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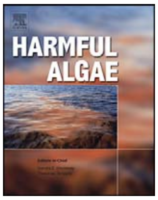

Fraser river sockeye salmon marine survival decline and harmful blooms of *Heterosigma akashiwo*

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ABSTRACT

A two-decade decline of Fraser River sockeye salmon, historically the most valuable west coast Canadian and United States salmon fishery, was linked with blooms of the harmful raphidophyte flagellate *Heterosigma akashiwo* in the Strait of Georgia ("Strait"), British Columbia. This region has the most intense and prolonged *Heterosigma* blooms of all B.C. regions analyzed. Marine survival of Chilko stock averaged 2.7% in years when juvenile sockeye salmon seawater migration in the Strait coincided with major *Heterosigma* blooms versus 10.9% in no or minor bloom index years. Since the mid 1990s, September young-of-the-year ("YOY") herring abundance was strongly correlated with marine survival rates of Chilko stock Fraser River sockeye salmon and *Heterosigma* bloom timing in the Strait. Juvenile sockeye salmon and YOY herring co-occur for only six weeks in mid-May through June during initial salmon migration in the Strait. Sockeye salmon marine survival rates were therefore determined in that early period. Fraser River discharge was a bloom-controlling factor with earlier and larger spring and early summer flows linked to major blooms in that period. *Heterosigma* is a most versatile and allelopathic harmful algal bloom species and may adversely affect sockeye salmon through acute and chronic toxicity or food web impoverishment.

1. Introduction

The most significant fish-killing harmful algal bloom (HAB) species in coastal waters of the Pacific Northwest, i.e., British Columbia (B.C.) and Washington State, is the golden brown, raphidophyte flagellate *Heterosigma akashiwo* (Hada) Sournia (herein, *Heterosigma*). It occurs on the North American west coast in an area that includes nearshore or inland sea waters from Mexico to the northern B.C. coast (Band-Schmidt et al., 2004; other references herein). In this paper we examine evidence that the Fraser River sockeye salmon (*Oncorhynchus nerka*) are being adversely affected by recurring *Heterosigma* blooms in coastal waters. The abundance (total catch plus escapement) and recruitment per spawner of this once prolific salmon run have been declining for two decades to record low levels in the past few years, despite careful management that allows for adequate numbers of spawners and resultant outmigrating smolts. The salmon run's abundance began to decline after peaking in the late 1980s, coinciding with commencement of major, sometimes basin-wide *Heterosigma* blooms that also killed farmed fish. The Fraser River sockeye decline was recently reviewed by a team of experts in B.C. who proposed that recent poor survival was related to loss of juvenile salmon after they began their seaward migration and that the food web may be involved (Simon Fraser University, 2009). They highlighted the need for increased research on the marine coastal environment where the juvenile sockeye initially migrate, and on climate impacts. Mortality of juvenile salmon migrating from their natal rivers and through coastal seas has long been thought to be an important factor limiting survival of salmonid populations (Ricker, 1976). The primary sources of total fish mortality have generally been attributed to fishing, predation by fish, seabirds and marine mammals, competition for prey, nearshore habitat loss, disease and food web perturbations from weather or climate factors. Previously, harmful algae have never been directly linked with significant losses of wild salmon in coastal oceans, although some observations of dead wild salmonids in shallow inlets or along beaches of deeper areas have occurred with every major *Heterosigma* bloom observed in North Puget Sound in the past two decades and recurring wild fish kills have occurred in other regions, as described below.

