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Evidence for depressed growth of juvenile Pacific salmon (*Oncorhynchus*) in Johnstone and Queen Charlotte Straits, British Columbia

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ABSTRACT

Juvenile salmon traveling northwestward to the Pacific Ocean from the Strait of Georgia migrate through and take residence in both Johnstone and Queen Charlotte Straits. Johnstone Strait is a narrow and deep passage that is strongly tidally mixed daily, resulting in a nearly isothermal water column, surface to the bottom (approximately 250 meters). The trophic gauntlet hypothesis (McKinnell et al., 2014) suggests that Johnstone Strait provides a poor growth environment for fish required to transit this area during their migration, due to the oceanographic conditions found there. Using insulin-like growth factor-1 (IGF1), a hormone used to assess short-term growth (within 5 – 7 days) in fishes, growth was measured in individual juvenile salmon from five species in the Northern Strait of Georgia, Johnstone Strait, Queen Charlotte Strait, and Queen Charlotte Sound in the summer of 2012, 2013, and 2014. All five juvenile salmon species had significantly lower IGF1 concentration in both Johnstone and Queen Charlotte Straits as compared to the Northern Strait of Georgia. These results are consistent with some aspects of the tropic gauntlet hypothesis as growth of juvenile salmon in both Johnstone and Queen Charlotte Strait was significantly lower than found in the Northern Strait of Georgia across all salmon species and all years. In addition, these results demonstrate the utility of growth indices for assessing the effects of environmental variation on juvenile salmon regardless of species when cohabitating in the presence of a strong ecological driver such as low primary productivity.

Key words: Oncorhynchus, trophic gauntlet, Strait of Georgia, IGF1, growth

INTRODUCTION

The Strait of Georgia is a highly productive freshwater fed marine fjord bound on the west by Vancouver Island and on the east by mainland British Columbia. The Strait of Georgia serves as an important early marine residence and adult return pathway for Pacific salmon (*Oncorhynchus* spp.) (Healy, 1980; Thomson, 1981). Each year, hundreds of millions of juvenile salmon undertake a seaward migration into the Strait of Georgia where they remain for weeks to months before heading to the open waters of the North Pacific Ocean (Tucker et al., 2009; Beamish et al., 2012; Beacham et al., 2014, Beacham et al., 2016). Many juvenile salmon appear to leave the Strait of Georgia through a northern route via Johnstone and Queen Charlotte Straits (Groot and Cooke, 1987; Tucker et al., 2009, 2016; Melnychuk et al., 2010; Beacham et al., 2014).

Johnstone Strait and Discovery Passage together comprise the narrowest, coldest, and often deepest sections of the primary inside passage of costal British Columbia. The physical properties of Johnstone Strait lead to extreme tidal water column mixing that prevents stratification and the development of a thermocline such as found in the nearby Strait of Georgia (Thomson, 1981). McKinnell et al. (2014) suggests that Johnstone Strait exists in a state of "perpetual biological winter" due to the inhibition of phytoplankton production by the tidal mixing and as such provides a poor growth environment for juvenile salmon due to a lack of prey availability. Therefore, McKinnell et al. (2014) propose that the migratory corridor of Johnstone Strait presents a consistent trophic challenge for juvenile salmon as they migrate out of the Strait of Georgia to the Pacific Ocean.

The trophic gauntlet hypothesis (McKinnell et al., 2014) suggests that on occasions when the consistently poor feeding conditions of Johnstone Strait are coupled with poor feeding conditions in Queen Charlotte Strait and/or Queen Charlotte Sound, salmon migrating into the Pacific Ocean from the Strait of Georgia (through the trophic gauntlet) have compromised energetic reserves, resulting in an increased risk of predation (Tucker et al., 2016), and experience depressed growth rates. Subsequently, after transiting the gauntlet, juvenile salmon mortality is hypothesized to be high and thus depressed adult returns may result in later years. This sequence of events may have occurred in 2007, resulting in the lowest return on record of sockeye salmon (*O. nerka*) to the Fraser River in 2009 (DFO, 2012; McKinnell et al. 2014).

Suggestions that juvenile salmon growth may be related to adult survival are neither unique to the trophic gauntlet hypothesis nor this aquatic system. Growth during early marine residence has been related to juvenile salmon survival to adulthood across many species and ecosystems (Parker, 1962; Healey, 1982; Cross et al., 2009; Beamish et al., 2010; Duffy and Beauchamp, 2011). What is unique about the trophic gauntlet hypothesis is that it links a specific oceanographic condition, strong tidal mixing, to a specific geographic location, Johnstone Strait, and posits a direct ecological effect, depressed growth of juvenile salmon.

A direct test for depressed growth rate of juvenile salmon in Johnstone Strait has not previously been conducted. Ferriss et al. (2014) inferred that juvenile salmon in

Queen Charlotte Strait, the area immediately northwest of Johnstone Strait, exhibit lower growth relative to juvenile salmon collected on the continental shelf of British Columbia (years: 2009, 2010, and 2011). Growth in this study was assessed by measuring circulating plasma concentrations of the hormone insulin-like growth factor 1 (IGF1), a hormone produced in and released from the liver that directly stimulates cell growth and division (Duan, 1998). Multiple laboratory experiments have shown that plasma IGF1 concentrations vary with feeding rate (Beckman et al., 2004; Shimizu et al., 2009) and are correlated to short-term growth (5 – 7 days) in juvenile Pacific salmon as well as other fish (Beckman, 2011; Picha et al., 2008). While IGF1 concentration as an index of growth is well established in laboratory experiments, its use in assessing growth of field-captured fish is still relatively novel (Bond et al., 2014; Ferriss et al., 2014). Here, we directly test a key component of the trophic gauntlet hypothesis, depressed growth of juvenile salmon in Johnstone Strait, by utilizing IGF1 concentration as an indicator of region-specific growth across five species of juvenile salmon distributed within and outside of Johnstone Strait across 3 different years (2012, 2013, 2014).

We assessed regional variation in growth by measuring IGF1 concentration in juvenile salmon. The location of these regions allowed us to directly test whether growth was lower in Johnstone Strait than in the surrounding regions, a result that would be consistent with the hypothesis of reduced food resources in Johnstone Strait, which is an essential component of the Trophic Gauntlet Hypothesis. However, we will also validate the use of plasma IGF1 concentrations to index fish growth in specific marine regions at specific times. The ability to measure near real-time growth of individual fish in specific areas provides a tool of general applicability to a number of marine ecological and oceanographic questions across fish species.

