



Reduction in overwinter body condition and size of Pacific sand lance has implications for piscivorous predators during marine heatwaves

Clifford L. K. Robinson^{1,*}, Douglas F. Bertram^{2,3}, Hayleigh Shannon⁴,
Vanessa R. von Biela⁵, Wesley Greentree⁶, William Duguid⁶, Mayumi L. Arimitsu⁷

¹Fisheries and Oceans Canada, Pacific Biological Station, Nanaimo, British Columbia V9T 6N7, Canada

²Environment and Climate Change Canada, Institute of Ocean Sciences, Sidney, British Columbia V8L 4B2, Canada

³Center for Wildlife Ecology, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

⁴Fisheries and Oceans Canada, Institute of Ocean Sciences, Sidney, British Columbia V8L 4B2, Canada

⁵US Geological Survey, Alaska Science Center, Anchorage, Alaska 99508, USA

⁶Department of Biology, University of Victoria, Victoria, British Columbia V8P 5C2, Canada

⁷US Geological Survey, Alaska Science Center, Juneau, Alaska 99801, USA

ABSTRACT: Acute anomalous ocean warming events, including marine heatwaves (MHWs), have significant effects on reproduction and survival of piscivorous seabirds. Additionally, MHWs have negative effects on seabird fish prey, exacerbating these consequences and resulting in population implications for seabirds. We evaluated the relative body condition of Pacific sand lance *Ammodytes personatus*, an important seabird forage species, in Haro Strait, a highly productive region of southern British Columbia, Canada. We compared body condition and length of fish cohorts that experienced the 2016 MHW year (MHW cohorts) with fish hatched during 3 subsequent post MHW years (2017–2019). Age-0 MHW cohorts had a seasonal decline in body condition in age-0 fish from 100% in the summer to 81% in the winter, while age-1 fish showed a decline from summer–fall highs of 93.5% to wintertime low of 79.5%. In comparison, post MHW cohorts had a winter body condition that was 2–4 times higher than their MHW cohorts. Similar to previous studies in Alaska during the MHW, age-1 fish failed to grow and reach the typical size that distinguishes them from age-0 fish. Poor sand lance condition and growth in winter may explain the ramifications of a warming ocean for top predators, including seabirds and Pacific salmon, which depend on these prey fish in Haro Strait. Our results support the idea that Haro Strait, which is influenced by estuarine circulation resulting in cooler temperatures than surrounding areas, serves as a climate refugium for sand lance populations in summer and provides buffering capacity to ocean climate warming events.

KEY WORDS: *Ammodytes personatus* · Ocean warming · Haro Strait · Marine birds · Forage fish · Otoliths

1. INTRODUCTION

Acute anomalous ocean warming events are increasing in frequency, duration, and extent worldwide (Oliver et al. 2018), with large impacts on the basic functioning of marine ecosystems. Discrete prolonged anomalously warm water events in a par-

ticular location are known as marine heatwaves (MHWs; Hobday et al. 2016), and a multi-year Pacific MHW extended from California to Alaska, USA, from 2014 through 2016. This MHW was typified by a large mass of anomalously warm offshore water which extended into nearshore coastal waters, and coincided with the strong El Niño of 2015–2016

*Corresponding author: cliff.robinson@dfo-mpo.gc.ca

(Bond et al. 2015, Di Lorenzo & Mantua 2016). The Pacific MHW of 2014–2016 was linked to changes in the abundance, growth, survival, and distribution of many coastal species (e.g. Piatt et al. 2020, Arimitsu et al. 2021, Robinson et al. 2022). In particular, there was a disruption of energy flow through middle trophic level forage fish such as Pacific sand lance *Ammodytes personatus* that likely contributed to population declines, shifts in distribution, and breeding failures of seabirds in the Gulf of Alaska (von Biela et al. 2019, Arimitsu et al. 2021). The Pacific MHW resulted in little growth or lipid accumulation from July 2015 at age-0 to July 2016 at age-1 in Prince William Sound, Alaska, where Pacific sand lance were also 38% shorter and 13% lower in energy density compared to cooler years of 2012–2014 (von Biela et al. 2019, Arimitsu et al. 2021).

In British Columbia, Canada, poor recruitment of Pacific sand lance has been linked to warm sea surface temperatures and slower nestling growth of rhinoceros auklets *Cerorhinca monocerata* on the 3 largest colonies: Pine Island, Triangle Island, and Lucy Islands (Bertram & Kaiser 1993). Multidecadal time series on Triangle Island further quantified linkages between ocean climate variation, timing of spring bloom, Pacific sand lance recruitment, and rhinoceros auklet and tufted puffin *Fratercula cirrhata* reproductive performance (Bertram et al. 2001, Gjerdrum et al. 2003, Hedd et al. 2006). Poor nestling development and/or breeding failures were common on Triangle Island when Pacific sand lance were poorly represented in the diet, particularly during ocean warming events such as the large-scale El Niño of 1998.