This paper focuses on the Strait of Georgia (herein, the Strait) and Puget Sound, two adjacent and deep fjord-like estuaries and the two pathways that connect them to the open ocean: to the south via the Strait of Juan de Fuca and to the north through

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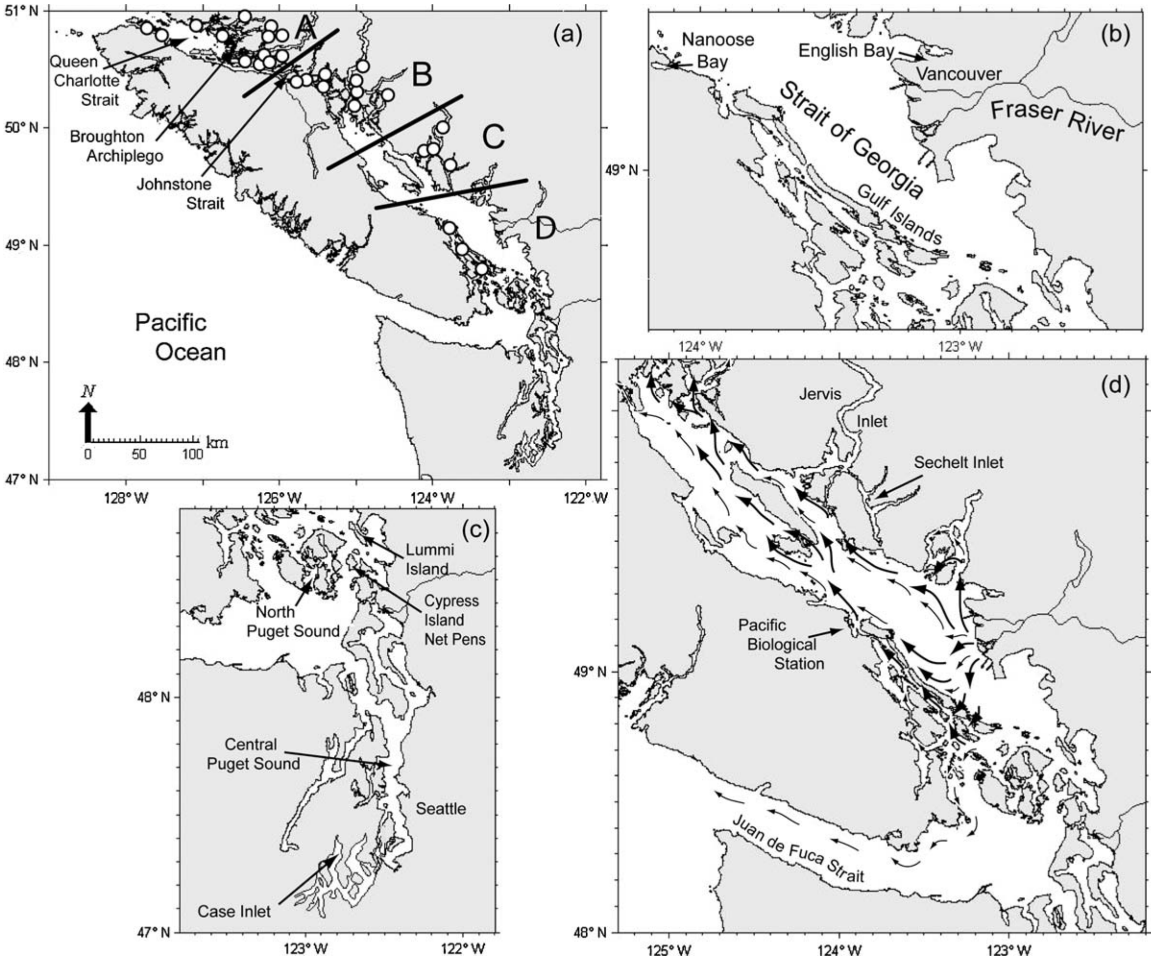


Fig. 1. Salish Sea place name maps including (a) Harmful Algae Monitoring Program regions A through D with open circles indicating sampling locations, (b) Southern Strait of Georgia locations, (c) Puget Sound locations and (d) juvenile sockeye salmon migration paths after Groot and Cooke (1987).

