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### Authors

Tunncliffe, Verena

Gasbarro, Ryan

Juanes, Francis

et al.

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Peer reviewed

**REGULAR PAPER**

# An hypoxia-tolerant flatfish: consequences of sustained stress on the slender sole *Lyopsetta exilis* (Pleuronectidae) in the context of a changing ocean

Verena Tunnicliffe<sup>1,2</sup>  | Ryan Gasbarro<sup>2,3</sup> | Francis Juanes<sup>1</sup> | Jessica Qualley<sup>1</sup> | Nicole Soderberg<sup>1</sup> | Jackson W. F. Chu<sup>1,4</sup>

<sup>1</sup>Department of Biology, University of Victoria, Victoria, British Columbia, Canada

<sup>2</sup>School of Earth & Ocean Sciences, University of Victoria, Victoria, British Columbia, Canada

<sup>3</sup>Department of Biology, Temple University, Philadelphia, Pennsylvania, USA

<sup>4</sup>Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, Newfoundland, Canada

**Correspondence**

Verena Tunnicliffe, Department of Biology, University of Victoria, PO Box 1700, Victoria, British Columbia, V8W 2Y2 Canada.  
Email: verenat@uvic.ca

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**Abstract**

Slender sole *Lyopsetta exilis* is an abundant groundfish on the continental shelf and inner waters of British Columbia, Canada, where it reaches a maximum standard length of 44 cm. Benthic image surveys coupled with oxygen measurements in Saanich Inlet document a dense population in bottom conditions near anoxia ( $0.03 \text{ ml l}^{-1}$  oxygen) where diel migrating zooplankton intersect the bottom; we confirm this species is a planktivore, which limits its depth range to the base of the migration layer. In a comparison with slender sole from a nearby well-oxygenated habitat, several probable effects of living in severe hypoxia emerge: both sexes are significantly smaller in Saanich and the sex ratio is male-skewed. Otoliths from the Saanich fish were difficult to read due to many checks, but both sexes were smaller at age with the largest female (20 cm) from the hypoxia zone registering 17 years. Hypoxia appears to have a direct consequence on growth despite good food supply in this productive basin. Hyperventilation, a low metabolic rate and a very low critical oxygen tension help this fish regulate oxygen uptake in severely hypoxic conditions; it will be particularly resilient as the incidence of hypoxia increases on the continental shelf. Data from small-mesh bottom-trawl surveys over four decades reveal an increase in mean annual catch per unit effort in southern regions of the province, including the outer shelf and the Strait of Georgia. The California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton database records a general decline in fish larvae on the Oregon–California shelf since 1990, but slender sole larvae are increasing there, as they are in the Strait of Georgia. We project that the slender sole will gain relative benefits in the future warming, deoxygenated northeast Pacific Ocean.

**KEYWORDS**

growth response, NE Pacific Ocean, otoliths, oxygen stress, population change, Saanich Inlet

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## 1 | INTRODUCTION

Deoxygenation of the global ocean in the past half century is well documented by long-term regional measurements in both ocean basins and coastal seas (Diaz & Rosenberg, 2008; Ito *et al.*, 2017; Keeling *et al.*, 2010; Whitney *et al.*, 2007). Causes include changing ocean circulation, decreasing ventilation, stronger stratification and reduced oxygen solubility in warmer water plus intensifying natural and anthropogenic eutrophication that increases microbial respiration at depth (Breitburg *et al.*, 2018; Ito *et al.*, 2017; Levin, 2018; Rabalais *et al.*, 2010). Climate-driven changes in distributions of heat, alkalinity and oxygen will have notable consequences for marine animals largely through increasing metabolic rates and oxygen demand as temperatures rise (Pörtner *et al.*, 2010; Sunday *et al.*, 2012). The effects of hypoxia and hypercapnia are linked in the ecophysiological responses at the organism level (Pörtner, 2012; Sokolova *et al.*, 2012). Because the additional stressor can also reduce metabolic and energy turnover rates (Pörtner, 2012), overall aerobic capacity is further reduced and the magnitude of response increased.

Oxygen is necessary to generate ATP thereby maintaining critical life processes, such as neurological function and to reduce the effects of acidosis generated in anaerobic metabolism (Nilsson & Östlund-Nilsson, 2008). The metabolic traits of animal species determine their ability to tolerate diminishing dissolved oxygen in the environment. In general, most water-breathing animals have a specific level of oxygen (critical oxygen tension:  $O_{2crit}$ ) below which oxygen demand exceeds the ability to regulate and supply the necessary levels of oxygen to meet aerobic requirements (Davis, 1975; Seibel, 2011). When animals are exposed to oxygen levels below their  $O_{2crit}$ , physiological impairment of standard life processes (e.g., cell growth) may occur because of the net loss in aerobic energy due to insufficient oxygen supply. Thus, standard metabolic rate, which represents the minimum oxygen requirements needed for normal life processes, is linked to environmental oxygen levels by the  $O_{2crit}$  of the species. As this physiological threshold varies greatly among species, hypoxia effects can differ among members of a community (Rabalais *et al.*, 2010). In their global analysis of  $O_{2crit}$ -based hypoxia thresholds, Chu and Gale (2017) showed that, on average, crustaceans in the northeast Pacific Ocean tolerate oxygen levels at  $0.88 \text{ ml l}^{-1}$  compared with the oft-cited level of  $1.4 \text{ ml l}^{-1}$  generated from study of mostly Atlantic Ocean species (Vaquer-Sunyer & Duarte, 2008), thus the relevant level of hypoxia differs between oceans.

Biological consequences of deoxygenation (coupled with temperature and pH changes) manifest in reduced fitness, altered behaviour, or extinction at the local population level and in wholesale shifts in distributions at the species level (Breitburg *et al.*, 2018; Deutsch *et al.*, 2015). Species range shifts result in new community structure and altered food webs (Doney *et al.*, 2011). Benthic community responses to severe hypoxia on continental shelves and coastal zones include expansion of microbial mats, emergence of infauna, migration of mobile fauna and species attrition in severe events (Levin *et al.*, 2009). Mobile finfishes can often evade deleterious hypoxia, but migration requires energy and may make them more vulnerable to predators or

fishers as they are pushed shallower (Gilly *et al.*, 2013; Stramma *et al.*, 2011). Another ecophysiological response to warming, hypoxic conditions, is reduced body size as developmental rates increase and fishes mature at smaller sizes (Sheridan & Bickford, 2011). Reduced feeding rates and growth rates in hypoxia are documented in many fish species that maintain lower oxygen requirements by processing less food (Pichavant *et al.*, 2001). The combination of species redistribution and diminishing size is causing a global-scale reduction in fish biomass (14 to 24%) and a shift away from lower latitudes (Cheung *et al.*, 2013).

Many species have high tolerance to severe hypoxia, thus may benefit as competitors and predators depart. Nematodes and annelids can be abundant sediment infauna in oxygen minimum zones (OMZ) regions exploiting accumulating organics from high surface productivity (Levin, 2003). Gallo and Levin (2016) document 77 species of demersal fishes that are recorded in the most depleted parts (often with sulphide) of OMZ although many may not spend extended periods there. Specific adaptations include low  $O_{2crit}$ , metabolic suppression, high haemoglobin affinity and increased gill surface area (Davis, 1975; Friedman *et al.*, 2012; Mandic *et al.*, 2009; Powers, 1980). In the Benguela upwelling system off Namibia, the bearded goby *Sufflogobius bibarbatus* (von Bonde 1923) is a critical component of the ecosystem, migrating daily from a deeper hypoxic zone to feed in the normoxic upper waters where it is also an important prey item for many species (Salvanes & Gibbons, 2018). It tolerates severe hypoxia and dissolved sulphides through physiological adaptations that include a very low  $O_{2crit}$ , metabolic depression and anaerobic ATP generation. Other benthic fishes have less mobility to access such regular re-oxygenation. Notable among them is the small slender sole *Lyopsetta exilis* (Jordan & Gilbert 1880) that has a similar  $O_{2crit}$  to the bearded goby (c.  $0.3 \text{ ml l}^{-1}$ ), but a lower metabolic rate (Chu & Gale, 2017).