Given the relative importance of Pacific sand lance to many piscivorous seabirds and other top predators like salmon *Oncorhynchus* spp. in the NE Pacific (Robards et al. 1999), it is important to understand the mechanisms of how this energy-rich forage fish responds to acute and chronic ocean warming events across its range. Unlike many forage fishes which tend to migrate between inshore spawning areas and offshore overwintering areas, Pacific sand lance are typically found in the same locations year after year because their anatomy and ecology are tied to persistent patches of habitat (Robards et al. 1999). Pacific sand lance lack a swim bladder for buoyancy, instead opting to bury in low silt sandy sediments in shallow nearshore waters (Robinson et al. 2021) to rest, minimize predation, and develop gonads in the late autumn, and for spawning in early winter (Huard et al. 2022). In summer, these fish feed in the water

column near their sandy burying habitat, returning daily to the same benthic patch (Haynes & Robinson 2011).

Due to their non-migratory life history strategy, juvenile and adult Pacific sand lance are potentially vulnerable to acute ocean climate events because they do not easily move to a new patch given the risks associated with abandoning good, uncommon burial habitat (Behrens et al. 2009). These acute ocean climate events are also likely particularly challenging for piscivorous seabirds because they impact an otherwise spatially reliable source of food, particularly during the breeding season. Overall, it is anticipated that a loss of Pacific sand lance habitat or habitat-use will occur with climate change. This is supported by observations in coastal Danish waters, where the congeneric lesser sandeel *A. tobianus* have been spatially excluded from about 8–23% of their nearshore coastal burying habitats due to occasional influxes of low-oxygen waters over the seabed. Furthermore, it was estimated that a 4°C increase in the next 100 yr, with an increase in the extent of oxygen deficient water, would result in a decrease of seabed habitat by 25 to 40% (Behrens et al. 2009).

In this study, we assessed the influence of the Pacific MHW on 2 age classes of Pacific sand lance. Fish were collected from key burying habitats in Haro Strait, British Columbia, Canada. We compared body condition (%) and body length (cm) for individuals that experienced the 2015–2016 MHW to 3 post MHW years (2017–2019). Body condition is considered a key indicator of individual- and population-level health, and fish with high relative body condition are predicted to have higher energy reserves to endure periods of low prey abundance (Gubiani et al. 2020). For breeding alcids, more energy-rich fish prey facilitates heavier bill loads, which can enhance nestling production (e.g. Wilson & Manuwal 1986, Bertram & Kaiser 1993, Hedd et al. 2006). We hypothesized that age-0 and age-1 Pacific sand lance would have lower relative body condition and smaller body lengths if they experienced the MHW, compared to the 3 subsequent cooler post MHW years.

2. MATERIALS AND METHODS

2.1. Study area

Haro Strait, in southern British Columbia (Fig. 1), is relatively shallow and tidally well-mixed throughout