Johnstone Strait and inland sea waters between Vancouver Island and the B.C. mainland. We use the recently adopted term "Salish Sea" to describe the entire subject area (the Strait north through Queen Charlotte Strait, Strait of Juan de Fuca and Puget Sound, Fig. 1). The objective of this paper is to evaluate available data and information relating to *Heterosigma* as a possible contributing factor to the decline of the Fraser River sockeye salmon. We utilized up to eleven recent years of weekly algal cell count data from samples collected in four geographically diverse regions of B.C. by fish farmers and analyzed by an algal taxonomist (coauthor N. Haigh). That information was compared and contrasted to publications, reports and observations from the same region over the past 20 years and from inland marine waterways of Washington State that are biogeographically contiguous with the B.C. waters. We examine how HAB-related mortality of large numbers of wild salmon could have gone undetected and suggest how other causes of Fraser sockeye salmon mortality, such as food web impoverishment or disease/parasite infection, may be interlinked with *Heterosigma* blooms. We first provide a brief review of the nature of *Heterosigma*, its distribution and mode of toxicity, followed by an overview of Fraser River sockeye salmon early marine migration and behavior patterns relative to the alga.

2. *H. akashiwo* in the Salish Sea

Heterosigma is a member of the algal Class Raphidophyceae and is characterized by having a flattened, ovoid to pyriform, asymmetric shape. It has no rigid cell wall so can change shape rapidly. An anterior-facing flagellum pulls the cell through the water while a posterior-facing flagellum is less active. The alga is relatively easy to identify in unpreserved live samples and can be enumerated in preserved samples by an experienced taxonomist. It is photosynthetic, and has numerous golden brown chloroplasts and mucocysts. As part of its life cycle, *Heterosigma* forms cysts that sink to the sea floor and, if conditions allow, can germinate subsequent year(s) and produce another crop of swimming cells. It has been termed the most versatile and allelopathic harmful algal bloom species for many reasons including its antagonistic effects on organisms with size ranging from bacteria to fish (Smayda, 2006) and its ability to vertically migrate (Wada et al., 1985; Hershberger et al., 1997; Bearon et al., 2004). *Heterosigma* is euryhaline, growing at 5 psu salinity but significantly faster at 10 psu or above, depending on the Puget Sound ecotype considered (Fredrickson et al., in press) or above 20 psu in another study (Martinez et al., 2010). Reduced surface water salinities are common in the Fraser River estuarine plume, the Strait in general and broad areas of North Puget Sound and the Strait of Juan de Fuca during the late spring and early summer.

Heterosigma kills of farmed salmon or trout and some species of wild salmon and marine fish have been recorded in Puget Sound (Rensel, 1995, 2007; Horner et al., 1997; Hershberger et al., 1997; Connell and Jacobs, 1999; Connell et al., 2001) and British Columbia (Gaines and Taylor, 1986; Taylor and Haigh, 1993; Taylor et al., 1994; Pacific Biological Station, 1999; Taylor and Harrison, 2002; Rensel and Whyte, 2003). Many other locations worldwide have been affected including Scotland (Smayda, 1998, 2006), Spain

(Fraga, 1988), Chile (Clément and Lembeye, 1993), Japan (Honjo, 1993), China (Tseng et al., 1993), Tasmania (Smayda, 1998) and New Zealand (Chang et al., 1990). The alga is likely present, but not yet documented, in other locations. Adverse effects of *Heterosigma* exposure have been reported for wild salmon and marine fish in Puget Sound (Hershberger et al., 1997) and with reduced invertebrate and fish populations and disruptions of food webs in bays of the Gulf of Mexico region (Livingston, 2007). *Heterosigma* abundance has been increasing since year 2000 in the State of Georgia (USA) coastal ponds and estuaries where it has been linked repeatedly to wild fish kills (Verity, 2010). Cultural eutrophication of ammonia and dissolved organic nitrogen in this case was significantly correlated with the increasing bloom trend.

Adverse and allelopathic effects of *Heterosigma* are also known for various marine invertebrates including zooplankton, oyster larvae (Connell et al., 1997), adult oysters (sublethal damage to digestive system, Keppler et al., 2005), pandalid shrimp (Littik, 1998) and scallops (Wang et al., 2006). Pacific oysters in B.C. had high clearance rates of exponentially growing *Heterosigma* but ceased feeding when presented with senescent cultures of the alga (Cassis, 2005). In Narragansett Bay, Rhode Island, zooplankton grazing was not related to the initiation or collapse of the bloom, but there appeared to be no natural predators as grazing rates were chronically low (Tomas, 1980). However, Clough and Strom (2005) found that toxicity and grazer avoidance to a single *Heterosigma* clone grown under different conditions varied greatly and that different protist grazers had effects ranging from toxic to no avoidance of feeding.