METHODS

Study location and sampling methods

Juvenile salmon were sampled in four regions (from south to north): the Northern Strait of Georgia, Johnstone Strait, Queen Charlotte Strait, and Queen Charlotte Sound (Fig. 1). These four regions represent distinct geographic areas before (Northern Strait of Georgia), during (Johnstone Strait), immediately following (Queen Charlotte Strait), and after a complete exit (Queen Charlotte Sound) of the proposed trophic gauntlet. These delineations represent distinct regions along a possible migratory pathway for juvenile salmon, however it is not assumed that individuals captured in Queen Charlotte Sound and Johnstone and Queen Charlotte Straits were resident in the Northern Strait of Georgia. It is assumed that individual IGF1 concentrations represent growth conditions of fish in the region in which they are captured. This allows region-to-region comparisons within and across years without the aid of additional specific individual analyses. Regional boundaries were kept consistent across all years, but exact tow locations and sample sizes within regions varied among years. Approximate linear distance across the regions sampled are: Northern Strait of Georgia, 48 km; Discovery Passage, 61 km (area between Northern Strait of Georgia and Johnstone Strait, no data collection); Johnstone Strait, 66 km; Queen Charlotte Strait, 90 km; and Queen Charlotte Sound, 90 km (Fig. 1).

Juvenile salmon were captured via fishing trawls aboard the C.C.G.S. W.E. Ricker and F/V Viking Storm (Queen Charlotte Sound 2012 only) in late June and early July of 2012, 2013, and 2014. Specifics of survey design and complete methods are detailed in Tucker et al. (2009). In this study, the species of juvenile salmon were identified by external characteristics, measured for fork length, and blood samples were collected via heparinized syringe. Blood samples were immediately centrifuged, the plasma removed from the red blood cells, and stored frozen (-20 °C). Plasma samples were transported frozen and stored at -80 °C until processing at the Northwest Fisheries Science Center (NWFSC) in Seattle, WA. Juvenile coho (*O. kisutch*), Chinook (*O. tshawytscha*), chum (*O. keta*), pink (*O. gorbuscha*) (2012 and 2014), and sockeye (2012 and 2013) salmon were collected. Water column conductivity, temperature, and depth/pressure (CTD) were measured on both vessels with SBE 911plus CTD (Seabird Scientific, Bellevue, WA).

Individual salmon were divided into 6 species by age classes. The first four classes were coho, chum, pink, and sockeye salmon of fork lengths less than 250 mm (fish of this size were in their first year of ocean residence for all species). Chinook salmon were divided into two year classes based on fork length. Individuals smaller than 150 mm in fork length were classified as Chinook-1 (in their first year of ocean residence having entered marine waters without spending a winter in fresh water) (Trudel et al., 2007) and those larger than or equal to 150 mm in fork length were classified as

Chinook-2 (in their first year of ocean residence having spent one winter in fresh water). Only regions with a sample size greater than 3 individuals for a given species by age class were included in analyses (to retain statistical power), resulting in fifteen total species sets (one juvenile species class per year): coho 2012, 2013, and 2014; Chinook-1 2013 and 2014; Chinook-2 2012, 2013, and 2014; chum 2012, 2013, and 2014; pink 2012 and 2014; and sockeye 2012 and 2013.

Laboratory techniques, statistical analyses, and oceanographic analyses

Concentration of plasma IGF1 for individual fish was measured each summer (2012, 2013, and 2014) following their collection using the time-resolved fluorescence immunoassay developed by Small and Peterson (2005) as modified by Ferriss et al. (2014). Uniformity and speed in processing samples was enhanced using an automated pipetting workstation (Perkin-Elmer, Shelton, CT). Across individual assays, all samples were standardized using inter-assay pools of juvenile coho salmon plasma at three known IGF1 concentrations (low, medium, and high), corresponding to approximately 75, 50, and 25 % binding in the immunoassay. Data standardization and complete laboratory techniques are detailed in Ferriss et al. (2014). Plasma 11-ketotestosterone (11-KT) concentrations were measured in coho salmon by immunosorbent assay (Cuisset et al., 1994) to exclude maturing coho salmon males, as their concentration of IGF1 is not exclusively indicative of relative growth (Beckman et al., 2004; Larsen et al., 2004). Maturing males were not found within the given size groups for other juvenile salmon species.

Mean IGF1 concentration and fork length were compared among regions using one-way analysis of variance (ANOVAs) tests independently for each combination of year and species. Tukey's range tests were used for each ANOVA to distinguish region to region differences within a year and species. The significance levels were not adjusted for multiple comparisons, as these tests were considered independent.

Length-standardized IGF1 concentrations were calculated in order to assess potential relationships between IGF1 concentration (ng/mL) and fork length (mm) as well as how the IGF1 concentration by fork length relationship varies between the four regions within a year and species using the following two linear models:

IGF1 concentration (ng/mL) ~ fork length (mm) [Model 1]

IGF1 concentration (ng/mL) ~ fork length (mm) + region [Model 2]

Length-standardized IGF1 concentrations were generated using Model 2 for each region based on a common (approximate mean) fork length for each species across all three years: 190, 130, 180, 130, 120, and 120 mm for coho, Chinook-1, Chinook-2, chum, pink, and sockeye salmon, respectively. These common fork lengths were used to interpret model output in lieu of linear y-intercepts for biological applicability. All statistical analyses were performed using the 'stats' package in RStudio (R Core Team, 2015).

CTD casts occurred in the same four geographic regions as the trawl locations. All temperature and conductivity data for a region in a given year were combined to generate mean temperature by depth plots for the region. Regional water column thermocline depths were estimated using the midpoint from the line with the maximum slope, where change in temperature is greater than 2 ºC within a distance of 10 meters (Defant, 1961; Reilly and Fiedler, 1994). Static water column stability (*E*) was calculated using change in average density at the top 3 meters and average density at 15 meters (given the shallow thermocline present in the Strait of Georgia) using the 'oce' package in RStudio (Kelly and Richards, 2015). Static stability measures greater than zero, equal to zero, and less than zero indicate a stable, neutral, and unstable water column respectively. Mean surface temperatures, presence/absence of a thermocline, and water column stabilities were used to assess differences in physical oceanography among years and regions.

RESULTS

Regional differences in IGF1 concentration

There was significant variation of IGF1 concentration among regions for all species in all years sampled ($p<0.04$, Supplemental Table 2). Juvenile salmon from Johnstone Strait had lower mean IGF1 concentration than salmon from the Northern Strait of Georgia in all tests. Of the 13 total IGF1 concentration comparisons, 12 were significantly lower in Johnstone Strait when compared to the Northern Strait of Georgia ($p<0.02$, Fig. 2). A non-significant difference for Chinook-2 was found in 2012.

Additionally, juvenile salmon from Queen Charlotte Strait had lower mean IGF1 concentration than salmon from the Northern Strait of Georgia in all comparisons. Of the

11 total IGF1 concentration comparisons, 9 were significantly lower in Queen Charlotte Strait when compared to the Northern Strait of Georgia ($p<0.04$, Fig. 2). The two non-significant IGF1 concentration comparisons were found in chum salmon (2012 and 2013).