*Lyopsetta exilis* is a right-eyed pleuronectid and the only species in the genus. As a native to the north east Pacific Ocean, the slender sole is known from the eastern Bering Sea to Baja California (Maslenikov *et al.*, 2013). While it ranges from 25 to 800 m depth, most adult occurrences are on the shelf and upper slope (AFSC, 2018). The slender sole has attracted little fisheries research attention, as it has no value as a market fish because of its small size. Nonetheless, it can be numerically abundant. On both the shelf in southern California (at 290 m; Cross (1987) and Hixon and Tissot (2007), respectively). The diet of slender sole taken off Oregon was mainly crustaceans that reflect a predominantly off-bottom feeding habit although a few benthic prey were present (Pearcy, 1978). In Saanich Inlet, on the southeast coast of Vancouver Island ( $48^{\circ} 38' \text{ N}$ ,  $123^{\circ} 30' \text{ W}$ ), Yahel *et al.* (2008) report slender sole abundances high enough to create turbid plumes of suspended sediments at the depths where they feed on diel-migrating zooplankton that intersect the bottom. Coincident with these dense fish aggregations was severely hypoxic water.

Water-column oxygen in Saanich Inlet has a well-described annual behaviour driven by deep-water renewal (Hamme *et al.*, 2015). It is a naturally eutrophic fjord (Parsons *et al.*, 1983) where plankton blooms are caused by nutrient upwelling induced by strong spring-summer tidal mixing (Gargett *et al.*, 2003). A shallow sill isolates the

212 m deep basin in which an oxygen deficit builds as the organic matter decays; in most years, anoxia is extensive below 150 m, and hydrogen sulphide evolves from the deeper sediments (Capelle *et al.*, 2018). Oxygen renewal initiates as cold, saline water entering over the sill sinks into the basin, gradually pushing upward and lifting anoxic and hypoxic water to shallower depths; this early-autumn event is linked to wider offshore upwelling and timing of neap tidal flows (Anderson & Devol, 1973; Herlinveaux, 1962). Manning *et al.* (2010) illustrate additional spring oxygen injections at mid-water depths. One consequence of the deep renewal is to compress the well-oxygenated zone and inundate much of the benthic habitat with hypoxic conditions both on steep walls (Tunncliffe, 1981) and over mud slopes (Chu & Tunncliffe, 2015a) where only a few sessile species that can withstand the conditions survive, such as brachiopods (Tunncliffe & Wilson, 1988) and certain sponges (*e.g.*, *Prosuberites saanichensis*; (Chu *et al.*, 2018)). The deep-water renewal that feeds Saanich flows through the adjacent Strait of Georgia and neighbouring channels. Johannessen *et al.* (2014) describe this phenomenon that can result in deep (300 m) oxygen levels at  $2.6 \text{ ml l}^{-1}$ , but levels never approach anoxia due to intense mixing entering the strait. Similarly, in the tidally mixed side channels of the strait, oxygen remains well above hypoxia.

A year-long camera deployment at 104 m in Saanich Inlet recorded the highest occurrences of slender sole during months of lowest oxygen ( $0.2\text{--}0.4 \text{ ml l}^{-1}$ ; Matabos *et al.*, 2012); the authors suggest a seasonal shift of the population on the mud slope coinciding with the fluctuating depth of the diel zooplankton migration that is curtailed by the near-anoxic boundary as described by Sato *et al.* (2013). Further work compiled data from over a decade of benthic transects recorded bottom imagery and associated oxygen from inlet basin to about 40 m depth to examine habitat compression as cyclical hypoxia encroached on and receded from the upper slope (Chu & Tunncliffe, 2015a). The slender sole was present in every survey and usually was the animal with deepest penetration into severe hypoxia. Chu and Gale (2017) demonstrate that slender sole can oxyregulate down to about  $0.2 \text{ ml l}^{-1}$  supported by a very low metabolic rate. As hypoxia expanded into the bay all mobile species migrated upslope resulting in overlapping depth ranges. During 2016, the most intense hypoxic incursion on record, these species suffered strong population declines, including a smaller decrease in slender sole numbers (Gasbarro *et al.*, 2019).

Our present study examines several features of this poorly known species with a primary purpose to determine whether there are evident consequences of prolonged exposure to hypoxia in the Saanich Inlet population. In that context, we test the hypothesis that fish from the hypoxic basin are smaller or grow slower than those in adjacent and broader regions of British Columbia (BC). As oxygen concentrations declined from 1979 to 2011 on the continental shelf and inner straits of southern BC (Crawford & Peña, 2013; Johannessen *et al.*, 2014), we also examine whether abundance of the slender sole has changed over time compared with other regions of the west coast. *Lyopsetta exilis* occupies one end of the hypoxia response spectrum; as there is no fishery for this species, it is a good subject to examine responses to climate-induced changes in the ocean at both the individual and the population levels.

## 2 | MATERIALS AND METHODS

Fish collection conducted by the authors was approved by the University of Victoria Animal Care Committee following guidelines of the Canadian Council on Animal Care. *Lyopsetta exilis* in Saanich Inlet was collected for this and associated studies; bycatch was very small in the hypoxic zone. Fish were killed upon collection or after studies not reported in this paper. No surgical procedures or experimental procedures were used in this work.

### 2.1 | Data and sample collection

We received data on slender sole from Fisheries and Oceans Canada (DFO) through special request to the Groundfish Biological Samples Database (GFBio; Groundfish Data Unit, Fisheries and Oceans Canada, Science Branch, Pacific Region). The groundfish survey trawl record (performed to assess stock abundance and overall groundfish composition) that we used spans 14 years from 2003 to 2016, during which time trawl gear was standardised (Table 1). Standard length ( $L_S$ ,  $\pm 0.1 \text{ cm}$ ) data were obtained for 42,166 slender sole from all fisheries management regions of British Columbia, both outer coast and near-shore waters; 97% of the fish were also sex-determined.

A second survey type used was DFO's shellfish surveys designed to catch smaller species for assessment of shrimp stocks, in which slender sole is bycatch. These trawls use a smaller mesh (Table 1) and report slender sole catch mass and trawl duration (length data are not available). Thus, we calculate catch per unit effort (CPUE,  $\text{kg h}^{-1}$ ). For years 1977–2015, we used the shellfish survey data from the north and central inner coast sections of DFO's northern shelf region (Figure 1; Fisheries & Oceans Canada, 2015a). To examine the southern shelf region and Strait of Georgia around Vancouver Island, we acquired the shrimp survey data available 2000–2015 (Fisheries & Oceans Canada, 2015b). As methods in these two survey sets differed (Table 1), the CPUE for northern and southern shelf regions are not comparable; however, the overall trends for each survey are relevant to our question. All survey data from DFO are fishery-independent. Area a (northern Hecate Strait;  $54^\circ 19' \text{ N}$ ,  $130^\circ 20' \text{ W}$ ) sees water temperatures of  $6\text{--}8^\circ \text{C}$ , salinity 31.5–33 and oxygen mostly  $>3 \text{ ml l}^{-1}$  (Crawford *et al.*, 2007) while values on the bottom near area b (Queen Charlotte Sound;  $52^\circ \text{ N}$ ,  $129^\circ \text{ W}$ ) show ranges of  $5.5\text{--}7.3^\circ \text{C}$ , salinity 33.2–34.2 and  $1.4$  to  $3.7 \text{ ml l}^{-1}$  oxygen where near-hypoxia is possible in the deeper (200 m) troughs (Whitney *et al.*, 2005). General bottom conditions in area b (Queen Charlotte Sound) are controlled by wind-driven circulation that changes seasonally with nutrient-rich water upwelling onto the shelf in late summer. Area c (west coast Vancouver Island) has experienced notable changes in ocean conditions over recent decades (Li *et al.*, 2019).