Taylor and Haigh (1993) note that vegetative *Heterosigma* cells have regularly appeared in late spring in the English Bay since 1967 when phytoplankton surveys were first initiated, several years before commercial aquaculture net pens were placed in Salish Sea waters. The first recorded *Heterosigma* bloom in Puget Sound was near Lummi Island in 1976 (Gaines and Taylor, 1986; R. Horner pers. comm. 2009, Fig. 1). The first B.C. fish kills due to *Heterosigma* blooms were reported from a former fish farm site in Nanoose Bay, north of Nanaimo, B.C. (J. Fulton pers. comm., in Gaines and Taylor, 1986). At least a few large and persistent blooms occurred in Departure Bay and the Strait of Georgia in the 1990s (Pacific Biological Station, 1999) which contrasted with similarly infrequent but much shorter duration blooms in Puget Sound during that same period starting in 1989 (Rensel, 2007). Routine recording of cell density throughout large areas of B.C. marine waters began in 1999 with the initiation of the Harmful Algae Monitoring Program (HAMP, the primary data source for this paper). A conceptual model of cyst germination and initial bloom development for the Strait showed the importance of 15 °C water temperature as a threshold for *Heterosigma* cyst germination following the spring diatom bloom (Taylor and Haigh, 1993; Taylor and Harrison, 2002). These authors also opined that *Heterosigma* blooms were facilitated by vertical stratification due to the annual massive peak discharge of the Fraser River in late spring or early summer, which flows without impediment of storage reservoirs and dams.

Several possible causes of fish mortality from exposure to *Heterosigma* have been proposed but no single cause has been indisputably identified. The most often cited hypothesis involves gill damage and respiratory failure caused by algal production of reactive oxygen species (ROS), including hydrogen peroxide, hydroxyl free and superoxide radicals (Oda et al., 1997). These substances may be produced by the alga to convert organically chelated and unavailable ferric iron to available forms, which may be in limited supply for the alga during large blooms. The ROS-gill damage hypothesis is supported by observations of Yang et al. (1995) that the presence of ROS-destroying catalase, an enzyme found in most plant and animal cells that decomposes hydrogen peroxide into oxygen and water, improved survival of rainbow trout exposed to *Heterosigma* bloom water by 80%. Enhanced ROS production could result from nitrogen starvation; significantly higher ROS production occurred in cultures reared at N:P molar ratio of 9 to 1 versus the alga grown at 18 or 36 to 1 ratios (Skeen et al., 2002). It is reasonable to expect nitrogen limitation in large blooms of *Heterosigma,* as was found in Puget Sound field measurements (Rensel, 2007) due to extensive algal biomass demands, but the alga is able to vertically migrate to shallow nutriclines that are common in the Strait.

Conflicting results indicate that ROS production by *Heterosigma* is insufficient to cause toxicity (Twiner et al., 2001) and point instead to an unidentified organic compound (Twiner et al., 2004, 2005) and in two reports from Japan, a brevetoxin-like compound (Khan et al., 1997; Haque and Onoue, 2002). However, recent studies of another fish-killing raphidophyte, *Chattonella marina*, concluded that ROS was responsible for fish mortality and brevetoxin and other proposed causes such as mucus blocking of gills were not probable causes (Woo et al., 2006). Oysters exposed to *Heterosigma* bloom water had digestive gland lysosomal destabilization rates similar to those exposed to purified brevetoxin (PBTx-3), but the authors noted that while this effect may have been caused by brevetoxin it may instead be a common physiological stress response (Keppler et al., 2005). It is possible that there is a brevetoxin-like compound involved in fish deaths during *Heterosigma* blooms, but if so, it is highly labile and not persistent (Black et al., 1991). Alternatively, the toxin(s) also may be isolated in organs or tissues (e.g., fish gills) that typically are not consumed by humans (Anderson et al., 2001). It is also possible that different clones or ecotypes of *Heterosigma* have different toxin-producing capabilities that may be expressed in different locations and times. For example, in British Columbia, some *Heterosigma* blooms have not caused acute mortality of salmon in fish farms, but in Washington State all observed major blooms have resulted in at least some mortality of pen-reared salmon.