Juvenile salmon from the outside waters of Queen Charlotte Sound followed a general trend of higher mean IGF1 concentration when compared to salmon from either Johnstone or Queen Charlotte Straits. In all six comparisons, mean IGF1 concentrations in salmon from Queen Charlotte Sound were significantly higher than in salmon from Johnstone Strait ($p<0.05$, Fig. 2). Additionally, in all six tests, mean IGF1 concentrations in salmon from Queen Charlotte Sound were higher than from salmon in Queen Charlotte Strait, with five of the six comparisons being significant ($p<0.05$, Fig. 2). Overall, fewer comparisons were possible between IGF1 concentrations in juvenile salmon found in Queen Charlotte Sound and other regions due to fewer juvenile salmon being collected in Queen Charlotte Sound.

Regional differences in mean fork length

There was significant variation of fork length among regions for coho 2012 and 2014, chum 2013 and 2014, Chinook-2 2012, and both years of pink and sockeye salmon ($p<0.05$, Supplemental Table 2). Mean fork lengths of juvenile coho, chum, and sockeye salmon were generally lower in the Northern Strait of Georgia than in other regions across all three years (Fig. 3). For Chinook salmon, mean fork length did not vary among the four regions for either Chinook-1 or Chinook-2 in either 2013 or 2014. For the remaining 11 significant species-specific comparisons of fork length, 9 means were significantly smaller in the Northern Strait of Georgia (the exception being pink salmon 2012 and 2014). For species sampled in Queen Charlotte Sound, mean fork length was significantly larger than the other regions in four of the six available comparisons: chum salmon 2012 and 2013, pink salmon 2012, and sockeye salmon 2012, but not sockeye salmon in 2013 or coho salmon in 2012.

Region specific relationships between IGF1 concentration and fork length

There was a positive or neutral relationship between IGF1 concentration and fork length in each species class for each year. Of these 15 linear regressions, 10 had significant and positive relationships between IGF1 concentration and fork length (Table

1, Model 1; $p<0.02$). Slopes for two of the non-significant relationships were slightly positive (coho, 2013; Chinook-2, 2014) and three slopes were approximately zero (coho, 2012; Chinook-2, 2012; and sockeye, 2013). No significant negative relationships were found.

Potential differences among regions for IGF1 concentration and fork length relationships were examined. Significant regressions of IGF1 concentration and fork length with Region as a covariate were found for all fifteen sets of data (Table 1, Model 2). R-squared values ranged from 0.19 (sockeye 2013, $p<0.05$) to 0.69 (chum 2012, $p<0.05$). The differences in results between Model 1 and Model 2 suggest that there is not a static relationship between fork length and plasma IGF1 concentration in any species. Rather, fork length and IGF1 concentration relationships are variable, presumably due to different environmental condition in different regions.

Length standardized IGF1 concentrations in salmon from the Northern Strait of Georgia were significantly greater than those from either Johnstone or Queen Charlotte Strait for all species in all years (Table 2, $p<0.05$). These results suggest that measured differences in IGF1 concentration between regions are independent of differences in regional fork length and thus reflect differences in growth between the regions. Length standardized IGF1 concentrations in Queen Charlotte Sound were greater than those found in the Northern Strait of Georgia for pink, chum, and sockeye salmon in 2012 and chum salmon in 2013.

Physical oceanography by region

Water column characteristics varied greatly among regions (Table 3). A thermocline was present in both the Northern Strait of Georgia and Queen Charlotte Sound in all years (Fig. 4). No thermocline was apparent in either Johnstone or Queen Charlotte Straits. Correspondingly, the greatest observed water column stabilities were calculated for the Northern Strait of Georgia and water column stability was near zero in all three years in Johnstone Strait and for two years in Queen Charlotte Strait. The strong tidal mixing present in Johnstone Strait is well demonstrated by the nearly isothermal water column, with mean temperature varying across depth by only 1.4, 0.8, and 0.7 °C across 2012, 2013, and 2014 compared to 4-8°C in Queen Charlotte Sound and the Northern Strait of Georgia for the same years (Fig. 4).

DISCUSSION

The results of this study are overwhelmingly consistent with the hypothesis of decreased growth for juvenile salmon in Johnstone Strait as compared to the Northern Strait of Georgia, developed from an application of the trophic gauntlet hypothesis (McKinnell et al., 2014). In all instances, across all juvenile salmon species, and across the three-year sampling period, average IGF1 concentration for each species was lower in Johnstone Strait than either the Northern Strait of Georgia or Queen Charlotte Sound. The pattern of decreased mean IGF1 concentration in Johnstone Strait is independent of fish size, species, and year; suggesting a consistent ecological challenge in Johnstone Strait as compared to nearby waters.

There are several caveats to these data that might affect our inference of lower growth in Johnstone Strait. Neither the freshwater origin, nor the migratory pathway and residence time of the individual juvenile salmon sampled is known. Thus, we cannot specifically determine whether the individual growth rate (IGF1 concentration) measured in a region accurately reflects the growth conditions in that region as we don’t know the exact residence time that region. Nonetheless, indirect data suggests than none of these issues directly invalidate the conclusion that juvenile salmon experience reduced growth within Johnstone Strait.

The individual point of entry of each fish into of the Strait of Georgia, Johnstone Strait, or Queen Charlotte Strait is unknown. For this study, it is assumed that most fish sampled entered marine waters in the Strait of Georgia. One might expect that recent emigrants from fresh water would be smaller and have lower growth rates than fish that had significant marine residence times. Mean fork length of juvenile salmon in the Northern Strait of Georgia was less than or equal to mean fork length measured in other regions, including Johnstone Strait (except pink salmon collected in 2014), across all three years. The fork length data is consistent with an interpretation of juvenile salmon entering the Strait of Georgia and then subsequently Johnstone Strait. Thus, the interpretation that lower IGF1 concentrations of salmon in Johnstone Strait were due to reduced food resources within Johnstone Strait does not seem to be biased by a significant number of recent marine immigrants within Johnstone Strait, as might be indicated if individuals from a given species were smaller in Johnstone Strait than in the Northern Strait of Georgia.

Individual fish must spend enough time in a given region for the growth rate measured in that area to reflect local environmental conditions. Although neither the exact ocean entry location or date, nor the path and speed of an individual salmon's migration prior to capture is known, the potential minimum residence time within the regions as a whole can be estimated. Assuming optimal travel speeds of 2, 1.5, and 1 body length/s (Trudel and Welch, 2005) the fastest swimming rate of individuals of 90, 150, and 250 mm long would be 17.0, 19.8, and 23.1 km per day, respectively. These three travel speeds and fork lengths are to account for both differences in species specific size and migration timing through the Strait of Georgia and Jonstone Strait. Given the approximate distance between the start of the Northern Strait of Georgia and the start of Queen Charlotte Sound (265 km), it would take approximately 11-16 days to travel this route by constantly swimming a direct straight line. While this is a rudimentary estimate, it is within the mean travel time of 8-18 days reported by Furey et al. (2015) for acoustically tagged juvenile sockeye salmon that were tracked between the northern end of Texada Island (southern most part of the Northern Strait of Georgia as defined in this study) to Queen Charlotte Strait (the midpoint of Queen Charlotte Strait as defined in this study). Assuming a constant swimming speed based on fork length, approximate minimum residence time within each region for these fish would be 2.1-2.8 days (Northern Strait of Georgia), 2.6-3.6 days (Discovery Passage, no sampling), 2.8-3.9 days (Johnstone Strait), and 3.9-5.3 days (Queen Charlotte Strait).