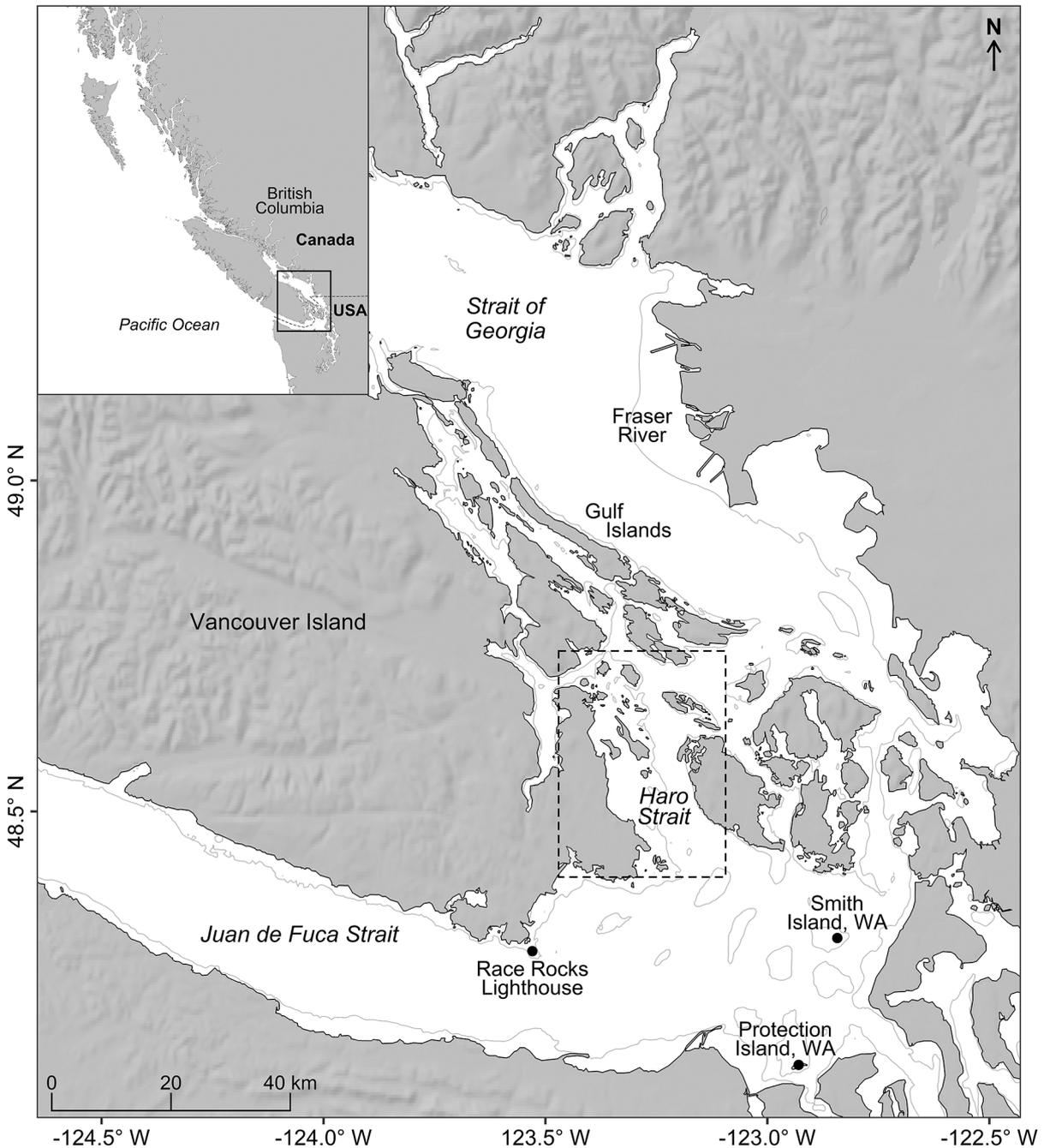


Fig. 1. Haro Strait study region located in southern British Columbia, Canada

the year, causing nutrient fluxes to remain high with associated high phytoplankton (e.g. diatom) production (Hobson & McQuoid 1997). The region also contains important and abundant Pacific sand lance burying and spawning habitats (Robinson et al. 2021, Huard et al. 2022). Furthermore, the Haro Strait region provides year-round foraging habitat for mar-

ine birds of many species (Bertram et al. 2023) and is recognized internationally, with Important Bird Areas (IBAs) established for Sidney Channel, Chain Islets, and Great Chain Island (Birds Canada 2022), in addition to 2 long-standing Migratory Bird Sanctuaries, namely Victoria Harbour and Shoal Harbour (see Bertram et al. 2023).

2.2. Heatwave days

To characterize MHWs in Haro Strait, we used the assessment methods discussed by Hobday et al. (2016, 2018) and implemented via the R package 'heatwaveR' (Schlegel & Smit 2018). Daily sea surface temperature (SST) data from Race Rocks lighthouse (Fig. 1) maintained by Fisheries and Oceans Canada (www.pac.dfo-mpo.gc.ca/science/oceans/data-donnees/lighthouses-phares/index-eng.html) were used to characterize the extent of anomalously warm oceanic conditions throughout the years 2014 to 2019. Although Pacific sand lance samples were not collected in 2014 and 2015, we identified the heatwave days for these years to provide the full context of the MHW in our study region. In addition, the age-1 Pacific sand lance collected in 2016 had hatched during the 2015 calendar year. MHW events were defined using the criteria of Hobday et al. (2016) when at least 5 consecutive days exceeded the 90th percentile of the 30 yr (1980–2010) baseline SST climatology for Race Rocks lighthouse. Once MHW events were identified, we counted days within an event and summarized them by calendar month and Pacific sand lance life history phase.

2.3. Fish collections

Pacific sand lance were collected from seabed sediments opportunistically during each year from 2016 to 2019 in the Haro Strait study area (see Fig. 2 in Robinson et al. 2021 for more details). A 15 l Van Veen benthic grab sampler was used to collect fish buried in the sediments, and at each station, any Pacific sand lance caught were placed in plastic bags, labeled (e.g. date, time, location), and frozen for later age analysis at the Institute of Ocean Sciences, Sidney, British Columbia.

To gauge the importance of Pacific sand lance to marine predators within the broader Salish Sea study region, we used independent data from the University of Victoria Adult Salmon Diet Program (W. Duguid unpubl.). This program engages recreational fishers who voluntarily submit the digestive tracts of Chinook salmon *Oncorhynchus tshawytscha* and coho salmon *O. kisutch* (Quindazzi et al. 2020). We present 2017–2021 data on the frequency of occurrence of Pacific sand lance in Chinook and coho salmon digestive tracts during the summer (April–September). The total number of salmon sampled at each site and the number of salmon containing Pacific sand lance at each site were mapped. The

Pacific sand lance samples from adult salmon diets were partially digested, so they were not used to calculate body condition as outlined below.

2.4. Pacific sand lance age and relative body condition

Otoliths were extracted from fish collected by grab sampling, dried, and examined under reflected light using a Zeiss SteREO Discovery V8 dissecting microscope. Under reflected light, translucent zones appear dark and opaque zones appear white. Translucent bands forming on the otolith edge were considered incomplete, assuming a 1 January birth date for Pacific sand lance (Dick & Warner 1982, von Biela et al. 2019). Age was assigned by counting translucent annular rings on sagittal otoliths by 2 independent readers (von Biela et al. 2019). The readers were blind to fish length to avoid bias in aging. In the event of disagreement in age assignment, readers re-examined an otolith jointly and assigned a consensus age for analysis.

Metrics of relative body condition allow for comparisons of different individuals independent of length (Wege & Anderson 1978, Froese 2006). The relative body condition factor of Pacific sand lance was calculated as the ratio of measured weight (g) of a fish at a given length (cm) to the expected weight of a fish of the same length as determined from a length–weight regression. The regression was derived from an independent data set of 331 fish collected prior to the study period (2004–2012) from the west coast of British Columbia, an area 200–300 km to the north of the Haro Strait study area (Siegle et al. 2014). The expected weight of a fish, $\log_e(\text{wt})$, was calculated using the length–weight regression from Siegle et al. (2014), whereby $\log_e(\text{wt in g}) = -6.075 + 3.222 \times \log_e(\text{length in cm})$. Relative body condition for Pacific sand lance was then reported as percent, whereby values of 100% indicated average body condition, <100% were perceived as low relative body condition for a given length of fish, and >100% indicated high body condition.