Some species of fish may be more or less resistant to the adverse effects of *Heterosigma*. Salmonid fishes including wild and farmed chinook (*Oncorhynchus tshawytscha*), coho (*O. kisutch*), chum (*O. keta*), rainbow trout (*O. mykiss*) and Atlantic (*Salmo salar*) salmon are all susceptible to the alga with varying survival rates in different blooms (e.g., Hershberger et al., 1997; Pacific Biological Station, 1999; Anderson et al., 2001). We know of no published reports of wild pink salmon (*O. gorbuscha*) mortality from exposure to the alga, although there have been recent observations of extensive adult pink salmon mortality associated with a *Heterosigma* bloom on the B.C. mainland (Klemtu area, A. Haslam, pers. comm. to N. Haigh, 2010). Pink salmon juveniles outmigrate seaward in coastal areas early in the spring, before *Heterosigma* blooms occur. Sockeye salmon (*O. nerka*) susceptibility to gill injury from harmful algae relative to other salmonids has not been studied. Sockeye salmon (*O. nerka*) may be at enhanced risk of gill injury from harmful algae as they have numerous and closely spaced gill rakers used to strain the water for plankton. Other salmonids including those reared in B.C. fish farms (Atlantic and chinook salmon), have fewer and more widely spaced gill rakers. Complicating efforts to understand the etiology of fish mortality, it has been impossible to kill fish in the laboratory with axenic (without bacteria or other algae) cultures of *Heterosigma*. However, non-axenic raw seawater from an apparent unialgal *Heterosigma* bloom has killed fish in the laboratory (e.g., Yang et al., 1995), but it is not possible to state with certainty the cause(s) of fish death, leading some to conclude that bacteria may be required for toxicity (e.g., Carrasquero-Verde, 1999). Individual ecotypes have different physiological capabilities of growth rate, photosynthetic ability, swimming speed, cyst formation, vegetative state activation, sensitivity to viral lysis and toxin production (Nagasaki and Yamaguchi, 1998; Nagasaki et al., 1999; Han et al., 2002; Cattolico and Deodato, 2009; Fredrickson et al., in press). Cryptic genetic variation among *H. akashiwo* ecotypes has been documented by comparative analysis of mitochondrial gene sequences. Recent data demonstrate that at least five ecotypes co-exist in the Salish Sea (M. Black and R.A. Cattolico, pers. comm., 2010); Fredrickson et al. (in press) report physiology and genetic differences of four ecotypes. Further, different cell type morphologies observed in blooms could be different life stages or ecotypes and cells may be motile or non-motile (possibly pre-cyst phases). These factors, and others such as nutrient limitation, discussed herein, may explain variations of *Heterosigma* toxicity observed by fish farmers in British Columbia.

3. Juvenile Fraser River sockeye salmon migration and behavior

Fraser River sockeye have a predominantly four year life cycle, with most juveniles rearing one winter in a lake prior to outmigration in their second year, followed by two winters at sea before returning to spawn as adults (Burgner, 1991; Roos, 1991). For example, juvenile sockeye entering the sea in 2007 would return as maturing adults in 2009. There are many different stocks of Fraser River sockeye, with juveniles having specific seaward migration patterns. Stock-specific freshwater production locations, growth rates, survival, and population behavioral differences result in differing freshwater and marine migration timing and behavior traits. For the purposes of management, adult returns are divided into four main run groups, aggregated by similar adult migration timing through marine approach areas to the river. These groups are the "Early-Stuart" run, with peak migration through approach areas in early July; "Early-Summer" run, with peak migration in mid to late July; "Summer-run" with peak migration in early to mid August; and the "Late-run" with peak migration in late August (Burgner, 1991). Adult sockeye of these groups return to the Fraser River using either of two coastal routes (Fig. 1): a northern approach through Johnstone Strait and the Strait of Georgia, or a southern approach along the west coast of Vancouver Island and through the Strait of Juan de Fuca and North Puget Sound (Groot and Quinn, 1987). The proportion of the run using each migration route to the river varies by stock group, year and migration week. In recent years, the percent of the total annual adult return migrating through the northern approach route has increased substantially (McKinnell et al., 1999; PSC, 2006).