For Saanich Inlet (Figure 1), most of the fish specimens were retrieved in three trawls executed by us in 2005 and 2012; a few additional fish were available in 2013 for otolith work. The majority of fish were captured at 104 m depth. For comparison, DFO donated

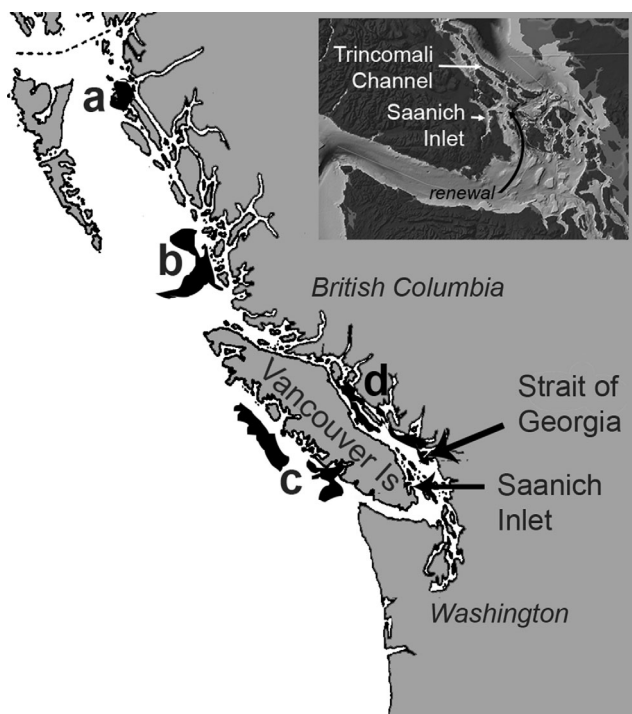
**TABLE 1** Gear type and mesh specifications for bottom trawls used and data gathered in this study of *Lyopsetta exilis*

Survey	Gear	Net mesh size	Cod-end liner mesh	Data extracted
DFO Groundfish (GF) Surveys 2003–2016	Atlantic Western IIA box trawl with Thyboron 104 Doors	127 mm	19 mm	Length
DFO Strait of Georgia GF Survey 2012 & 2015	Yankee 36 bottom trawl <sup>a</sup>	89 mm	25 mm	Length & diet
DFO Strait of Georgia GF Survey Trincomali Channel 2014	Yankee 36 bottom trawl <sup>a</sup>	89 mm	25 mm	Length & age
DFO Shellfish Survey <sup>b</sup> Northern Region: 1974–2015	18.6 m high-rise net with tickler chain	38 mm	13 mm	CPUE (kg h <sup>-1</sup> )
Southern Region 1973–2015	17.7 m high-rise otter trawl with Nordmore separator grate	38 mm	6.3 mm	
Saanich survey 2005	3 m Otter trawl	25 mm	None	Length, weight, diet
Saanich survey 2012	3.7 m Beam trawl	25 mm	None	Length, sex weight, age

Note: DFO: Department of Fisheries & Oceans, Canada.

<sup>a</sup>King *et al.* (2013) records full specifications.

<sup>b</sup>DFO Shellfish Survey areas are shown on Figure 1.



**FIGURE 1** The coast of British Columbia, Canada: the main location in which *Lyopsetta exilis* was studied, Saanich Inlet, is located on south-eastern Vancouver Island. Areas covered by Fisheries and Oceans Canada shellfish surveys in four regions are shown in black shading: a, northern shelf bioregion; b, central shelf bioregion; c, southern shelf bioregion; d, Strait of Georgia bioregion. Inset: The lower Strait of Georgia and Vancouver Island showing locations of Trincomali Channel and Saanich Inlet. —→, Direction of influx of renewal water in late summer that is mixed through Haro Strait and flushes into Saanich Inlet

160 slender sole retrieved during their 2014 groundfish survey from a site (Trincomali Channel, 48° 58.6' N, 123° 34.6' W) 30 km north of Saanich Inlet. The bottom depth is 70 m in this tidally flushed side

channel of the Strait of Georgia. Water-column information in this channel derives from conductivity–temperature–depth (CTD) casts in 2009 and 2010 where bottom oxygen values range from 4.5 to 6.0 ml l<sup>-1</sup> with temperatures 8.4 to 10.3°C. Trawl net information for all sampling is listed in Table 1.

## 2.2 | Image acquisition in Saanich Inlet

Video observations from a remotely operated vehicle (ROV) form the basis for determining slender sole distributions with depth and oxygen in Saanich Inlet. Between 2006 and 2013, we ran the same transect 10 times from 180 m to c. 40 m depth (some transects were truncated for operational reasons) into Patricia Bay (48° 39' 30" N, 123° 27' 30" W). The ROV maintained altitude as close to the bottom as possible with a bow-mounted video camera oriented forward and down; after 2007, the camera was high definition. A Sea-Bird SBE19plus (or V2) CTD with an SBE43 oxygen sensor ([www.seabird.com](http://www.seabird.com)) was mounted with the intake c. 0.5 m above bottom during transit. Details on image analysis are available in Chu and Tunnicliffe (2015a) but, in brief, with a slow, near-bottom transit, we can enumerate fish, even when mostly buried and determine distribution with respect to oxygen levels measured coincident with observation. Fish counts (individuals s<sup>-1</sup> of video) from Chu and Tunnicliffe (2015b) were summarised into 20 m<sup>2</sup> sections along individual transects and standardised to density (individuals m<sup>-2</sup>). Densities then were pooled into 11 oxygen regimes to calculate the average fish density by oxygen level. We assessed fish length from video captured by a secondary downward-looking HD camera with lasers mounted planar to the seafloor; only fish that were aligned with the lasers were used on video stop-frames from one transit in October 2013. The objective was to test that there is no effect of size on spatial distribution. As error in this method may exceed 0.5 cm and *in situ* fish may differ in length from dead fish (Chesnes, Waldner, & Krahforst, 2009), we assess results without comparison to sizes of trawled fish.

## 2.3 | Measurements

In all surveys except Trincomali,  $L_S$  ( $\pm 0.1$  cm) was measured on the landed fish. For Saanich fish, individual total mass ( $M_T$ ,  $\pm 0.01$  g) was also recorded before freezing. The Trincomali fish were first frozen shipboard. To adjust frozen to live length and mass, 60 Saanich fish were thawed, re-measured for  $L_S$  and  $M_T$  and compared with the original landed measurements; average changes were 4% for  $L_S$  and 0.4% for  $M_T$ . Trincomali data were adjusted to live  $L_S$  and  $M_T$  using these factors. After outlier analysis, a few specimens were re-measured to correct errors, then lengths of each sex were tested for differences between the sites using Kolmogorov–Smirnov tests. For  $L_S$ : $M_T$  comparison between these two sites, Saanich data from the 70 m trawl (the same depth as the Trincomali trawl) were examined separately from the Saanich 104 m trawl. We used ANCOVA to compare the  $L_S$ : $M_T$  relationship of females between sites (small sample size and larger males in Trincomali did not allow a similar comparison). For *in situ* measurements, we used Pearson correlations to test for potential relationships between  $L_S$  and both oxygen and depth using the data registered by the ROV sensors at the time a fish was imaged on the seafloor.

Sex determination was made by dissection in most cases. Testes appeared as two small, yellowish-white opaque masses on either side of the body cavity. Ovaries were much larger, bright orange to yellow longitudinal egg sacs. It was also possible to sex and stage development non-destructively using a bright light to illuminate gonads once dissection confirmed the interpretation.

## 2.4 | Otolith processing

Otoliths were extracted from sexed fish and cleaned of surrounding tissue prior to drying for 12 h. Each otolith was weighed to the nearest mg ( $\pm 0.0001$  g; Denver APEX Analytical Balance; www.denverinstrumentusa.com); for analysis, mass of both otoliths from each fish were averaged (there was no lateral bias in otolith mass). Surface areas (plan view) were calculated from images (Olympus SX16 stereomicroscope with a DP26 CCD camera; www.olympus-bioscience.com) using the ImageJ program (www.imagej.nih.gov); again, areas were averaged and mass-to-area relationships plotted for each otolith pair. We used regression models to examine fish  $L_S$  and otolith area across sites to examine whether fish size, not age, determined otolith size. To determine whether the hypoxic environment affected calcification of the otoliths as reported in other studies (Morales-Nin, 2000), we compared the mass-to-area relationship for otoliths between sites in the region of size overlap, using averages of right and left otoliths, with a Mann–Whitney  $U$ -test on de-trended residuals.

To age the fish, left otoliths were thin-sectioned first, but band interpretations were difficult and too variable between readers, especially for Saanich fish. The Sclerochronology Lab at the Pacific Biological Station recommended the break-and-burn method (Chilton & Beamish, 1982) after assessing a subset of right otoliths from both Saanich Inlet and Trincomali Channel. We completed the right otolith set at the University of Victoria. The clearest light-to-dark pattern

usually occurred along, or near, the sulcus, but if the sulcus edge was damaged, the closest readable axis from core to margin was chosen. An annulus was defined as an opaque light band paired with a translucent dark band (under reflected light) that form 1 year of growth. A growth check was identified as a dark band that merged with an adjacent dark band and was not continuous around the otolith, therefore it was excluded from the age estimate. As fish from both sites were captured late in the year, marginal light (opaque) growth was assigned to the collection year and, using the January 1st birthdate convention, estimated age was equal to the number of dark (translucent) growth zones observed. Otoliths were aged blindly, in random order. Both halves were aged in succession and a final age was determined if both halves produced the same age. If there was discrepancy between aged halves, the half with the clearest pattern was chosen as the final age. Von Bertalanffy growth curves were generated using Solver in Microsoft Excel (www.microsoft.com). All data for Saanich Inlet and Trincomali fish are provided in Supporting Information Table S1.