The time required for decreases in food consumption to result in measurable decreases in IGF1 concentration in laboratory-reared fish varies, depending on feeding regime (Beckman, 2011), but may be a minimum of 3 days (Pierce et al., 2005). Travel time between the end of the Northern Strait of Georgia and the end of Johnstone Strait was estimated to take about 5-7 days of constant, directed travel, suggesting that measured IGF1 concentration in Johnstone Strait is indicative of the feeding and growth conditions encountered in Johnstone Strait. Furthermore, IGF1 concentrations measured in the eastern section of Queen Charlotte Strait as defined by this study may reflect growth conditions found in Johnstone Strait, as fish sampled in Queen Charlotte Strait may have exited Johnstone Strait within the past 2 or 3 days. Precise determination of growth conditions in Queen Charlotte Strait would require more extensive sampling, enabling the comparison of IGF1 concentrations in the Eastern, Central and Western portions of this region. However, no significant difference existed between the eastern and western sections of Queen Charlotte Strait for the individuals examined in this study (when appropriate sample sizes were available to assess this from the data herein).

Primary factors influencing growth, and thus IGF1 concentration, are the quantity and/or quality of food consumed and water temperature (Brett et al., 1969; Beauchamp 2009). Basic environmental conditions known to influence the abundance of juvenile salmon prey gives some insight into variation in food abundance among different regions where juvenile salmon were sampled. The optimal stability window defined by Gargett (1997) suggests that primary production is highest in regions where water column stability is intermediate, allowing some mixing of nutrients above the thermocline and limiting mixing of phytoplankton below the photosynthetic zone. In contrast, limited productivity is expected in a well-mixed water column, because phytoplankton do not spend enough time in the photosynthetic zone to grow well. In all three years sampled, waters of Johnstone Strait were well mixed, with water column stabilities near zero. In contrast, waters of the Northern Strait of Georgia had a defined thermocline at approximately 15 meters. The observed water column characteristics lead to the prediction of higher plankton productivity in the Northern Strait of Georgia than in Johnstone Strait. These water column properties are consistent with previous measurements of Johnstone Strait productivity compared to surrounding regions (McKinnell et al., 2014), all suggesting that food abundance could be low in Johnstone Strait.

In addition to food quality and quantity, water temperature can also affect growth. Upper water column temperatures in Johnstone Strait were cooler than other regions assessed. However, water temperatures across all regions lie within the upper range of thermally defined optimal growth curves for juvenile salmon (Brett et al., 1969; Plumb and Moffitt, 2015), thus temperature alone is not responsible for the IGF1 concentration differences measured. Moreover, experimental data demonstrates that temperature differences do not bias the ability of IGF1 concentration to index growth (Beckman et al., 2004). Differences in food resources among regions remain the simplest explanation for differences in growth between regions.

Regardless of annual mean IGF1 concentration or fork length, a consistent pattern of decreased growth within Johnstone Strait was found across year and species, indicating that a common underlying environmental condition exists. The complete mixing of the water column within Johnstone Strait is not unique to the coastal Pacific, but the length of the migration corridor through this region for northwestward bound juvenile salmon migrants from the Strait of Georgia is unusual. The presence of this pattern of reduced growth in juvenile salmon provides an example of the influence that regional ocean conditions may have upon the physiology and ecology of juvenile salmon (Ferriss et al., 2014). The findings reported herein do not predict poor survival for salmon of any given species or year; rather, they reflect a cross species physiological response to an environmental challenge in a given region. The impact of this challenge on marine survival of juvenile salmon is likely dependent on the quality of the marine environment encountered in Queen Charlotte Sound and beyond in any given year (McKinnell et al., 2014). The inter-annual oceanography of Queen Charlotte Sound and the Northeast Pacific as well as inter-annual variation in the survival of salmon originating from the Strait of Georgia are beyond the bounds of this report. A more complete understanding of how the oceanography of Johnstone and Queen Charlotte Straits affect the ecology of juvenile salmon would require measures of phytoplankton production, prey abundance, and feeding by juvenile salmon. In addition, identification of juvenile salmon by stock would provide greater resolution to questions of residence time and migration by these fish within Johnstone and Queen Charlotte Straits. Nevertheless, the common pattern of depressed growth by juvenile salmon across species and years clearly demonstrates the presence of a powerful ecological process operating in this region. This report should stimulate further work to elucidate the causes and consequences of this process and it’s effect on salmon populations.

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REFERENCES

Beacham, T.D., Beamish, R.J., Candy, J.R., Wallace, C., Tucker, S., Moss, J.H. and Trudel, M. (2014) Stock-specific migration pathways of juvenile sockeye salmon in British Columbia waters and in the Gulf of Alaska. *Trans. Am. Fish. Soc.* 143:1386-1403.

Beacham, T.D., Beamish, R.J., Neville, C.M., Candy J.R., Wallace, C., Tucker, S. and Trudel, M. (2016) Stock-specific size and migration of juvenile coho salmon in British Columbia and Southeast Alaska waters. *Mar. Coast. Fish.* 8:1:292-314.

Beamish, R.J., Sweeting, R.M., Lange, K.L., Noakes, D.J., Preikshot, D. and Neville, C.M. (2010) Marine survival of coho salmon in the Strait of Georgia declines to very low levels. *Mar. Coast. Fish.* 2:424-439.

Beamish, R.J., Neville, C.M. and Sweeting, R.M. (2012) An early marine life history strategy for Fraser River sockeye salmon. *N. Pac. Anadr. Fish Comm.* Doc. 1423, 23 pp.

Beauchamp, D.A. (2009) Bioenergetic ontogeny: linking climate and mass-specific feeding to life-cycle growth and survival of salmon. *Am. Fish. Soc. Symp.* Vol. 70.

Beckman, B.R., Shimizu, M., Gadberry, B. and Cooper, K.A. (2004) Response of the somatotropic axis of juvenile coho salmon to alterations in plane of nutrition with an analysis of the relationships among growth rate and circulating IGF-I and 41 kDa IGFBP. *Gen. Comp. Endocrinol.* 135:334-344.

Beckman, B.R. (2011) Perspectives on concordant and discordant relations between insulin-like growth factor 1 and growth in fishes. *Gen. Comp. Endocrinol.* 170:233-252.

Bond, M., Beckman, B.R., Rohrbach, L., and T. Quinn. (2014). Differential growth in estuarine and freshwater habitats indicated by plasma IGF1 concentrations and otolith chemistry in Dolly Varden charr *Salvelinus malma*. *J. Fish Biol.* 85:1429-1445.