Non-parametric statistical analyses were used to determine if age-0 or age-1 Pacific sand lance body conditions differed significantly during summer, fall, and winter periods in the MHW year or in the post MHW years. Non-parametric analyses were used because of unequal sample sizes among months and years, small numbers of fish in some months, and inability to meet parametric assumptions of normality and equal variance. For age-0 Pacific sand lance, a

Kruskal-Wallis 1-way ANOVA on ranks test was performed on body condition partitioned into July/August, September/October, November, and December during the MHW year, and a second Kruskal-Wallis test on those same months for body condition collected during post MHW years. For age-1 Pacific sand lance, a Kruskal-Wallis test was conducted on body condition partitioned into April–May, July–October, and November–December for MHW cohorts and a Kruskal-Wallis test for those same months in post MHW cohorts. The MHW cohorts were hatched in 2015 and 2016 and captured as age-1 fishes in 2016 and 2017, respectively. For each non-parametric Kruskal Wallis test with a significant result, a Dunn's multiple comparison Z-value test was conducted to test which median values of pairwise comparisons were significantly different. Bonferroni test values were used to indicate significance.

A non-parametric Mann-Whitney test was also used to compare median body condition of age-0 and age-1 fish during the winter months between MHW and post MHW cohorts, while a second Mann-Whitney test was used to examine for length differences of age-0 versus age-1 Pacific sand lance caught in each study year from 2016 to 2019.

3. RESULTS

3.1. MHW days

The highest number of MHW days in a calendar year occurred in 2015 and 2016 when 45 and 47%, respectively, of the total number of calendar days met the definition of anomalously warm. The average monthly SSTs in 2015 and 2016 were as high as 1.2–1.3°C above the 30 yr long-term averages (7.8°C in winter to 11.6°C in summer). In comparison, the total number of MHW days in 2017–2019 ranged from 2 to 6% (Table 1), and their monthly average SSTs were within 0.1–0.3°C of the 30 yr long-term averages. During the gonad-development and spawning period (September to November), the MHW days ranged between 18 and 36 d during 2015–2016 compared to 0 MHW days from 2017–2019. During the larval phase (February to May), the number of MHW days ranged from 58 to 80 d during 2015–2016 com-

Table 1. Life history phases of age-0 and age-1 Pacific sand lance, and the number of marine heatwave (MHW) days detected in sea surface temperatures by month from Race Rocks Light Station, the nearest daily time series to Haro Strait, British Columbia, Canada

Month	Life history phase		MHW (d)					
	Age-0	Age-1	2014	2015	2016	2017	2018	2019
Jan	Hatching	Spawning	0	31	20	0	0	16
Feb		Spawning	0	28	29	0	0	0
Mar	Larvae		0	20	26	0	0	0
Apr			0	10	20	0	0	0
May			0	0	5	0	8	0
Jun		Foraging	0	10	0	6	0	6
July			0	12	11	1	0	0
Aug			0	15	23	8	0	0
Sep	Foraging		0	6	6	0	0	0
Oct		Maturing	13	5	4	0	0	0
Nov			28	7	26	0	0	0
Dec		Spawning	23	19	0	0	0	0
Total			64	163	170	15	8	22
Percentage			18	45	47	4	2	6

pared to 0 d from 2017 to 2019 (Table 1). The Pacific sand lance age-0 foraging phase (May to December) had a range of 74–111 MHW days in 2015–2016 but only ranged from 6 to 15 MHW days in 2017–2019. Finally, the age-1 pelagic foraging period (March to September) experienced 73–91 MHW days in 2015–2016 compared to 6–15 MHW days in 2017–2019 (Table 1).

3.2. Pacific sand lance age, body condition, and length

A total of 281 Pacific sand lance otolith and fish body measurements were made across all years. The majority of fish caught (68%) were age-0 in the year of capture (193 of 281; Table 2), and 56% (108 of 193)

Table 2. Number of age-0 and age-1 Pacific sand lance samples collected by Van Veen grabs in Haro Strait, British Columbia, Canada, during the peak marine heatwave (MHW) and post MHW years

Age class	Collection period	MHW 2016	Post MHW 2017–2019
Age-0	August	38	24
	September	28	26
	November	23	26
	December	19	9
Age-1	Apr/May	19	25
	July–Oct	8	12
	Nov/Dec	14	10
Total		149	132

Table 3. Non-parametric comparisons of Pacific sand lance body length by age class during the marine heatwave (MHW; 2016) and post MHW years (2017–2019). Significant differences ($p < 0.05$) in fish body length between the 2 age classes in a given year are indicated by an asterisk (*)

Year-age class	Number	Median length (cm)	Mann-Whitney Z-statistic	Probability
2016-0	108	7.9	1.473	0.14
2016-1	15	8.2		
2017-0	26	8.3	-3.87	<0.001*
2017-1	26	9.6		
2018-0	29	7.9	-4.168	<0.001*
2018-1	18	9.9		
2019-0	30	7.5	-4.876	<0.001*
2019-1	41	8.6		

of all age-0 fish were caught in the MHW year 2016. Age-1 fish ($n = 88$) were caught from 2016 to 2019. Age-1 fish were significantly longer than age-0 fish in each post MHW year, but lengths were not significantly different during the 2016 MHW year (Table 3, see Fig. 3).

