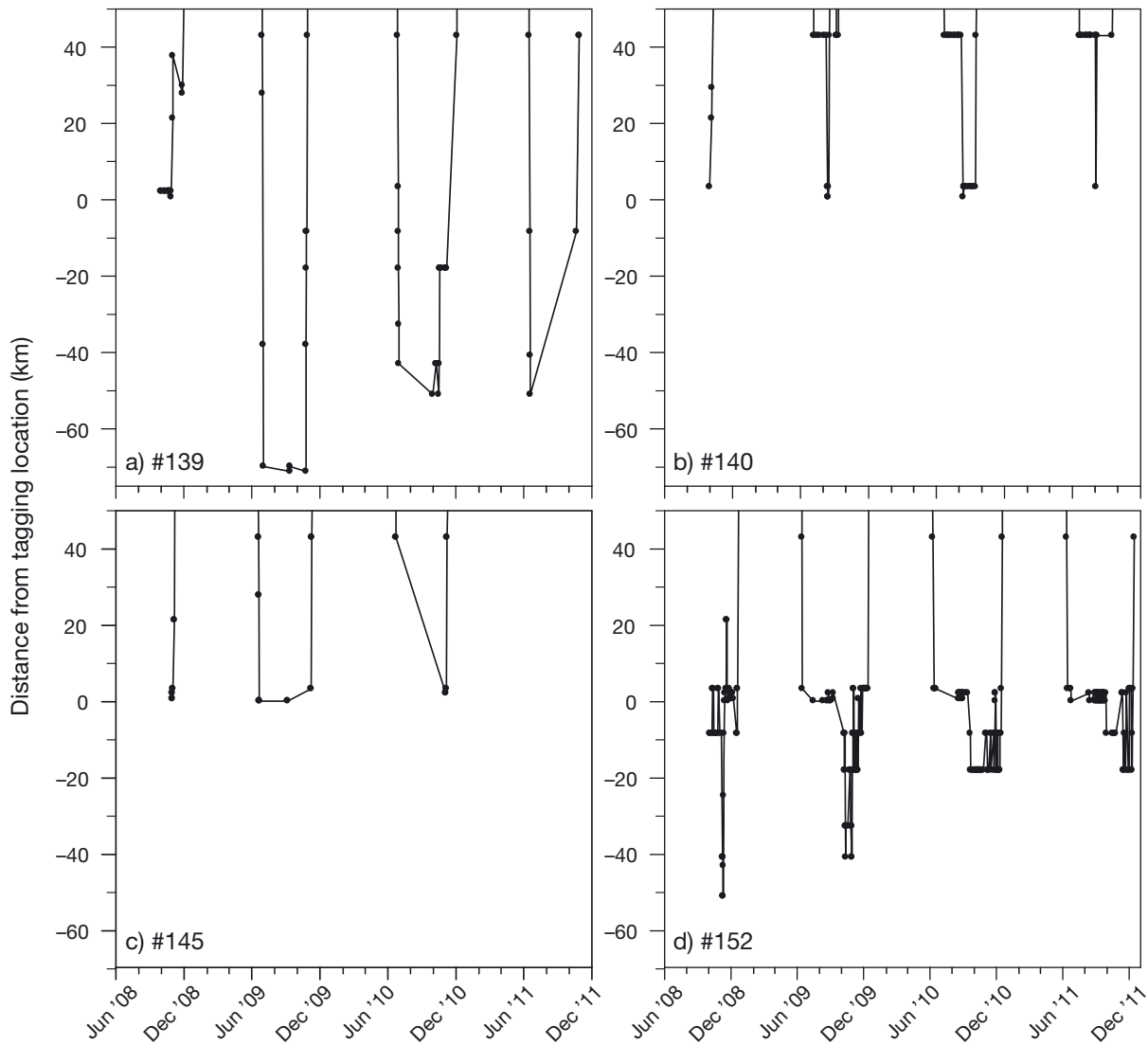


Fig. 4. *Squalus suckleyi*. Movement of different individuals (a to d) inside Puget Sound, Washington, USA. Negative values represent distances south of tagging location, while positive values represent distances north of tagging location