Brett, J.R., Shelbourn, J.E. and Shoop, C.T. (1969) Growth rate and body composition of fingerling sockeye salmon, *Oncorhynchus nerka*, in relation to temperature and ration size. *J. Fish. Res. Board. Can.* 26(9):2363-2394.

Cross, A.D., Beauchamp, D.A., Moss, J.H. and Meyers, K.W. (2009) Interannual variability in early marine growth, size-selective mortality, and marine survival for Prince William Sound pink salmon. *Mar. Coast. Fish.* 1:1:57-70.

Cuisset, B., Pradelles, P., Kime, D.E., Kuhn, E.R., Babin, P. and Le Menn, F. (1994) Enzyme immunoassay for 11-ketotestosterone using acetylcholinesterase as label: application to the measurement of 11-ketotestosterone in plasma of Siberian sturgeon. *Comp. Biochem. Physiol.* 108:229-241.

Defant, A. (1961) Physical Oceanography, Vol. 1. p.729. Oxford, Pergamon Press, London.

DFO (2012) Assessment of Area 23 Sockeye and 2010 Forecast (Barkley Sound and Alberni Inlet). *DFO Can. Sci. Advis. Sec. Sci. Advis. Rep.* 2012/033.

Duan, C. (1998) Nutritional and developmental regulation of insulin-like growth factors in fish. *J. Nutr.* 128(2):306S-314S.

Duffy, E.J. and Beauchamp, D.A. (2011) Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, Washington. *Can. J. Fish. Aquat. Sci.* 68:232-240.

Ferriss, B.E., Trudel, M. and Beckman, B.R. (2014) Regional and inter-annual trends in marine growth of juvenile salmon in coastal pelagic ecosystems of British Columbia, Canada. *Mar. Ecol. Prog. Ser.* 503:247-261.

Furey, N.B., Vincent, S.P., Hinch, S.G., and Welch, D.W. (2015) Variability in migration routes influences early marine survival of juvenile salmon smolts. *PLoS ONE.* 10.10:e0139269.

Gargett, A.E. (1997) The optimal 'stability window': a mechanism underlying decadal fluctuations in North Pacific salmon stocks? *Fish. Oceanogr.* 6.2:109-117.

Groot, C. and Cooke, K. (1987) Are the migrations of juvenile and adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in near-shore waters related? *Publ. Spec. Can. Sci. Halieut. Aquat.* 96:53-60.

Healy, M.C. (1980) The ecology of juvenile salmon in Georgia Strait, British Columbia, p. 203-229. In: W.J. McNeil and D.C. Himsworth (eds.) Salmonid ecosystems of the North Pacific, Oregon State University Press, Corvallis, OR.

Healey, M.C. (1982) Timing and relative intensity of size-selective mortality of juvenile chum salmon (*Oncorhynchus keta*) during early sea life. *Can. J. Fish. Aquat. Sci.* 39:952- 957.

Kelley, D. and Richards, C. (2015) oce: Analysis of Oceanographic Data. R package version 0.9-17. http://CRAN.R-project.org/package=oce

Larsen, D.A., Shimizu, M., Cooper, A., Swanson, P. and Dickhoff, W.W. (2004) Androgen effects on plasma GH, IGF-I, and 41- kDa IGFBP in coho salmon (*Oncorhynchus kisutch*). *Gen. Comp. Endocr*. 139:29-37.

Melnychuk, M.C., Welch, D.W. and Walters, C.J. (2010) Spatio-temporal migration patterns of Pacific salmon smolts in rivers and coastal marine waters. *PLoS ONE* 5(9): e12916.

McKinnel, S., Curchitser, E., Groot, K., Kaeriyama, M. and Trudel, M. (2014) Oceanic and atmospheric extremes motivate a new hypothesis for variable marine survival of Fraser River sockeye salmon. *Fish. Oceanogr*. 23:4,322-341.

Parker, R.R. (1962) Estimation of ocean mortality rates for Pacific salmon (*Oncorhynchus*). *J. Fish. Res. Board Can.* 19:561-589.

Picha, M.E., Turano, M.J., Beckman, B.R. and Borski, R.J. (2008) Endocrine biomarkers of growth and applications to aquaculture: A minireview of growth hormone, insulin-like growth factor (IGF)-I, and IGF-Binding proteins as potential growth indicators in fish. *N. Am. J. Aquacult.* 70:196-211.

Pierce, A.L., Shimizu, M., Beckman, B.R., Baker, D. M., and Dickhoff, W.W. (2005) Time course of the GH/IGF axis response to fasting and increased ration in Chinook salmon (*Oncorhynchus tshawytscha*). *Gen. Comp. Endocr*. 140:192–202.

Plumb, J.M. and Moffitt, C.M. (2015) Re-estimating temperature-dependent consumption parameters in bioenergetics models for juvenile Chinook salmon. *T. Am. Fish. Soc*. 144:2:323-330.

R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reilly, S.B. and Fiedler, P.C. (1994) Interannual variability of dolphin habitats in the eastern tropical Pacific. I: Research vessel surveys, 1986-1990. *Fish. Bull.* 92.2: 434-450.

Small, B.C. and Peterson, B.C. (2005) Establishment of a time-resolved fluoroimmunoassay for measuring plasma insulin-like growth factor I (IGF-I) in fish: effect of fasting on plasma concentrations and tissue mRNA expression of IGF-I and growth hormone (GH) in channel catfish (*Ictalurus punctatus*). *Dom. Anim. Endocrinol.* 28:202-215.

Shimizu, M., Cooper, K.A., Dickhoff, W.W. and Beckman, B.R. (2009) Postprandial changes in plasma growth hormone, insulin, insulin-like growth factor (IGF)-I and IGF-binding proteins in coho salmon fasted for varying periods. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 297:352-361.

Thomson, R.E. (1981) Oceanography of the British Columbia coast. *Can. Spec. Pub. Fish. Aquat. Sci.* 56:291.

Trudel, M. and Welch, D.W. (2005) Modeling the oxygen consumption rates in Pacific salmon and steelhead: model development. *Trans. Am. Fish. Soc.* 134(6):1542-1561.

Trudel, M., Jones, S.R.M., Thiess, M.E., Morris, J.F.T., Welch, D.W., Sweeting, R.M., Moss, J.H., Wing, B.L, Farley Jr., E.V., Murphy, J.N., Baldwin, R.E. and Jacobson, K.C. (2007) Infestations of motile salmon lice on Pacific salmon along the west coast of North America. *Am. Fish. Soc. Symp. Ser.* 57:157-182.

Tucker, S., Trudel, M., Welch, Candy, J.R., Morris, J.F.T., Theiss, M.E., Wallace, C., Teel, D.J., Crawford, W., Farley, E.V. and Beacham, T.D. (2009) Seasonal stock-specific migrations of juvenile sockeye salmon along the west coast of North America: implications for growth. *Trans. Am. Fish. Soc.* 138:1458-1480.