For age-0 Pacific sand lance, and in both MHW and non-MHW years, the Kruskal-Wallis 1-way ANOVA on ranks indicated significant seasonal changes in fish body condition ($H = 62.98$, $df = 3$, $p < 0.001$; $H = 10.65$, $df = 3$, $p = 0.014$, respectively; Fig. 2A). A Dunn's multiple comparison test, using Bonferroni correction, indicated that medians were significantly different if the Z-value was >2.638 . In MHW years, the July/August body condition was significantly higher compared to November ($Z = 5.202$) and December ($Z = 6.366$), while in the post MHW period, only the July/August body condition was significantly higher than December body condition ($Z = 2.745$; Fig. 2A).

For age-1 Pacific sand lance MHW cohorts, a Kruskal-Wallis 1-way ANOVA on ranks indicated a significant seasonal change in fish body condition ($H = 18.626$, $df = 3$, $p < 0.001$); post MHW cohorts did not show a significant seasonal change in condition ($H = 4.941$, $df = 3$, $p = 0.845$; Fig. 2B). A Dunn's multiple comparison test, using Bonferroni correction, indicated which medians were significantly different if Z-values were >2.394 . During the MHW year, the April/May body condition was significantly better than November/December ($Z = 4.227$), and the July/October condition was also significantly better than November/December ($Z = 2.709$; Fig. 2B).

Age-0 winter body condition reached a lower median value during the MHW (81.2%) compared to

post MHW (2017–19; 94.9%; Mann-Whitney test, $Z = 5.28$, $p < 0.001$). Age-1 fish also showed significantly lower winter body conditions for MHW cohorts (79.5%) compared to post MHW cohorts (104.2%; Mann-Whitney test, $Z = 2.928$, $p = 0.002$).

Body length was not significantly different for age-0 and age-1 Pacific sand lance during the MHW year, with a median length of 8.2 cm for age-1 fish and 7.9 cm for age-0 fish ($Z = 1.473$ and $p = 0.14$). Age-1 fish were significantly longer than age-0 fish in each of the 3 post MHW years examined (2017–2019; see Mann-Whitney results in Table 3, Fig. 3).

Chinook salmon and coho salmon diets from the Salish Sea demonstrate the high frequency of occurrence of Pacific sand lance in salmon digestive tracts from Haro Strait in summer compared to other regions in the Strait of Georgia (Fig. 4).

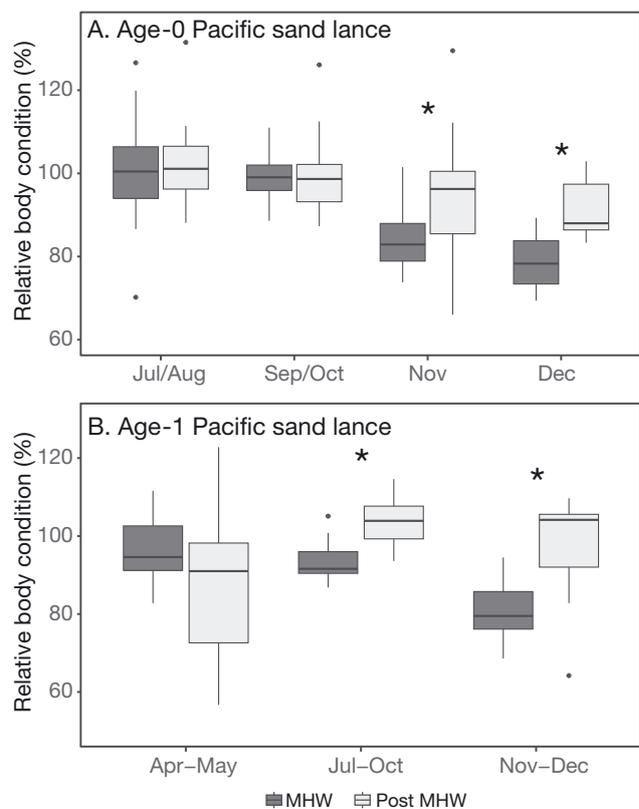


Fig. 2. Relative body condition of (A) age-0 and (B) age-1 Pacific sand lance cohorts in month of capture during the MHW (2015–2016) and post MHW (2017–2019) years. Box plots show median relative body condition as a horizontal line, the box represents the first and third quartiles, the whiskers extend to $1.5 \times$ the inter-quartile range, and points denote outliers. Significant differences ($p < 0.05$) between pairs are indicated by asterisk (*)