## 2.5 | Ichthyoplankton analysis

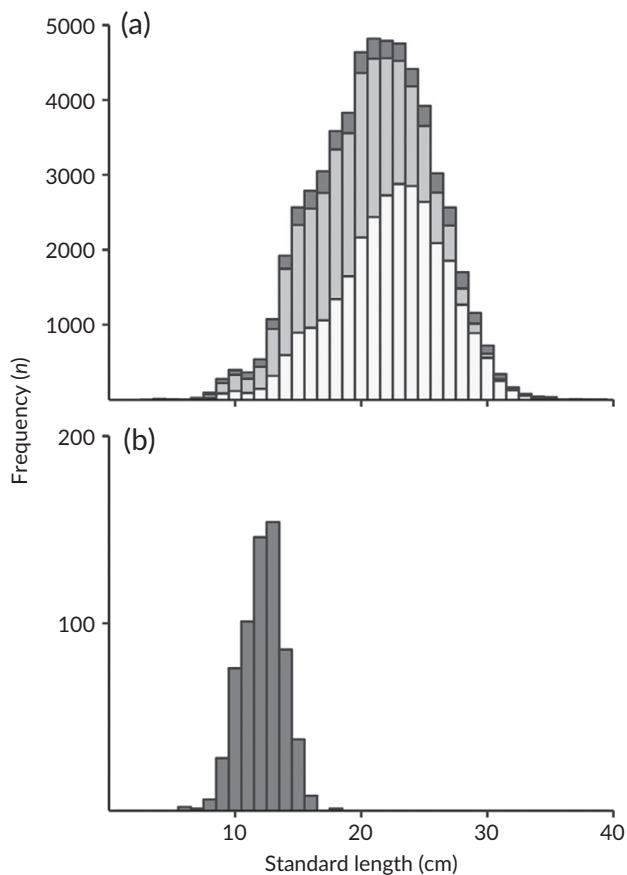
Data were drawn from the ichthyoplankton survey dataset of the California Cooperative Oceanic Fisheries Investigations (CalCOFI; www.new.data.calcofi.org) throughout the California Current System (CCS; records from Baja, Mexico to southern British Columbia); the objective was to test the prediction that the overall abundance of slender sole larvae has increased from the years 1980 to 2011 as oxygen declined in the CCS (Bograd *et al.*, 2008). The annual trend in larval slender sole abundance was compared to the trend in all ichthyoplankton species using linear regressions to test whether slender sole trends differed from those of other larval fish. Four hundred and forty nine records of slender sole and 94,853 records of total ichthyoplankton  $10\text{ m}^{-2}$  (ocean surface) comprised the full data set. Exploratory analyses revealed no significant spatial (*i.e.*, longitudinal or latitudinal) or seasonal patterns in ichthyoplankton abundances that had the potential to bias the results.

# 3 | RESULTS

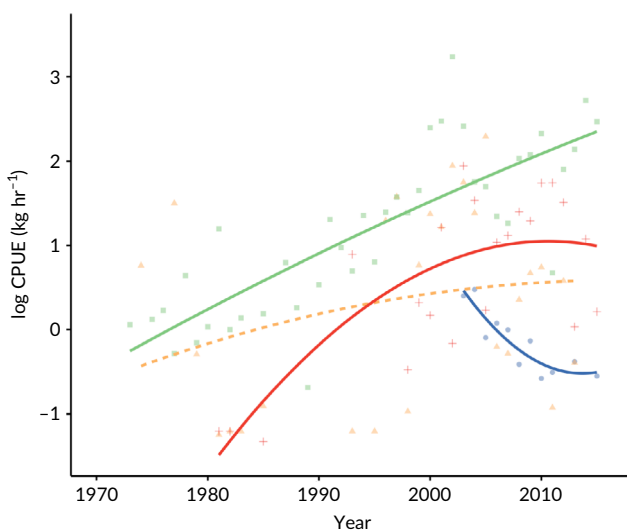
## 3.1 | Size and abundance in British Columbia

Slender sole were collected over the full depth range of the DFO Groundfish Surveys: 25 to 420 m. The size structure (standard length) of >42,000 *Lyopsetta exilis* retrieved over 14 years along the coast is shown in Figure 2a. The largest fish recorded was 41.0 cm while female mean length was 22.0 cm and male was 19.2 cm (both  $\pm 0.02$  cm SE); females were significantly longer than males (Welch's  $t = 76$ ,  $P < 0.01$ ). Sex ratio was female-biased to 1.22.

The DFO small-mesh shellfish survey data were more likely to include the smaller end of the size range of slender sole and thus a good estimate of mean annual CPUE over four decades (Figure 3). CPUE ( $\text{kg h}^{-1}$ ) for slender sole (see Figure 1 for locations) decreases in



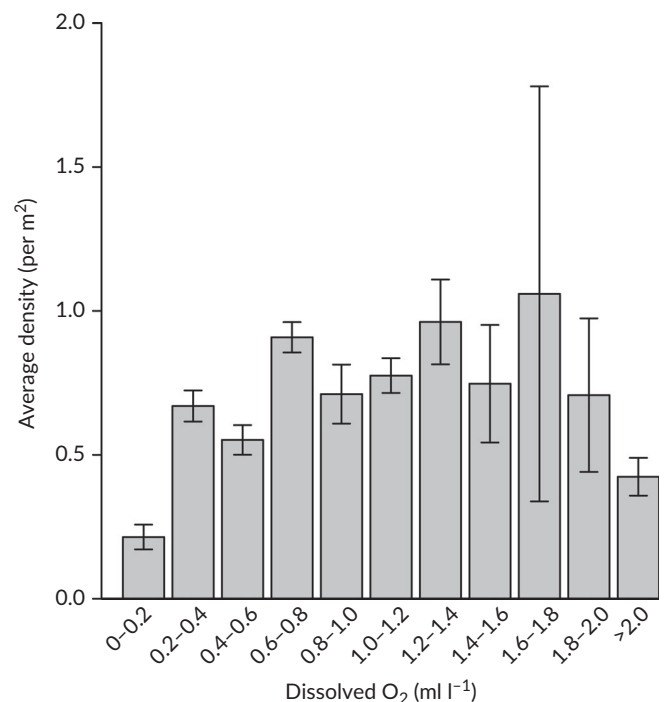
**FIGURE 2** Standard length frequency distributions of *Lyopsetta exilis* from (a) Fisheries and Oceans Canada groundfish survey trawl data off British Columbia from 1983 to 1916 ( $n = 42,126$  and (b) Saanich Inlet trawl data at 103 m in 2012 ( $n = 647$ ). (□) Female, (▒) male, and (■) unknown



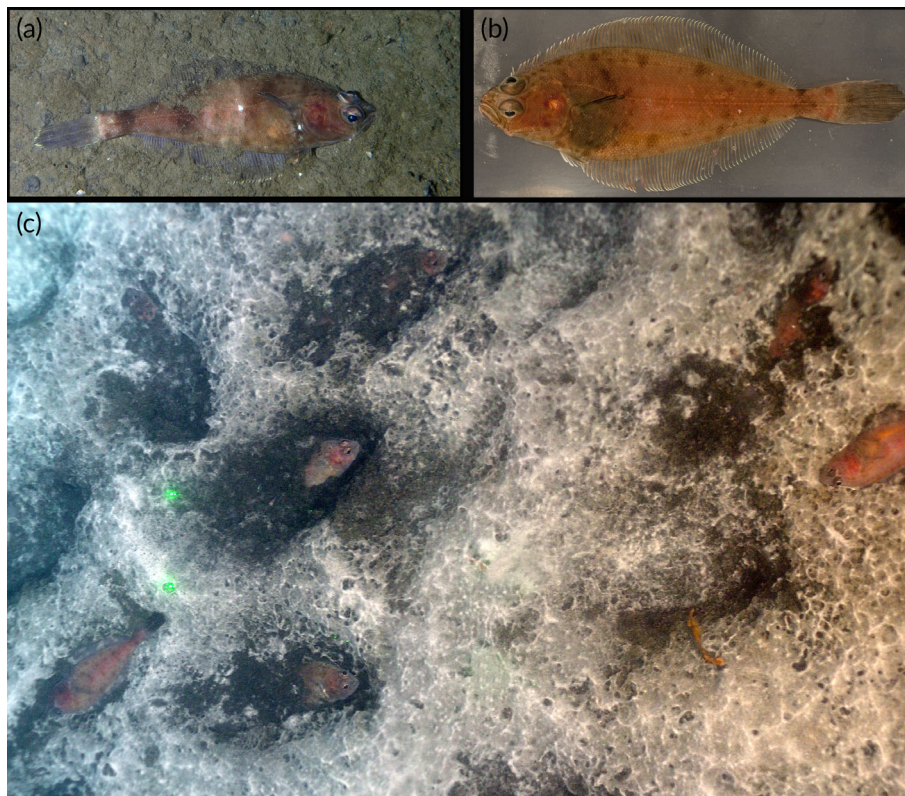
**FIGURE 3** The Fisheries and Oceans Canada shellfish survey trawl hauls from which catch per unit effort (CPUE) of *Lyopsetta exilis* was calculated in four regions (a–d; Figure 1) of British Columbia. Change in the central region (b) CPUE was not significant ( $P > 0.05$ ) while the north region (a) CPUE declined, and the southern shelf (c) and Strait of Georgia (d) bioregions increased. (—●—) a, (—▲—) b, (—■—) c, and (—+—) d