Tucker, S., Hipfner, J.M. and Trudel, M. (2016) Size- and condition-dependent predation: a seabird disproportionately targets substandard individual juvenile salmon. *Ecology*. 97(2):461-471.

Tukey, J. (1949) Comparing Individual Means in the Analysis of Variance. *Biometrics.* 5(2):99-114

Table 1. Statistical model output for two linear models of IGF1 concentration (ng/mL), fork length (mm), and region per species per year. Model 1 is a linear regression of IGF1 concentration and fork length. Model 2 is a linear regression of IGF1 concentration and fork length with Region as a covariate. ND indicates inadequate sample size collected for that region in that year (n<3). Significant (p<0.05) R-squared noted with asterisk.

Table 2. Length standardized IGF1 concentration (+ Standard Error) (ng/mL) per region at mean fork length (mm) for all regions within a year as calculated from Model 2 (Table 1). Mean fork length for coho, Chinook-1, Chinook-2, chum, pink, and sockeye salmon were: 190, 130, 180, 130, 120, and 120 mm, respectively. ND indicates inadequate sample size collected for that region in that year (n<3). NS indicates that the region was not sampled in that year.

Table 3. Average locations of CTD casts per region shown by mean latitude, mean longitude, number of casts per year, and presence or absence of thermocline. NS indicates that the region was not sampled in that year.

Supplemental Table 1. Sample size per region for each species in all years sampled for IGF1 concentration. ND indicates inadequate sample size collected for that region in that year (n<3). NS indicates that the region was not sampled in that year.

Supplemental Table 2. Simple analysis of variance (ANOVA) statistical results for effects of regions on IGF1 concentration (ng/mL) or fork length (mm) for a given species in a given year. ND indicates inadequate sample size collected for that region in that year (n<3).

Figure 1. Map of study area in British Columbia, Canada. The tow locations from all three sample years (2012, 2013, 2014) are shown and color coordinated by region: Queen Charlotte Sound (QCSND), Queen Charlotte Strait (QCST), Johnstone Strait (JS), and the Northern Strait of Georgia (NSOG) in white, light gray, dark gray, and black; respectively. Sampling conducted in late June and early July on W.E. Ricker.

Figure 2. Average IGF1 (± standard error) concentration (ng/mL) per region per species per year. Statistically significant differences between regions are represented above a given column in a given year, with differences represented by different letters (ANOVA; $p<0.05$). Queen Charlotte Sound (QCSND) in white, Queen Charlotte Strait (QCST) in light gray, Johnstone Strait (JS) in dark gray, and the Northern Strait of Georgia (NSOG) in black. Sample size per region per year for QCSND, QCST, JS, and NSOG can be found in Supplemental Table 1.

Figure 3. Average fork length (± standard error) (mm) per region per species per year. Statistically significant differences between regions are represented above a given column in a given year with differences represented by different letters (ANOVA; $p<0.05$). Queen Charlotte Sound (QCSND) in white, Queen Charlotte Strait (QCST) in light gray, Johnstone Strait (JS) in dark gray, and the Northern Strait of Georgia (NSOG) in black.

Figure 4. Water column temperature from individual CTD casts in each region (North to South): Queen Charlotte Sound, Queen Charlotte Strait, Johnstone Strait, and the Northern Strait of Georgia are shown in gray. Mean water column temperature per region is shown in black. Thermocline presence per region per year is indicated by dashed line.

Table 1.

Species & Year		Model 1 R^2	Model 2 R^2
coho	2012	0.03	0.52*
	2013	0.02	0.45*
	2014	0.08*	0.36*
chum	2012	0.07*	0.48*
	2013	0.06*	0.45*
	2014	0.12*	0.42*
Chinook-2	2012	0.01	0.38*
	2013	0.29*	0.45*
	2014	0.02	0.44*
Chinook-1	2012	ND	ND
	2013	0.34*	0.52*
	2014	0.17*	0.51*
pink	2012	0.30*	0.49*
	2013	ND	ND
	2014	0.09*	0.23*
sockeye	2012	0.21*	0.37*
	2013	0.01	0.19*
	2014	ND	ND

Table 2.

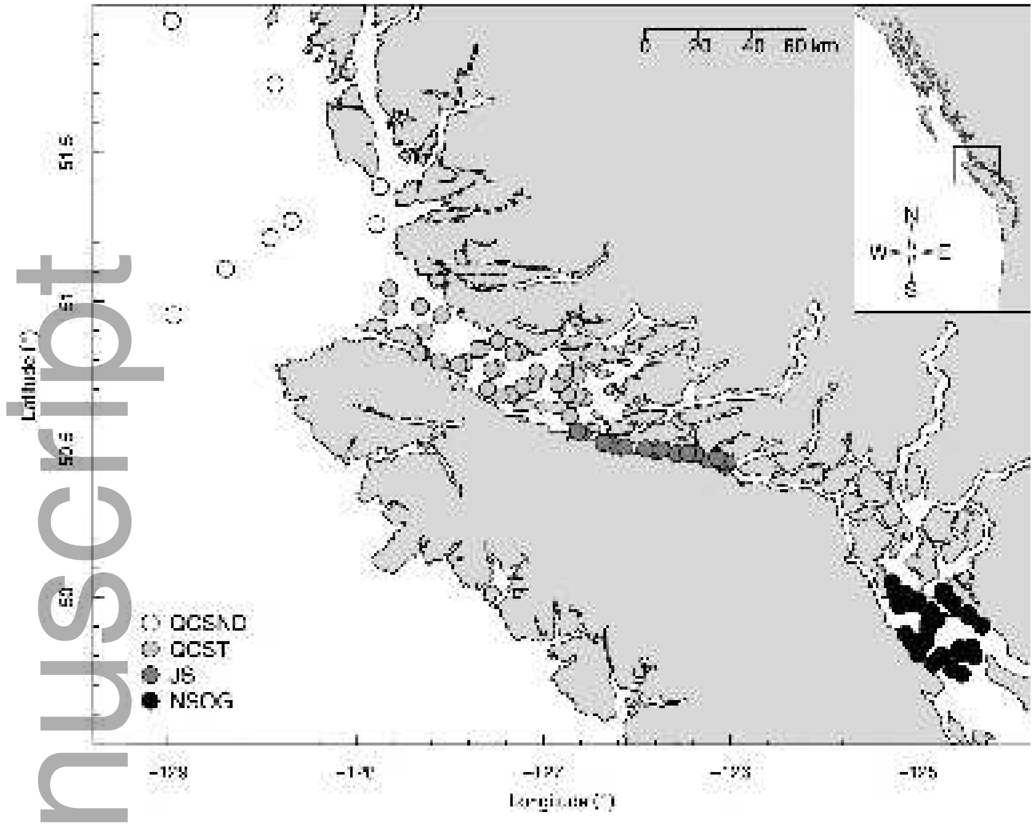
Species & Year	Calculated IGF1 Concentration + SE (ng/mL) at Annual Mean Fork Length			
	NSOG	JS	QCST	QCSND