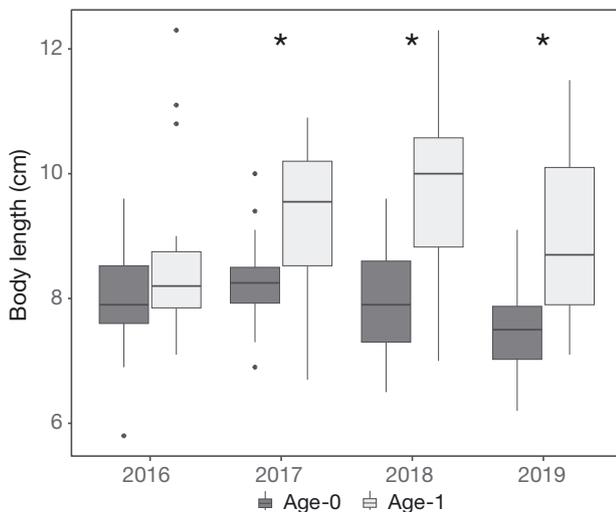


Fig. 3. Pacific sand lance standard body length (cm) by age-class for fish caught in each study year. Age-1 fish body length was not significantly different from age-0 length during the marine heatwave (MHW) in 2016, while age-1 fish lengths during post MHW years (2017, 2018, and 2019) were significantly longer than lengths of age-0 fish. Box plot parameters as in Fig. 2

4. DISCUSSION

The Pacific Marine Heatwave of 2014–2016 resulted in a noticeable increase in 2015 and 2016 water temperatures in Haro Strait in winter compared to the 3 years post MHW (2017–2019). The Pacific sand lance cohort with the strongest response to the MHW were those that hatched in 2015 and experienced the 2 strongest MHW years, 2015 at age-0 and 2016 at age-1. This cohort of fish failed to grow and improve body condition from age-0 to age-1 such that they were indistinguishable in body length from age-0 fish captured in 2016. This is consistent with the warm period from December 2015 until April 2016, which had 65% of days classed as MHW days. Our results are similar to those of von Biela et al. (2019), who found that the 2015 Pacific sand lance cohort in Prince William Sound, Alaska, USA (about 1300 km north of our study site) had the strongest MHW response with a similar failure for age-1 fish to reach longer lengths and stored lipids compared to age-0 fish. There is a seasonal difference between the 2 responses, with Prince William Sound Pacific sand lance only sampled in summer (July) near the peak of body condition and Haro Strait Pacific sand lance sampled throughout the year with the MHW influence apparent only during the winter low body condition. From a predator perspective, larger and lipid-rich Pacific sand lance were

missing for at least part of 2016 in both regions and may help explain the widespread seabird die-off and reduced reproductive success across the northeast Pacific Ocean (Piatt et al. 2020).

Individuals that experienced the 2016 MHW year as age-0 fish in Haro Strait had short-lived declines in body condition during winter 2016 and quickly returned to typical condition and size post heatwave. This seasonal decline in relative body condition was 2–4 times more pronounced during the MHW at 16–22% compared to post MHW years. The more dramatic seasonal decline in body condition during November 2016 was likely related to the 26 MHW days that were on average 1.2°C higher than the post MHW period, which would have resulted in a substantial increase in standard metabolic rate of the age-0 fish when foraging opportunities would be seasonally low. By 2017 when this cohort was age-1, individuals grew enough to distinguish themselves from age-0 fish, and age-1 fish hatched during the MHW were similar in size to fish caught in 2018 and 2019. This recovery in growth suggested that foraging conditions quickly returned to normal with cooler water temperatures. Indeed, the heatwave ended abruptly, as no days were categorized as MHW days from December 2016 to May 2017. Our results are similar to recent studies that found little interannual difference in summer length and whole-body energy in age-0 Pacific sand lance in Prince William Sound, south-central Alaska (60.7° N) (von Biela et al. 2019), and in summer body condition of age-0 fish on St. Lazaria Island, southeast Alaska (57° N; Thompson et al. 2019).

A seasonal decline in Pacific sand lance body condition from summer peaks was expected because zooplankton abundance declines from summer to early winter such that fish must draw on stored energy reserves. In a typical year, this decline appears to be smaller for age-0 Pacific sand lance compared to age-1 because the former distribute energy toward growth rather than lipid storage (Anthony et al. 2000). The congeneric sandeel *Ammodytes marinus* has the same energy allocation strategy that favors growth over storage in small fish (<95 mm) and results in the need to acquire energy from actively feeding during winter (van Deurs et al. 2011). Small Pacific sand lance (<80 mm) in Haro Strait likely feed in winter as well given that they are consumed by pelagic-feeding Chinook salmon during December (W. Greentree unpubl. data). Thus, the larger seasonal decline in body condition of age-0 fish could be related to increased metabolic demands and poor foraging conditions.