northern BC (area a: quadratic regression  $r^2 = 0.83$ ,  $P < 0.001$ ,  $F_{2,8} = 18.99$ ), shows no change in central BC (area b:  $P > 0.05$ ) and increases markedly in both offshore (area c: Southern Shelf Bioregion, quadratic regression  $r^2 = 0.64$ ,  $P < 0.001$ ,  $F_{2,37} = 32.47$ ) and inshore (area d: Strait of Georgia, quadratic regression  $r^2 = 0.60$ ,  $P < 0.001$ ,  $F_{2,19} = 13.82$ ) regions of lower BC; this last area has > two orders of magnitude change. Using an average value of  $M_T = 0.039$  kg for slender sole (Drazen *et al.*, 2015), trawls in area c returned maximum numbers around 44,500 slender sole  $h^{-1}$  in 2002 and 13,500  $h^{-1}$  in 2013.

The hypoxic water in Saanich Inlet inundates the bays with variable intensity each year; for example, a level of 1.4  $ml\ l^{-1}$  occurred at 110 m in the February 2009 survey, but as shallow as 56 m in September 2013. Thus, over the slope, the amount of low oxygen bottom habitat changes markedly over time and space. In 10 visual ROV surveys over 8 years, slender sole was nearly always the first animal recorded during ascent from anoxia to normoxia with first encounters as deep as 184 m and as shallow as 103 m (at oxygen 0.03  $ml\ l^{-1}$ ). As oxygen levels changed with depth and season, the overall oxygen range for slender sole was broad, but the fish was common in oxygen below 0.2  $ml\ l^{-1}$ , and rarely observed above 2.0  $ml\ l^{-1}$  (Figure 4); the average oxygen recorded for these 12,809 fish was 0.96  $ml\ l^{-1}$  ( $\pm 0.75\ ml\ l^{-1}$  SD). Most of its range, and the highest densities, were in hypoxic conditions (Supporting Information Video S1) where fish were common in bacterial mats (Figure 5). Examining distributions over the 10 years, we see no consistent change in densities with respect to



**FIGURE 4** Distribution of dissolved oxygen recorded for each of 12,809 slender sole sightings on ROV transects between 2006 and 2013 in Saanich Inlet. Abundances per 20  $m^2$  of transect are binned into oxygen intervals (standard error bars do not include zero counts) and presented per 1  $m^2$



**FIGURE 5** (a) *Lyopsetta exilis* (standard length c. 12 cm) *in situ* in Saanich Inlet at 95 m, (b) typical specimen of slender sole and (c) seven individuals in bacterial mats at 110 m depth in Saanich Inlet; area is 0.5 m<sup>2</sup>; ●, laser marks 10 cm apart

**TABLE 2** Densities of *Lyopsetta exilis* estimated from trawl hauls in Saanich Inlet, plus one site in the adjacent Trincomali Channel; area derived from vessel speed, time on bottom and trawl width

Sample	Depth fished (m)	Area trawled (m <sup>2</sup> )	<i>L. exilis</i> as proportion of flatfish catch <sup>a</sup>	Density (n 100 m <sup>-2</sup> )	Biomass (kg 100 m <sup>-2</sup> )
February 2005: All flatfish	70	1250	0.53	4.6	0.22
February 2005: <i>L. exilis</i> only	70	1250	–	2.4	0.07
July 2005: All flatfish	95	1060	0.99	23.6	0.60
July 2005: <i>L. exilis</i> only	95	1060	–	23.4	0.59
August 2012	104	2220	1.00	30.4	0.63
October 2013	104	1200	1.00	18.8	na
January 2014: Trincomali, <i>L. exilis</i> only	70	14,000	na	0.01	0.07

Note: na: not available.

<sup>a</sup>Other flatfish species encountered in Saanich were English sole and rock sole in shallower areas.

either depth or oxygen concentration, probably due to the variable timing of surveys relative to seasonal hypoxia that redistributed mobile benthos.

In shallower reaches of the bay, slender sole encounter frequency decreased while other flatfish species increased. Densities of flatfish in trawl surveys within the inlet are summarised in Table 2. Other flatfish collected were English sole *Parophrys vetulus* Girard 1854 and rock sole *Lepidopsetta bilineata* (Ayres 1855). Slender sole is the dominant flatfish at depths below 85 m and is the only flatfish below 104 m. Despite the low oxygen levels measured as 0.60 to 0.70 ml l<sup>-1</sup> in August 2012 at 104 m depth, slender sole density was over 30 individuals 100 m<sup>-2</sup>. Visual counts in the same area are about three times higher than those from the trawls.

### 3.2 | Population features in Saanich Inlet

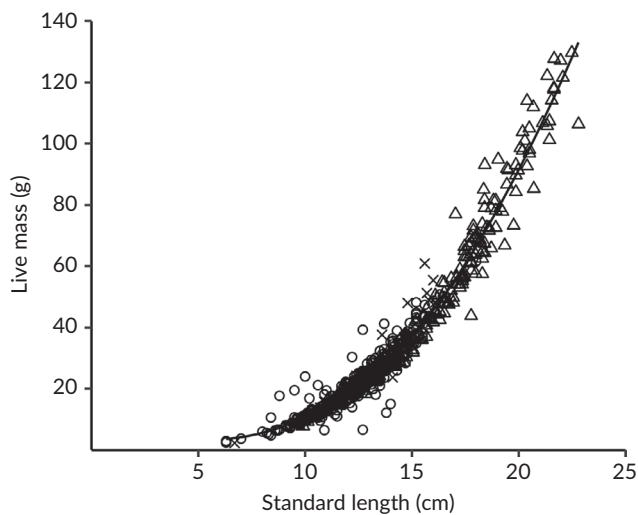
The average slender sole  $L_S$  from trawls in the inlet was 12.2 cm with a range of 6.3–20.0 cm; a notably smaller range than the all-BC dataset (Figure 2). A subset of animals from these trawls was assessed to determine sex-specific lengths and compared with DFO groundfish data from trawls in Strait of Georgia in 2012 and 2015 (Table 3). Both sexes are significantly smaller in Saanich Inlet compared with the neighbouring populations (female Kolmogorov–Smirnov  $D = 0.68$ ,  $P < 0.01$ ; male  $D = 0.58$ ,  $P < 0.01$ ). In 217 individuals, the Saanich sex ratio (♀:♂) is 0.79 compared with 1.30 from Strait of Georgia ( $n = 2042$ ). Using ROV imagery of coarse (resolution c. 1 cm) measurements of *in situ* fish length between 41 and 148 m depth (oxygen



**TABLE 3** Numbers ( $n$ ) of female and male *Lyopsetta exilis*, sex ratios and standard lengths ( $L_S$ ) in Saanich Inlet compared with DFO trawl samples from Trincomali Channel and in sites around Strait of Georgia. Trawl mesh sizes in these studies were similar

	Saanich Inlet 2005 & 2012	Trincomali Channel 2013	Strait of Georgia <sup>a</sup> 2012 & 2015
Females ( $n$ )	96	135	1135
Males ( $n$ )	122	25	907
Sex ratio (♀:♂)	0.79	5.40	1.25
Female $L_S$ range (cm)	7.0–20.0	11.9–22.8	11–29
Female mean $L_S$ (cm)	13.5	17.8	21.8
Male $L_S$ range (cm)	7.0–15.3	9.9–18.8	11–27
Male mean $L_S$ (cm)	11.9	15.7	18.8

<sup>a</sup>Data from King et al. (2013).