coho	2012	80.3 + 5.0	48.2 + 18.5	58.6 + 5.4	62.0 + 5.3
	2013	68.0 + 2.6	47.8 + 8.3	ND	ND
	2014	83.0 + 3.1	64.0 + 9.0	60.0 + 2.9	NS
chum	2012	39.8 + 5.3	29.3 + 4.1	33.2 + 3.4	62.8 + 4.9
	2013	46.0 + 2.2	36.2 + 3.1	43.4 + 2.5	63.1 + 2.6
	2014	60.0 + 2.0	41.0 + 5.4	43.8 + 1.5	NS
Chinook-2	2012	84.5 + 9.9	61.4 + 37.5	53.7 + 11.6	ND
	2013	87.3 + 10.1	68.2 + 63.0	ND	ND
	2014	93.0 + 8.6	66.2 + 29.1	61.8 + 9.6	NS
Chinook-1	2012	ND	ND	ND	ND
	2013	60.3 + 13.7	ND	45.4 + 4.4	ND
	2014	69.1 + 5.1	44.8 + 19.8	ND	NS
pink	2012	38.2 + 3.9	26.4 + 10.1	31.0 + 3.7	48.6 + 4.5
	2013	ND	ND	ND	ND
	2014	48.6 + 2.4	38.7 + 4.1	35.2 + 1.8	NS
sockeye	2012	47.0 + 14.7	ND	30.6 + 6.6	60.5 + 5.9
	2013	54.8 + 3.9	43.1 + 13.5	ND	55.9 + 3.8
	2014	ND	ND	ND	NS

Table 3.

Region & Year		CTD casts			
		Mean Latitude	Mean Longitude	# of casts	Stability (E)
NSOG	2012	49.85	-124.81	6	0.6
	2013	49.91	-124.88	7	0.5
	2014	49.94	-124.93	7	0.3
JS	2012	50.49	-126.37	6	0.0

	2013	50.51	-126.40	5	0.0
	2014	50.49	-126.32	7	0.0
QCST	2012	50.81	-127.28	20	0.0
	2013	50.75	-127.17	8	0.1
	2014	50.82	-127.33	16	0.0
QCSND	2012	51.22	-128.40	5	0.1
	2013	51.12	-128.67	4	0.1



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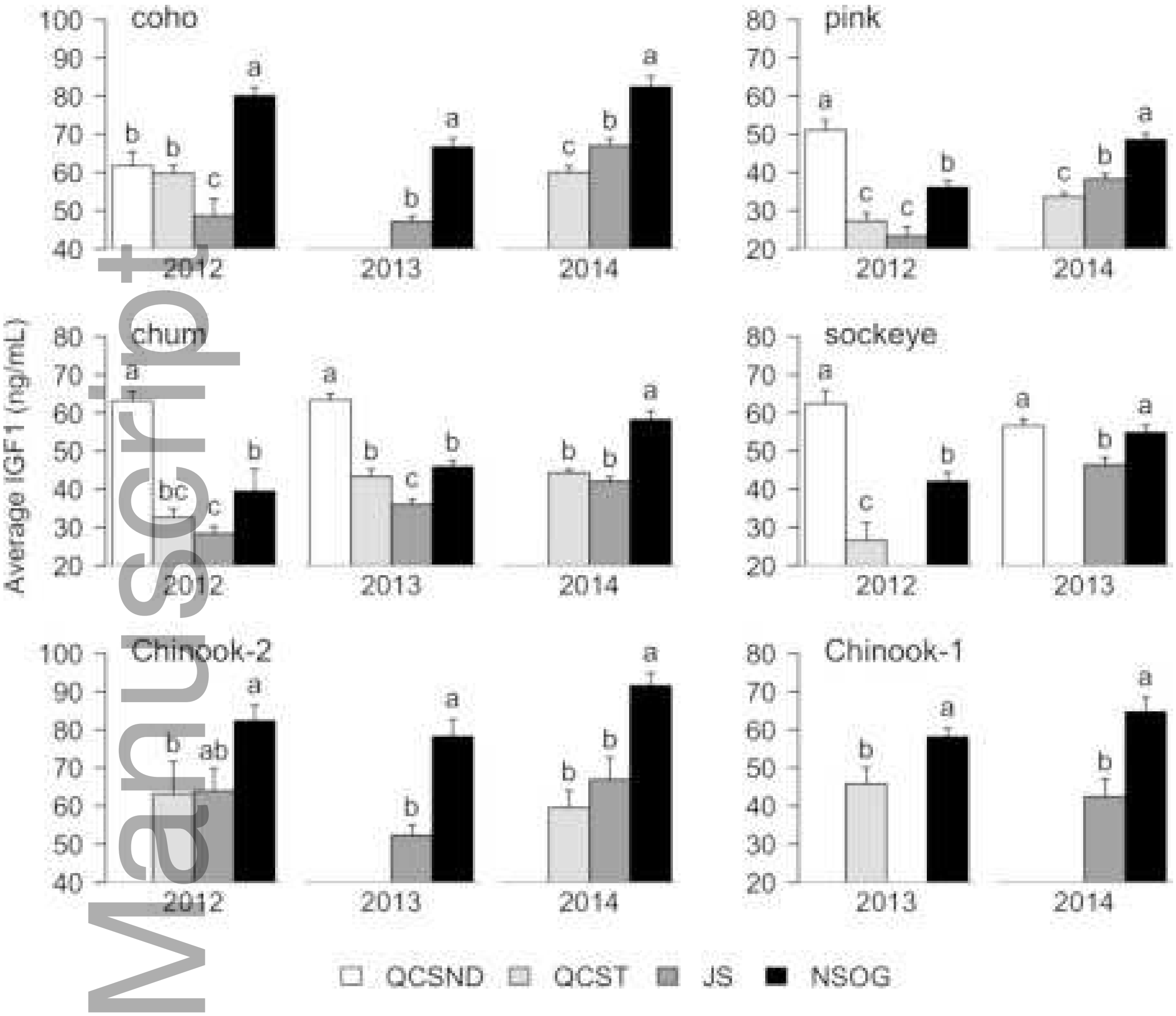