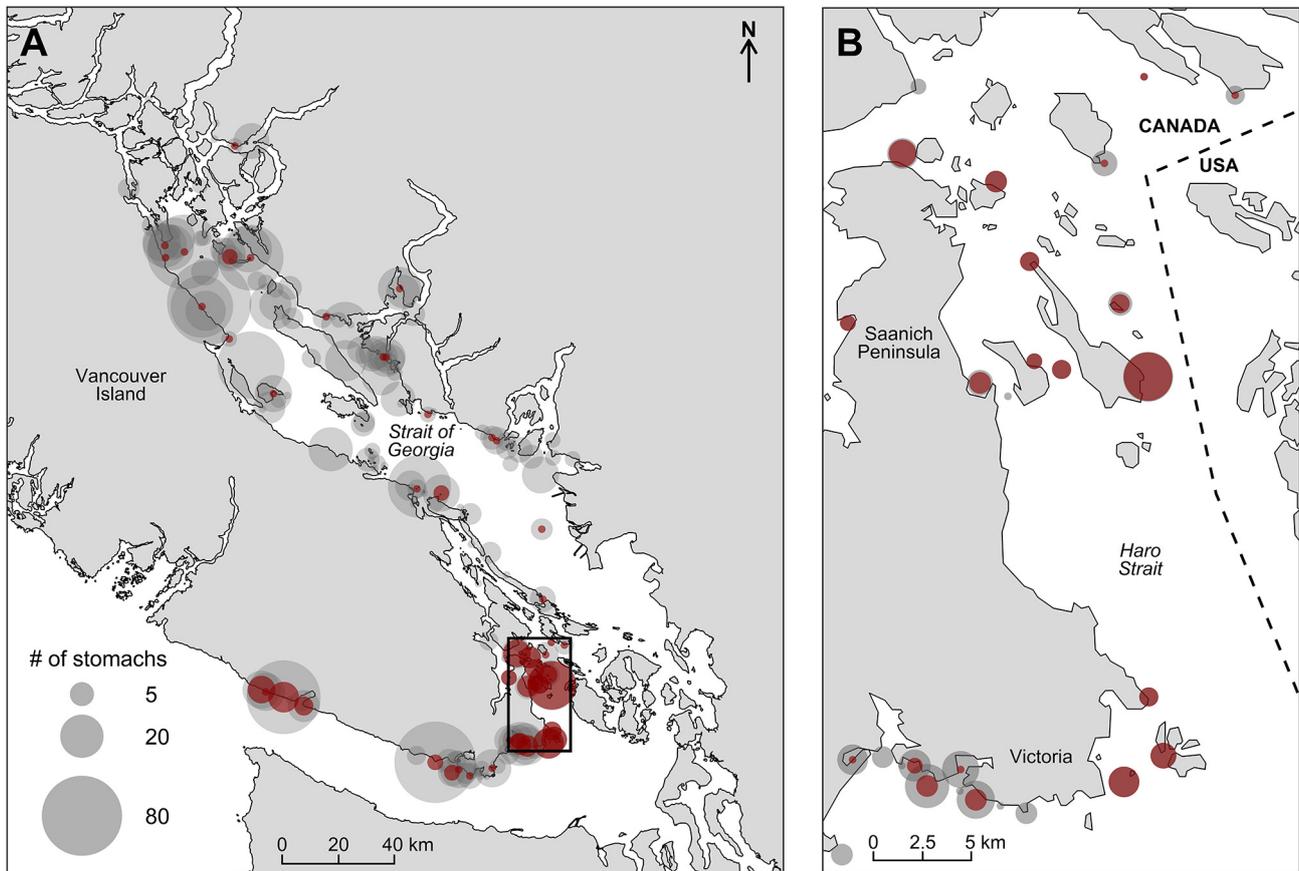


Fig. 4. Distribution of Pacific sand lance in Chinook and coho salmon digestive tracts during the summer in the (A) Strait of Georgia and (B) Haro Strait study area. The size of grey bubbles indicates the total number of salmon sampled at each site. The size of red bubbles indicates the number of salmon containing Pacific sand lance at each site. For most cases in Haro Strait, all digestive tracts sampled contained Pacific sand lance, and the grey bubble is covered by the overlaid red bubble. Data are from the adult salmon diet program (W. Greentree unpubl. data, W. Duguid unpubl.)

We also observed a seasonal decline in the relative body condition of age-1 Pacific sand lance from summer peaks to a November–December low, and this seasonal decline was more exaggerated for MHW cohorts (19–25%) compared to post MHW cohorts (4–11%). Given that peak body condition was similar for MHW and post MHW cohorts, it seems unlikely that food availability was the primary determinant of body condition difference as demonstrated for Pacific sand lance in a previous study (Robards et al. 2002). Instead, the decline in body condition for MHW cohorts of age-1 Pacific sand lance examined here was more likely related to increased winter metabolic costs from warm water temperatures rather than poor foraging conditions. Mature sandeels are known to balance increased metabolic costs of warmer temperatures by reducing gonad mass (Wright et al. 2017), and we anticipate that MHW cohorts of Haro Strait Pacific sand lance followed a similar strategy. By prioritizing estivation, a process

that can be cued by diminished fat reserves and/or warmer thermal conditions (Tomiya & Yanagibashi 2004), *Ammodytes* are able to survive periods of poor environmental conditions and rebound more quickly because they can continue to develop gonads compared to other forage fish that do not estivate.

Our study on forage fish was conducted largely within the Sidney Channel IBA of Haro Strait. In a companion study on marine birds, we conducted year-round shipboard surveys (2015–2019) and observed large numbers of piscivorous rhinoceros auklets in each year during summer, with a hotspot in the Sidney Channel IBA (Bertram et al. 2023). It is well established that the diet of rhinoceros auklet nestlings on nearby Protection Island and Smith Island (well within the foraging distance of our study site, Cunningham et al. 2018) is dominated year after year by Pacific sand lance (Wilson & Manuwal 1986, Wagner et al. 2023). In addition, breeding birds on

Protection Island appeared to be resilient to historical variation in ocean climate by showing limited response to the large 1998 ENSO, in contrast to colonies on the outer Pacific coast (Wilson 2005, Hedd et al. 2006). However, in 2016, at the peak of the Pacific MHW, bill loads on Protection Island were the lightest recorded in 14 yr of sampling (Hipfner et al. 2018). The seabird researchers reported that Pacific sand lance collected in 2016 were 30% shorter and 24% lighter than the average of the previous 7 yr (S. F. Pearson et al. unpubl. data) and consequently, reproductive performance was the poorest on record (2006 to 2020: Wagner et al. 2023). Our study results are consistent with the observations of anomalous nestling diet and low reproductive performance on Protection Island in 2016 that were part of a wider, synchronous pattern of seabird breeding failure and mortality across the northeast Pacific associated with the Pacific MHW (Piatt et al. 2020).