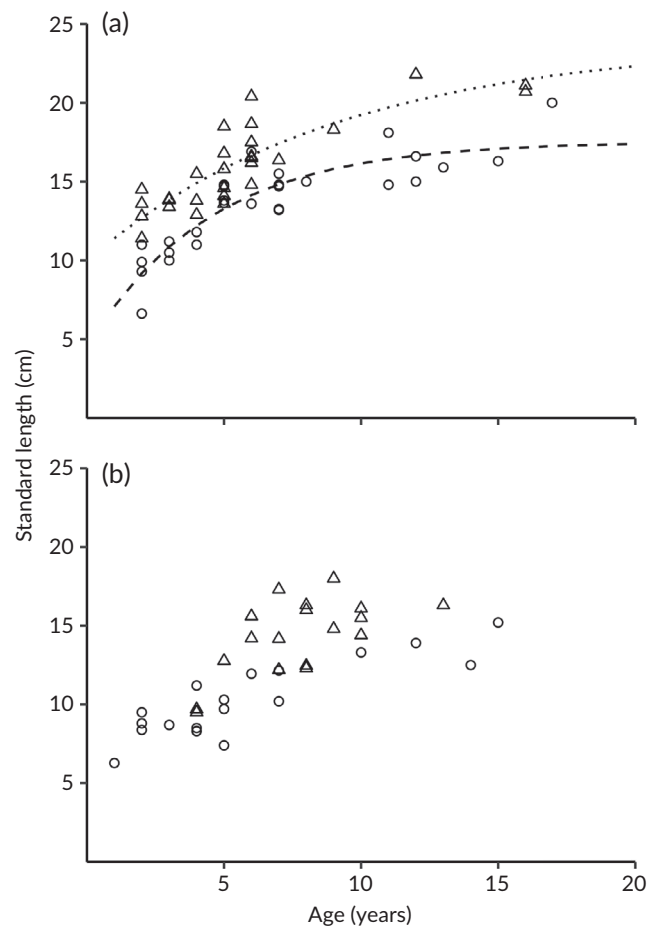
**FIGURE 6** Standard length–live mass relationship for *Lyopsetta exilis* from Saanich Inlet (two samples from 70 and 103 m depth) and Trincomali Channel (one sample from 70 m depth). ( $\Delta$ ) Trincomali Channel 70 m, ( $\times$ ) Saanich Inlet 70 m, ( $\circ$ ) Saanich Inlet 103 m

from 0.01 to 3.26 ml l<sup>-1</sup>, we could determine no relationship with either oxygen or depth ( $P > 0.05$ ).

The  $L_S$ – $M_T$  curve (Figure 6) shows a smooth transition from Saanich Inlet through to the Trincomali Channel fish. The ANCOVA model to test the effect of site on female mass found no significant differences between sites ( $F_{1,226} = 1.14$ ,  $P > 0.05$ ). Resultant scaling coefficients for females and males, respectively, are  $a = 0.0061$ ,  $0.0077$  and  $b = 3.18$ ,  $3.21$ ).

### 3.3 | Age analysis

The most effective otolith preparation technique was break-and-burn, as sectioning and polishing produced less pronounced banding. Otoliths from Saanich fish were distinguished by the presence of many growth checks and lower band resolution than those from Trincomali Channel. Owing to either unreadable otoliths or to reader disagreement, we only



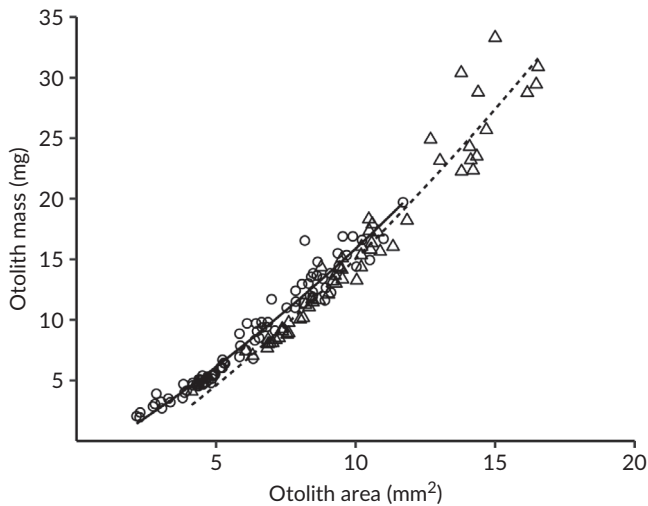
**FIGURE 7** Von Bertalanffy growth curves for (a) female *Lyopsetta exilis*: from Saanich Inlet and Trincomali Channel, and (b) for males, where data are too few to fit a curve but show smaller size at age in Saanich Inlet. ( $\Delta$ ) Trincomali Channel and ( $\circ$ ) Saanich Inlet

have adequate comparison for 28 females each from inside and outside the inlet (Figure 7a). Saanich fish ranged from 2 to 17 years in age; 10 females (seven in Saanich) were >10 years in age. In Trincomali, ages ranged from 2 to 16 years. Von Bertalanffy growth curves differ with  $L_\infty$  at 17.5 cm ( $r^2 = 0.78$ ) for Saanich and 23.9 cm ( $r^2 = 0.73$ ) for Trincomali. Although fewer data for males do not support a good curve fit, Saanich males also appear smaller at age (Figure 7b).

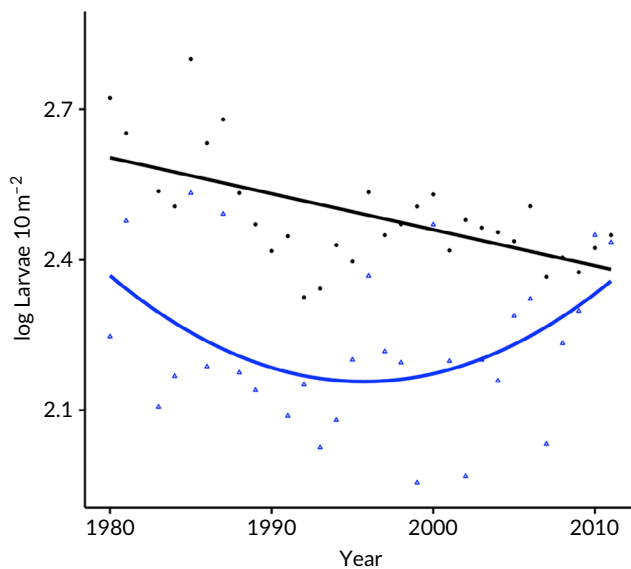
For a total of 164 fish from both Saanich and Trincomali, the relationship of fish length to surface area of otoliths is nearly linear (regression  $r^2 = 0.95$ ). When comparing the relationship between sites (Figure 8, both fitted curves: regression  $r^2 = 0.97$ ), in the region of the curve where otolith area overlaps between sites (4 to 12 mm<sup>2</sup>), otoliths from Saanich are heavier at size (residuals on detrended data, Mann–Whitney  $U = 2687$ ,  $P < 0.001$ ). Thus, an older fish at a given size in Saanich has more calcified otoliths.

### 3.4 | Ichthyoplankton

For 95,302 records of log-transformed species abundances in ichthyoplankton tows from the CalCOFI data set, we determined that



**FIGURE 8** Relationship between *Lyopsetta exilis* otolith area and mass from Saanich Inlet (—) and Trincomali Channel (-----); in the region of size overlap, Saanich otoliths are heavier. (Δ) Trincomali Channel and (○) Saanich Inlet



**FIGURE 9** California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton data 1980–2016 showing an overall decrease in total fish larval abundance off California (—●—), driven largely by *Engraulis mordax* and *Merluccius productus* ( $\text{adj-}r^2 = 0.25$ ), while larvae of *Lyopsetta exilis* (—△—) show a marked recovery beginning in 1996 to a level in 2010 comparable with 1980 (quadratic regression curve  $\text{adj-}r^2 = 0.13$ ). (—) Overall and (—) *Lyopsetta exilis*

larval fish abundance decreased per tow in each year (linear regression  $P = 0.02$ ,  $F_{1, 30} = 11.14$ , adjusted  $r^2 = 0.25$ ) from 1980–2011 in the California Current System. Slender sole larval abundance, on the other hand, does not show a linear change ( $P = .80$ ,  $n = 449$ ) in the sampling period. However, a non-significant quadratic regression ( $P = 0.055$ ,  $F_{2,28} = 3.214$ , adjusted  $r^2 = 0.13$ ) through the data indicate about a four-fold increase after a period of low abundance from 1992–2001 (Figure 9).