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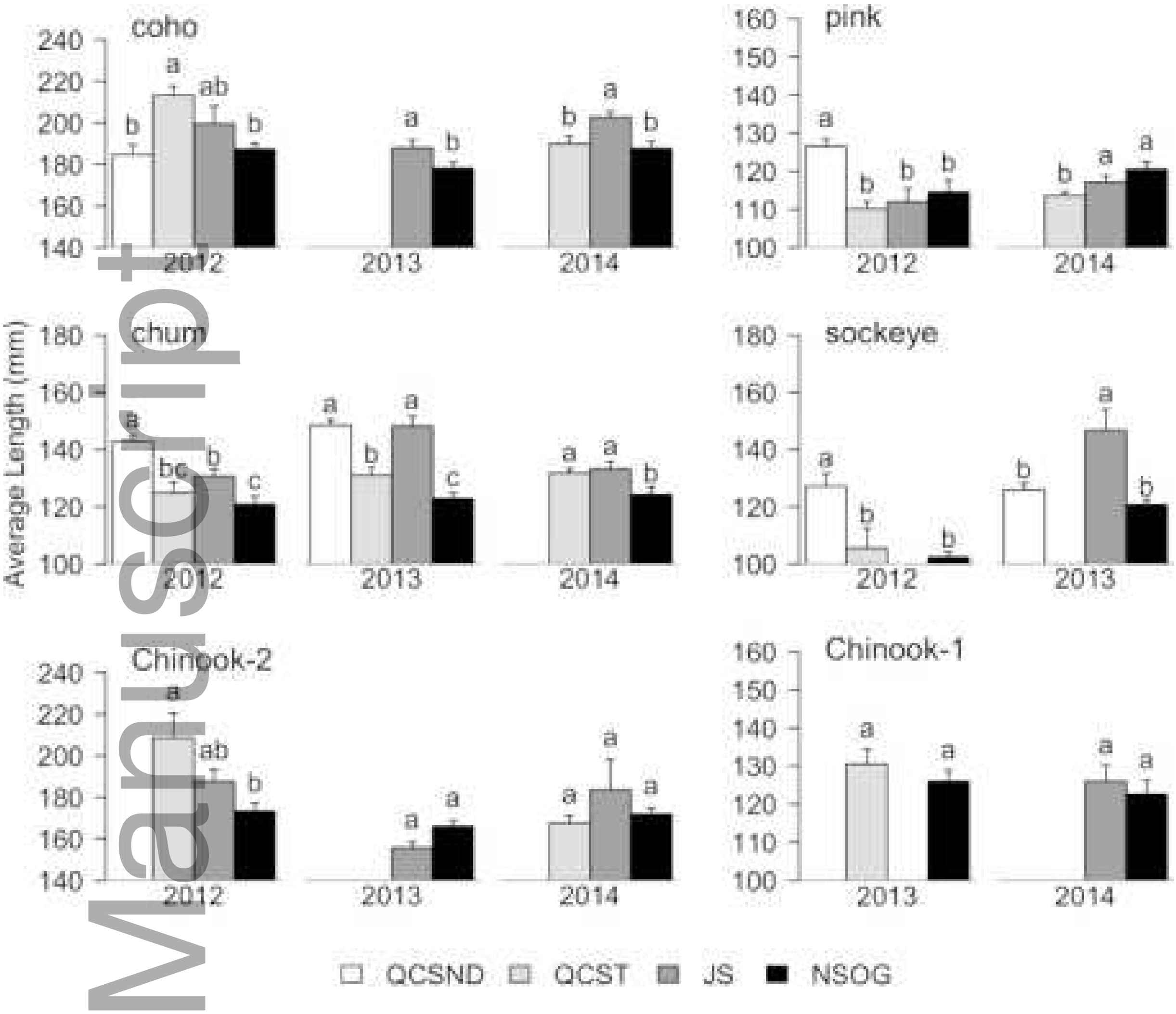

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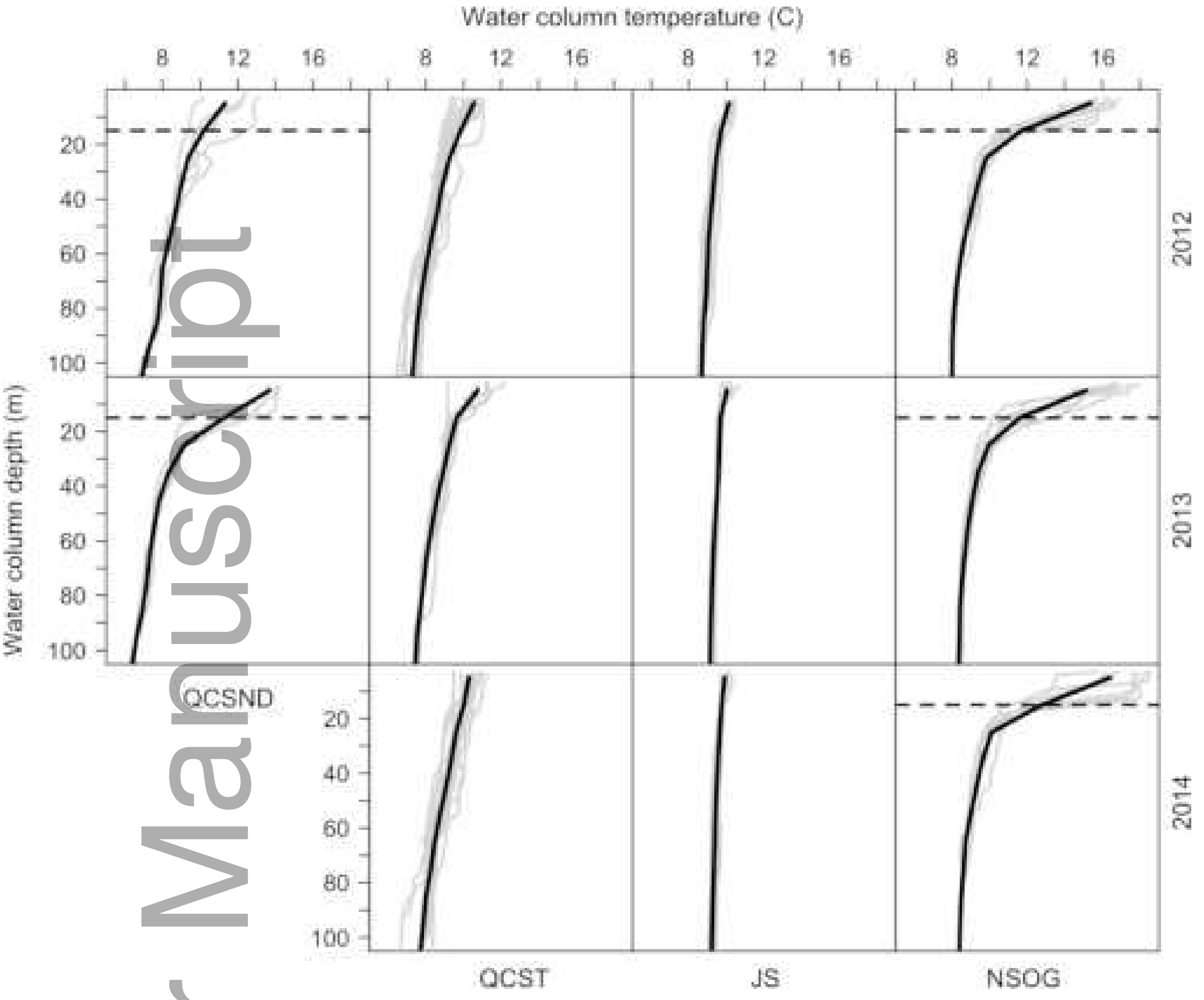

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