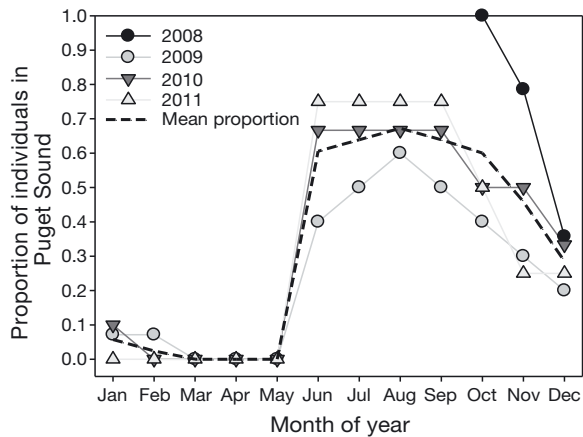


Fig. 5. *Squalus suckleyi*. Proportion of tagged spiny dogfish detected in Puget Sound from 2008 to 2011

absent (Fig. 6). This led to a 48% decrease in total Puget Sound prey consumed by spiny dogfish, and the decrease was seasonal in nature. In the summer, monthly consumption decreased by ~30% from the baseline model due to variation in the timing of arrival, the timing of departure, and the frequency of annual occurrence across individual dogfish. As dogfish gradually departed over the fall, the adjusted prey consumption decreased until winter, when total monthly prey consumption decreased by ~70% relative to the null model condition. Overwinter consumption by dogfish did not cease entirely because we conservatively assumed that <70 cm individuals remained in Puget Sound year-round.

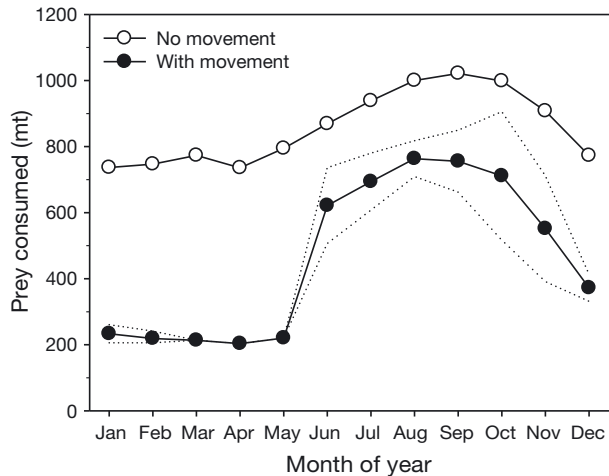


Fig. 6. *Squalus suckleyi*. Biomass of prey consumed by spiny dogfish in the central basin of Puget Sound each month when movement dynamics are included and excluded. Error bands (dotted lines) around consumption 'with movement' were calculated using ± 1 SD of the mean proportion of tagged individuals inside Puget Sound each month

DISCUSSION

General movement patterns

At the broadest scale, we found that most North Pacific spiny dogfish *Squalus suckleyi* tagged in Puget Sound made annual migrations through the Strait of Juan de Fuca to the outer coast, where they remained during winter and spring months before returning. The timing and duration of residency in Puget Sound was consistent from year to year within individuals, but varied across individuals. Local fishermen note the presence of dogfish all year, and mark-recapture studies in Puget Sound have shown that individuals are recaptured during all months of the year (Taylor et al. 2009). However, our findings are consistent with surveys of recreational catch in Puget Sound, which show that >90% of dogfish are caught in July and August, and that catch-per-unit-effort rates are an order of magnitude higher in July and August (0.05 dogfish trip⁻¹) than in all other months (0.002 dogfish trip⁻¹; D. Lowry, Washington Department of Fish & Wildlife, pers. comm.). Together, these findings suggest that a large proportion of the dogfish population emigrates from Puget Sound in the winter, while a minority remains throughout the year.