## 4 | DISCUSSION

As hypoxia intensifies in many parts of the ocean, insight into the responses of even a single species to this stressor can support predictions of consequences for marine populations. Slender sole demonstrates high tolerance for hypoxic conditions where it can maintain very high population numbers. Nonetheless, compared with conspecifics throughout the region, this Saanich Inlet population does not produce large fish at maturity and growth rates appear to be slower. While predator and competitor evasion may push the slender sole into hypoxic water, it is more likely the pull of food, such as plankton intersecting the seafloor, that explains their presence. Although the physiological adaptation to hypoxia in slender sole is not outstanding, its sedentary nature and easy prey access appear to support metabolic needs that are met in the reduced oxygen environment.

### 4.1 | Biology of *Lyopsetta exilis*

The BC province-wide dataset records slender sole sizes up to 40 cm in length. The mean size of 20.6 cm is greater than the largest fish in Saanich Inlet. Similar mean size (20.4 cm) and range were recorded for over 1000 fish in the adjacent Strait of Georgia (King *et al.*, 2013) confirming a size distribution that is consistent throughout BC. The Trincomali fish are larger than Saanich, but smaller than the Georgia Strait individuals. The reason is not clear, but we note that, for the fish that were aged, there was a preponderance of younger, smaller females; possibly this side channel of the Georgia Strait harbours younger fish.

While the mean size (12.2 cm) of the Saanich population is much smaller than elsewhere in BC, it is nearer the size reported from the southern extreme of the range in Baja California where individuals range from 7.2 to 22.2 cm (Martinez-Munoz *et al.*, 2013; Rodríguez-Romero *et al.*, 2008). The small sizes in Saanich could result from a predominance of younger fish that migrate out of the inlet to complete the life stages in the Georgia Strait. However, both gonad and otolith data indicate that these are adult fish, some of which exceed 10 years in age. The  $L_{\infty}$  in Saanich fish is less than the comparative population (already a small-end subset of a larger population). In their review, Nilsson and Östlund-Nilsson (2008) find that hypoxia tolerance is independent of fish size. Similarly, there is no relationship between  $O_{2\text{crit}}$  and body mass in slender sole from Saanich (Chu & Gale, 2017), which suggests that the smaller size in Saanich is a consequence of, not an adaptation to, low oxygen. Several studies record reduction in growth rates of fish as oxygen declines [*e.g.*, Atlantic cod *Gadus morhua* L. 1758 (Chabot & Dutil, 1999), summer flounder *Paralichthys dentatus* (L. 1766) and winter flounder *Pseudopleuronectes americanus* (Walbaum 1792) (Stierhoff *et al.*, 2006) and yellow perch *Perca flavescens* (Mitchill 1814) (Roberts *et al.*, 2011)] in response to lowered food intake as metabolism decreases.

In 54 trawl survey trips around British Columbia, DFO records sex ratios varying from 0.7 to 3.4 (F:M) with an overall proportion of 1.4 ( $n = 2142$ ). Only seven times does the proportion fall below 1.0,

as it does in Saanich Inlet where 0.78 is the second lowest record. Environmental sex determination occurs in many teleosts including pleuronectids in which higher temperatures at the time of sex differentiation causes a significant increase in the proportion of males (Luckenbach *et al.*, 2009). Juvenile flatfishes are abundant in shallow (<5 m) water in the inlet where summer temperatures near 20°C may contribute to the male dominance. While we neither collected nor saw juvenile slender sole in the deep inlet, it is possible that exposure of developing eggs to severe hypoxia affects subsequent development; male-dominated hatchlings result from zebrafish *Danio rerio* (Hamilton 1822) eggs exposed to brief anoxia (Robertson *et al.*, 2014).

While we did not examine gut contents in our study, a pilot project at the same site found pelagic crustaceans in nearly all slender sole examined ( $n = 30$ ; T. Ingram pers. comm.). Similarly, King *et al.* (2013) reported that over 75% of slender sole stomachs in Strait of Georgia had small crustaceans such as copepods. We often saw slender sole darting off bottom, especially in swarms of migrating plankton; these movements resuspended sediments to the point of creating dense turbidity layers near bottom in severe (<0.5 ml l<sup>-1</sup>) hypoxia (Katz *et al.*, 2012; Yahel *et al.*, 2008). Hypoxia intensity on the Saanich margins changes over the year, and mobile animals show strong responses as zooplankton adjust the depth of their diurnal migration (Sato *et al.*, 2013) while epibenthic animals move up and down slope (Chu & Tunnicliffe, 2015a). As a plankton feeder, slender sole congregates where the scattering layer intersects with the bottom (Matabos *et al.*, 2012). Some zooplankton in Saanich are highly tolerant of severe hypoxia, possibly using the conditions to avoid pelagic predators (De Robertis, 2002); densities of euphausiids, copepods and amphipods are very high in this migrating layer (Mackie & Mills, 1983; Sato *et al.*, 2013). Thus, food availability is unlikely to be a limitation for slender sole at this site. A diet dominated by pelagic crustaceans explains the abundance of slender sole in the demersal fish assemblage on the shelf (200 to 300 m) from Baja California to Oregon where diel plankton migration reaches the bottom (Cross, 1987; Hixon & Tissot, 2007; Robinson & Goómez-Gutierrez, 1998). It also probably accounts for the absence of this species noted by Gallo and Levin (2016) on the deeper continental slope in the oxygen minimum zone.

Slender sole densities in our 95–105 m trawls in Saanich inlet were c. 20 to 30 fish 100 m<sup>-2</sup> and 50 to 200 fish 100 m<sup>-2</sup> in visual surveys at oxygen <2 ml l<sup>-1</sup>. These numbers are much higher than those reported for the species elsewhere where highest numbers are between 1–5100 m<sup>-2</sup> (Hixon & Tissot, 2007; Martinez-Munoz *et al.*, 2013; Powell *et al.*, 2018). Indeed, only two other circumstances support similar or greater densities of any flatfish: nursery areas (Stoner *et al.*, 2007) and hydrothermal vents (Tunnicliffe *et al.*, 2013). Slender sole extend much deeper into the hypoxic zone than either rock sole *Lepidopsetta bilineata* (Ayres 1855) or English sole *Parophrys vetulus* Girard 1854, but when encroaching hypoxia compresses the habitat (Chu & Tunnicliffe, 2015a), species overlap ensues (Gasbarro *et al.*, 2019). Both diet differences (benthic for rock and English sole) and differential hypoxia tolerance likely dictate these distributions.

## 4.2 | Living in hypoxia

Slender sole is highly tolerant of severe hypoxia. In addition to the transects summarised in Section 3, a year-long study used a camera that captured sub-daily images at our study site to record the benthic community responses to severe hypoxia (Chu *et al.*, 2018). As oxygen steadily diminished over 3 months from 1.0 to 0.1 ml l<sup>-1</sup>, slender sole occurred in 38% of the records (each c 2.6 m<sup>2</sup> seafloor, 200 images). In addition to its small size and thus lower total oxygen requirements, a low metabolic rate and critical oxygen threshold (mean O<sub>2crit</sub> is 0.36 ml l<sup>-1</sup>) allows slender sole to regulate oxygen uptake at low environmental oxygen levels (Chu & Gale, 2017). Hyperventilation appears to enable this regulatory ability: we observed increasing opercular amplitude in severe hypoxia that exposed gill filaments both *in situ* and in respiration chambers. By increasing the volume of water flowing over the gills, presumably hyperventilation helps to maintain the partial pressure differential required for oxygen diffusion into the blood during counter-current exchange (Schmidt-Nielsen, 1997). Similar behaviour occurs in other flatfishes (Hughes, 1960). Adaptations seen in fish in hypoxic environments may also be used by the slender sole including cutaneous oxygen uptake (Le Moigne *et al.*, 1986), cardiovascular adaptations to increase oxygen uptake and delivery efficiency (Gamperl & Driedzic, 2009), metabolic rate suppression to lower energy demands (Richards, 2009), and adjustment of haemoglobin levels and oxygen binding affinities (Wells, 2009).

While fish are generally sensitive to low oxygen levels (Vaquer-Sunyer & Duarte, 2008), many species are notable for their severe hypoxia tolerance. Pacific hake *Merluccius productus* (Ayres 1855) also occur frequently in hypoxia (Chu & Tunnicliffe, 2015a), but they are transients in the depleted water as their occurrence and persistence is unpredictable. Such highly mobile fish can rapidly retreat to oxygenated water and larger fish have a higher capacity for anaerobic glycolysis (Nilsson & Östlund-Nilsson, 2008). Slender sole also appear to move as their abundance in the time-lapse camera had a diurnal signal. (Chu *et al.*, 2018) although we did not see large distribution changes in the 2 day–night transects that we compared. It is unlikely they are long-range swimmers like the bearded goby of Namibia that inhabits severely hypoxic water and migrates 60 m vertically at night to feed and re-oxygenate (Salvanes & Gibbons, 2018).