The magnitude and intensity of the Pacific MHW and associated biological responses appear to vary somewhat spatially, with more moderate responses in cooler and more productive areas that arise from unique oceanographic conditions (Arimitsu et al. 2021). In Haro Strait in summer, estuarine circulation contributes to cooler temperatures than the surrounding region, which appears to create a climate refugium when regional ocean temperatures rise. The Haro Strait ecosystem is highly productive and a biological hot spot, with peak diatom production occurring during summer (Hobson & McQuoid 1997), due primarily to the influence of strong tidal mixing and to strong estuarine outflow of the Fraser River. Peak River discharge occurs by the end of June, and the movement of freshwater in the top 5 m through Haro Strait towards the continental shelf on the western coast of Vancouver Island is replaced by deep cool and nutrient-rich oceanic waters from the continental shelf that flow up Juan de Fuca Canyon into Haro Strait (Thomson 1981). These cool, nutrient-rich waters are then mixed into the shallow surface waters by high tidal currents interacting with the Victoria sill and contribute to high plankton production in Haro Strait (Hobson & McQuoid 1997). Unlike much of the greater region, Haro Strait includes a substantial area of unique sand waves from glacial relic seabed sediments (Barrie et al. 2009) for Pacific sand lance to bury when not foraging in the water column (Robinson et al. 2021). Haro Strait also provides nursery areas for juvenile Pacific herring *Clupea pallasii*, which school with Pacific sand lance in summer (Bertram et al. 2023), likely reducing predation risk and perhaps conferring survival advantages

to both species. We suspect that these unique features of Haro Strait (cooler, highly productive, and burying habitat) restricted the measurable impacts of the MHW on Pacific sand lance body condition to winter, as normal condition was observed in summer 2016.

Results from other studies also reinforce Haro Strait as a unique region that provides a degree of resilience to ocean warming. A long-term study (1995–2012) estimated 6605 murrelets annually during summer surveys and identified the San Juan Islands as highly productive, and some of the most heavily used marine areas in the southern US range. In ENSO years, numbers increased to 8500 birds, suggesting that this area may provide ‘refugia marine habitat’ for murrelets when prey availability along the outer Pacific Coast is poorer than usual (Lorenz & Raphael 2018). For colonial alcids, the persistence of large breeding colonies reflects predictable prey within their foraging range (Mackas & Galbraith 1992). It follows that the rhinoceros auklet colony on Protection Island, among the world's largest (36 145 breeding pairs in 2008, Pearson et al. 2013), is supported by the Pacific sand lance refuge habitat in Haro Strait where breeding birds are known to forage (Movebank 2023, Bertram et al. 2023). Because these properties extend into the San Juan Islands, USA, it is likely the entire southern Salish Sea serves as an important refuge for Pacific sand lance and their various fish, bird, and mammal predators (e.g. Lorenz & Raphael 2018).

In addition to seabird nestling diets, the importance of Haro Strait to Pacific sand lance and fish predators is corroborated by recent diet studies of Chinook and coho Salmon (W. Duguid unpubl.). The frequency of occurrence of Pacific sand lance in summertime Chinook and coho salmon diets is far higher in Haro Strait compared to other regions of the Canadian Salish Sea. Chinook salmon support economically and culturally valuable fisheries, and are also the primary prey of the endangered Southern resident killer whale *Orcinus orca* population (Ford et al. 2010), illustrating the importance of Haro Strait to the economy and regional ecosystem.

In summary, we have described how acute ocean warming affected a key forage fish in one of the most productive regions of the northeast Pacific Ocean. Our study supports information needs related to Critical Habitat for marbled murrelet *Brachyramphus marmoratus* under Canada's Species at Risk Act (ECCC 2023) and rhinoceros auklet populations breeding on Protection Island and Smith Island (Bertram et al. 2023). Our year-round sampling highlighted the

importance of monitoring periods of seasonal low body condition in regions where productivity is high. We hypothesize that Haro Strait's high productivity and expansive burying habitat allowed Pacific sand lance to encounter adequate foraging opportunities during summer, but questions remain about winter survival. If Pacific sand lance are able to survive winters with limited resources and higher metabolic demands, Haro Strait may be able to sustain populations of Pacific sand lance, seabirds, and other predators like Chinook salmon for the foreseeable future. Continued research efforts are needed to determine if Haro Strait and the San Juan Islands serve as important climate refugia. Similar climate refugia have been identified in freshwater (Isaak et al. 2015, Mauger et al. 2017) areas with cold water and upper-elevation terrestrial (Brighenti et al. 2021) habitats with cold air and higher snow-pack or glaciers (Arimitsu et al. 2008). Across ecosystems, land resource managers often target these climate refugia for special conservation protections aimed at maintaining populations, broader ecosystem functions, and species diversity (Morelli et al. 2020).

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