Our broad-scale findings also contrasted with mark-recapture data from nearby Canadian waters. Among spiny dogfish tagged in the Strait of Georgia, 83% (Beamish et al. 1992) and 91% (McFarlane & King 2003) of recaptures occurred in the Strait of

Georgia, leading the authors to conclude that the dogfish were resident. None of our tagged sharks were detected moving north through the line of acoustic receivers across the Strait of Georgia (see Fig. 1), and McFarlane & King (2003) observed relatively little movement of Strait of Georgia dogfish into other basins such as Puget Sound. These studies suggest limited interaction between dogfish populations in Puget Sound and the Strait of Georgia. However, mating may occur in coastal waters, where both Puget Sound (present study) and some Strait of Georgia (McFarlane & King 2003) individuals spend part of the year, which, in turn, could influence stock structure and management considerations for spiny dogfish in the inside waters of the Northeast Pacific.

Similar to the large-scale patterns, we found that movement within Puget Sound waters was consistent from year to year within individuals, which visited the same sites during the same months each year (Fig. 4). This repeating pattern suggests a certain level of philopatry or homing for dogfish that has been observed in other sharks (Bonfil et al. 2005, Edrén & Gruber 2005). However, there were stark differences in localized movements across individuals. Some moved directly to the southern reaches of Puget Sound, some were very active in the central basin, while others only frequented the north. This individual variation in movement and habitat use is noteworthy considering that all dogfish were tagged on 2 consecutive days at 1 location in the central basin. Stable isotope data from Puget Sound have shown that dogfish collected in the same trawl had more similar isotopic signatures than dogfish collected in separate tows, suggesting that individuals caught together had been feeding on similar prey items for several months (Reum 2011). On the outer coast, dogfish are often encountered in large schools (Mecklenburg et al. 2002) that may be segregated by size and sex depending on maturity level (Bigelow & Schroeder 1953). However, our acoustic data suggest that Puget Sound dogfish do not form long-term schools or aggregations. Schooling behavior in Puget Sound dogfish may be more dynamic, with individuals schooling and dispersing more rapidly as prey densities may be more limited or environmental conditions may vary on a smaller scale than in coastal waters.

Possible mechanisms underlying dogfish movement

For many species, estuaries such as Puget Sound serve as nursery grounds for young, immature individuals (Percy & Myers 1974, Heck et al. 2003,

Heupel et al. 2007). For example, immature sixgill sharks *Hexanchus griseus* are year-round residents in Puget Sound waters for several years before they leave for the outer coast (Andrews et al. 2010). For Puget Sound spiny dogfish, however, the mechanism behind migrations and residency appears to be more complex and variable than maturity level alone can explain. Coastal dogfish stocks in the Northeast Pacific are thought to mate in winter between December and February (Ketchen 1972), which corresponds to the timing of dogfish leaving Puget Sound for the outer coast. However, most of our tagged dogfish were probably immature. Based on size-maturity relationships for Puget Sound dogfish, female size at 50% maturity is 88.2 cm (Taylor & Gallucci 2009, Gertseva & Taylor 2011). All but 4 of the sharks we tagged were between 70 cm (0.7% mature) and 88 cm; yet, they all migrated out of Puget Sound in the winter. It is unclear what incentive immature dogfish might have to migrate out of Puget Sound waters for the winter. By contrast, the largest tagged female (105 cm; 91% probability of maturity) also had the most distinct migration pattern. It exited Puget Sound the first year at the same time as the rest of the individuals, but unlike the others it never returned, instead inhabiting coastal California waters in the summers of 2009 and 2010 (Table 2).