Slender sole has an average O<sub>2crit</sub> among hypoxia-tolerant marine fish (Gallo & Levin, 2016). The resident population of slender sole in Saanich Inlet, however, is exposed to an order of magnitude greater oxygen variability relative to the stable conditions occupied by more hypoxia tolerant fishes living in oxygen minimum zones (Gallo & Levin, 2016). The high-frequency oxygen fluctuations (over minutes) in Saanich Inlet can expose slender sole to intermittent, but short duration, levels of higher oxygen thereby allowing the fish to occupy mean O<sub>2</sub> concentrations that are well below its O<sub>2crit</sub> (oxyconformation; Chu *et al.*, 2018). Nonetheless, functional impairment can occur when an animal oxyconforms to low O<sub>2</sub> concentrations. In natural field conditions, we cannot discriminate the contributions of intrinsic (physiology) or extrinsic (predation, food supply) factors in structuring population-level dynamics (Audzijonyte *et al.*, 2019). However, the

smaller age at size for slender sole in Saanich Inlet was probably a partial consequence of the cumulative life-time exposure to periods of reduced physiological oxygen supply induced by periods of oxyconformation. Laboratory studies have not accounted for high frequency hypoxic exposure centred on species-specific  $O_{2crit}$ , thus the influence of natural habitat variability on physiological oxygen supply and demand remains an open question.

The mean body size of the Saanich slender sole population is the smallest of all examined in British Columbia. While food may not be limiting, the ability to allocate energy to substantial growth is limited by oxygen availability. In general, principles concerned with shrinking fish associate oxygen limitation with shifting energy dynamics induced by warming (Cheung *et al.*, 2013). Controlled experiments with turbot *Scophthalmus maximus* (L. 1758) and European sea bass *Dicentrarchus labrax* (L. 1758) record similar growth decline in hypoxia when food is plentiful (Pichavant *et al.*, 2001). Energy conservation requires shunting metabolic resources away from food acquisition and processing, as well as from growth and reproduction under sustained hypoxia (Sokolova *et al.*, 2012). Our work documents the direct effect of hypoxia on growth *in situ*, whereas other studies implicate hypoxia effects as fish are crowded into oxygenated regions with subsequent density-dependent growth outcomes (Cottingham *et al.*, 2018; Eby *et al.*, 2005). Keller *et al.* (2010) note reduced condition in five of six species in oxygen under  $1.0 \text{ ml l}^{-1}$ .

The sustained exposure to hypoxia may also affect maturation rate in slender sole where only females over 11.5 cm (4 years) were mature compared to similar sized, but younger (2 years), females outside the inlet; however, as our sample size was small, wider comparison is needed. As there are many ways that hypoxia can affect reproduction (behavioural, biochemical, developmental, and recruitment: see Wu (2009)), it is likely some effects have manifested in this population. Otolith calcification appears to continue over time such that Saanich fish have heavier otoliths than those of the same size outside the fjord; hypoxia does not appear to inhibit calcification. But these otoliths, compared with the nearby population, were difficult to read because of poor definition in banding and irregular checks. In a review of exogenous and bioenergetics factors that affect opacity changes in otoliths, Grønkvær (2016) invokes a model in which energetic status of an individual drives the ability to allocate metabolic resources to growth. Thus, not only temperature and food availability, but hypoxia effects on metabolic rate and food assimilation will affect the growth opportunities reflected in the otolith (Morales-Nin, 2000). Similar work on this and other fish subject to hypoxia may support reconstruction of past conditions experienced by individuals and populations, such as demonstrated by Chung *et al.* (2019). Application of a dynamic energy budget model to otolith properties has proven useful in hindcasting metabolic control on anchovy *Engraulis encrasicolus* (L. 1758) growth (Pecquerie *et al.*, 2012). While we focus on hypoxia, other environmental stressors may also contribute to limitation of aerobic scope. For example, the cumulative effect of concomitant increase in  $p\text{CO}_2$  includes acidosis (increase in  $\text{H}^+$  concentration), which can cause metabolic depression as energy is diverted to maintain the acid–base balance in internal tissues (Pörtner, 2012).

Given that slender sole inhabits a wide range of depths and habitats in the NE Pacific, why is it largely restricted to the hypoxic zone in Saanich Inlet? There is an evident cost in growth and, possibly also in reproduction, yet the population is robust in numbers and persistence. Probably, the abundance of food is a key factor where zooplankton prey intersect the inlet slope in the hypoxic zone. Reduced oxygen means less metabolic energy to acquire and digest food; more active fish require a greater metabolic scope but the small meal and sedentary lifestyle may reduce metabolic scope as observed for the common sole *Solea solea* (L. 1758) (Chabot & Claireaux, 2008). Thus, food availability and reduced competition, as well reduced predation from piscivores, can enable these fish to push into hypoxic areas as seen in oxygen minimum zones (Levin, 2003; Salvanes & Gibbons, 2018).

While we detect a decrease in slender sole CPUE in northern BC waters, the southern areas show an increase. Similarly, several demersal species have positive anomalies in biomass on the west coast of Vancouver Island in recent years (Perry *et al.*, 2017); thus, generally favourable growth conditions probably prevailed. The interplay of a complex coastline with dynamic seasonal wind, current and ocean mixing patterns creates a suite of distinct ecozones along the coast that do not show coordinated long-term responses to climate or other forcing factors (Okey *et al.*, 2014). However, if or when hypoxia expands on the shelf, as is currently underway offshore (Crawford & Peña, 2013), slender sole may experience a relative benefit as competitors are reduced. Of 23 species examined during years of moderate hypoxia on the Oregon shelf, slender sole was one of two species that showed a negative density relationship with dissolved oxygen, while overall larval fish abundance was positively correlated with increasing dissolved oxygen (Johnson-Colegrove *et al.*, 2015). Then, in the year of most intense hypoxia (2012), juvenile slender sole numbers increased markedly compared with other species (Sobocinski *et al.*, 2018). Our synoptic analysis of the California Current System ichthyoplankton trends finds a notable increase in slender sole in recent years. In a comparison of ichthyoplankton in the Strait of Georgia between the early 1980s and late 2000s, Guan *et al.* (2015) report a 15 fold increase in slender sole larvae despite survey methods that 'likely underestimated in the recent surveys'. Over 38 years to 2009, Johannessen *et al.* (2014) record an overall oxygen decline around  $1 \text{ ml l}^{-1}$ . Thus, this species is poised to take advantage of environmental changes that disadvantage other fish. Morley *et al.* (2018) project large range expansions northward along the Pacific North American coast for many demersal species based on temperature models; at a projected 24% thermal habitat gain (conservative scenario), the slender sole is in the upper quartile of species habitat gain in the model. However, with rising temperature comes reduced tolerance to hypoxia; thus, the slender sole may be better adapted to occupying new habitat.

We present empirical evidence that there is a cost to living in hypoxia: growth of slender sole is slower than the comparative population, and its average size in Saanich Inlet falls in the first quartile of the regional population. Clearly, the slender sole has reached physiological limits in severe hypoxia although the adaptations of small size,

a low maintenance metabolism and very low critical oxygen pressure support its presence where nearly all other macrofauna are absent. We were not able to assess the fitness cost, but the slow growth implicates delayed maturation. As the ocean warms, the effects of rising temperature on oxygen demand in fish are compounded by hypoxia expansion also related to ocean heat. Fish with low oxygen  $O_{2crit}$  levels, such as slender sole, will be the relative beneficiaries at the expense of species of greater fisheries interest. However, even the slender sole will diminish in size as the ocean environment loses oxygen.

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## AUTHOR CONTRIBUTIONS

V.T. formulated the overall approach and many of the specific studies, analysed data and prepared the manuscript. R.G. collected and analysed data and contributed to the script. F.J. guided studies with ideas, interpretation and equipment and edited the script. J.Q. contributed ideas, generated and analysed data and helped prepare the manuscript. N.S. collected and analysed data and contributed to the script. J.W.F.C. formulated ideas, executed fieldwork, analysed data and contributed to the script.

## ORCID

Verena Tunnicliffe  <https://orcid.org/0000-0003-2791-6337>

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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