Alternatively, temperature and salinity have been shown to affect the distribution and abundance of elasmobranchs (Hopkins & Cech 2003), as well as control the timing of migration in other fishes (Quinn & Adams 1996, Sims et al. 2004). In Puget Sound, there appears to be a correlation between mean temperature and the proportion of tagged dogfish returning to Puget Sound each year (Fig. 5, Table A1). This supports the hypothesis that variations in water temperature influence the mean latitude of occurrence for coastal dogfish populations (Murawski 1993, Taylor et al. 2009). However, seasonal differences in water conditions cannot account for the different large-scale patterns we observed between mature and immature individuals. With potential increases in climate variability and ocean temperatures, it will become increasingly important to understand how migratory patterns may be affected by physical factors.

Other mechanisms, such as the distribution and abundance of prey, are likely contributing to patterns of movement. Dogfish, like many high-level trophic predators, show ontogenetic changes in their diet (Jones & Geen 1977a, Werner & Gilliam 1984, Ebert 1994). As they grow larger, larger prey items may be less abundant in Puget Sound in the winter and

necessitate leaving for coastal habitats on an annual basis; as they continue to feed on larger prey items, perhaps the largest dogfish leave Puget Sound permanently. Much work is necessary in order to evaluate the relative importance of mechanisms that may affect migration timing, but at a minimum, determining differences in movement patterns among a greater number and wider age-range of individuals for both sexes is needed.

Food web effects of dogfish migration

The behavior of predators, such as migration timing and duration of residency, can have strong effects on the behavior, health, survival, and ultimately the populations of other species with which they interact (Ritchie et al. 2012). Spiny dogfish have been identified as potential keystone predators in Puget Sound, based on their high degree of community-wide trophic impact relative to their abundance (Harvey et al. 2012). Spiny dogfish are generalist feeders preying on both pelagic and demersal prey communities, and many of their prey are also generalists (Harvey et al. 2010, 2012). Thus, there are numerous pathways for cascading effects through the food web as the abundance or consumption rates of dogfish vary in Puget Sound. However, the predatory impact of dogfish is dependent on how much time they spend foraging in each prey's habitat. Coupling the movement data with the bioenergetics model suggests that the impact of spiny dogfish predation on the Puget Sound food web is ~70% lower in the winter and ~30% lower in the summer than for a population that is resident year-long.

In developing their food web model of central Puget Sound, Harvey et al. (2010, 2012) assumed that roughly 30% of spiny dogfish feeding occurred outside of Puget Sound, based on the absence of dogfish in winter trawl samples (Reum & Essington 2011). The present study, however, indicated that a seasonally weighted average of 48% of spiny dogfish feeding occurred outside of Puget Sound, which may have a profound influence on food web simulations. For example, if spiny dogfish diets are rescaled in the Harvey et al. (2012) food web model, such that 48% of dogfish diet comes from external sources, the revised model predicts noticeable changes in a range of model outputs. For example, we ran simulations in the revised model, in which spiny dogfish biomass was either doubled or halved. Final biomass estimates of key groups such as Pacific herring *Clupea pallasii*, Pacific hake *Merluccius productus*, flat-

fishes, surf perches, small demersal fishes, crabs, shrimp, snails, and octopuses differed by >10% in the revised model relative to the original model (C. J. Harvey unpubl. data). Our study thus illustrates the importance of accounting for large-scale migrations of key species in food web models. The field and bioenergetics methods we presented here may help reduce uncertainty or bias concerning consumption and diet inputs for migratory species in ecosystem-scale models.

It has become a general conclusion of movement studies that individual variation is an important and dominant characteristic of many marine taxa (e.g. Austin et al. 2004, Egli & Babcock 2004, Tolimieri et al. 2009, Hammerschlag-Peyer & Layman 2010). Variation in the timing and duration of migration patterns among individual dogfish contributed directly to monthly variation in prey consumption in Puget Sound, and that variation could spread to other species or ecosystem processes through various ecological pathways. Thus, incorporating metrics of movement into food web or end-to-end ecosystem models will increase our understanding of species interactions and will improve our ability to predict changes in food web dynamics as individuals and communities respond to changing environmental and management scenarios.

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Appendix 1. Bioenergetics modeling specifics

For the bioenergetics modeling, we used water temperature data collected by the Washington Department of Ecology's Environmental Assessment Program (www.ecy.wa.gov/apps/eap/marinewq/mwdataset.asp?staID=63). We queried the 'Long-term marine water quality data' database for temperature data for depths from 0.5 to 213.5 m from 2008 to 2011 at the Admiralty Inlet (south) site (ADM003). For each month, we calculated the mean temperature across years using depths that were frequented by spiny dogfish in Puget Sound during each month (Table A1; K. S. Andrews unpubl. data). These mean temperature values were used in the bioenergetics modeling equations (Kitchell et al. 1977, Harvey 2009).

In order to ensure that spiny dogfish in the bioenergetics model were growing as expected, we iteratively adjusted the feeding rate (the proportion of maximum consumption) for each size class (see Harvey 2009) in order to fit the model's size-at-age estimates to those of the von Bertalanffy growth functions. For both sexes, we found good agreement between the age-weight relationship determined by the bioenergetics model and the expectation based on the von Bertalanffy growth function (Fig. A1).

Table A1. *Squalus suckleyi*. Mean temperature at the northern end of the central basin of Puget Sound using data from depths most frequently occupied by spiny dogfish detected in Puget Sound (K. S. Andrews unpubl. data). For months in which no detections were made (March to May), we used temperature data from depths frequented by dogfish in June

Month	Mean temperature (°C)	Depths frequented (m)
Jan	8.3	80–120
Feb	8.5	100–140
Mar	8.8	80–120
Apr	8.3	80–120
May	9.0	80–120
Jun	10.0	80–120
Jul	10.8	40–80
Aug	11.4	30–70
Sep	11.6	110–150
Oct	11.3	120–160
Nov	10.5	120–160
Dec	8.9	110–150

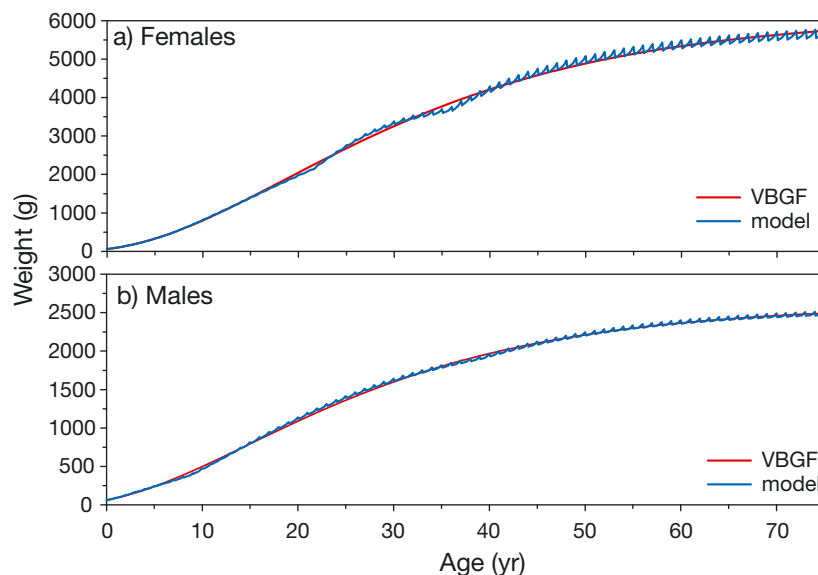


Fig. A1. *Squalus suckleyi*. Comparison of age-weight relationship between bioenergetics model and the expectation based on von Bertalanffy growth functions (VBGF) for (a) female and (b) male spiny dogfish