Sockeye smolts start to emigrate from the Fraser River sometime in the last two weeks of April (Groot and Cooke, 1987), with the majority of them leaving the river and migrating through the Strait in May and June (Birtwell et al., 1987; Groot and Cooke, 1987; Burgner, 1991; Tucker et al., 2009; M. Lapointe, PSC, pers. comm. 2009). The smolts first concentrate around the Fraser River mouth and by late May smolts disperse north through the Strait and Johnstone Strait or west towards the San Juan Islands and Strait of Juan de Fuca (Fig. 1D). Migration data collected by Groot and Cooke (1987) suggest that most smolts migrate seaward in a northerly direction through the Johnstone Strait route, some along the east shore of Vancouver Island after crossing the Strait and some near the B.C. mainland coast with no stock-specific route preference (Groot and Cooke, 1987; Groot et al., 1989; Welch et al., 2009). Simulation models indicated that surface currents within the Strait affect the seaward migratory route of Fraser River sockeye smolts (Peterman et al., 1994). Prevailing northwest wind conditions in spring and early summer would force smolts along the eastern shore of the Strait. Less frequent southeast winds would force many smolts residing within the Fraser River plume and plume boundary along the western shore of the Strait.

Recent acoustic telemetry research of tagged and hatchery-reared Cultus Lake (Late-run) sockeye smolts showed that most of the tagged fish migrated seaward using the Strait of Georgia/Johnstone Strait route in the years studied, generally swimming closer to the B.C. mainland coast than the Vancouver Island side (Welch et al., 2009). The relatively large smolts used exited the river in <6 days and migrated out of the Strait in 27–34 days. Trudel et al. (2010) compared the swimming speed of free-ranging Cultus Lake sockeye of normal size that were caught in the ocean during trawl surveys and showed that, when expressed in terms of body lengths per second, both the large acoustically tagged smolts and the smaller coded-wire tagged smolts swam at similar rates (0.5–2 and 1.1–1.4 BL/s, respectively). As the larger acoustically tagged smolts were about 17–18 cm long, smaller smolts would have achieved mean swimming speeds of about 50% of the acoustically tagged cohort, resulting in clearance times from the river and Strait of <2 weeks and <2 months, respectively. Data collected by Groot and Cooke (1987) suggest that Fraser sockeye smolts take about one month to travel from the river through the northern Strait. Based on a comparison of peak smolt catch timing data in the Fraser River plume and Canadian Gulf Islands, Beamish et al. (2003) reported that Fraser sockeye smolts move through the Strait in 20 to 30 days. These migration rate estimates indicate that the bulk of the annual sockeye smolt migration that enters seawater in May and June exit the Strait by late June or early July, and the northern portion of Johnstone Strait for open ocean areas at some slightly later date. Importantly to the context of this paper, within the Strait, most sockeye smolts have been found within 10 m of the surface and concentrated relatively close to shore (Groot and Cooke, 1987).

4. Adult Fraser River sockeye salmon migration and behavior

Ultrasonic telemetry studies of adult sockeye salmon migrating to the Fraser River from Johnstone Strait indicate a preference for near-surface waters (Quinn and terHart, 1987). Quinn et al. (1989) reported these fish in the Strait of Georgia spent much less time near the surface than when the fish were in Johnstone Strait. Results of sockeye tracking (Quinn and terHart, 1987; Quinn et al., 1989) in both mixed and stratified waters indicated that fish migrating to the Fraser River in inside-marine areas were generally surface-oriented in vertically mixed waters, but remained at or below the thermocline in stratified waters. As the migrating adult fish approach the Fraser River they generally move shallower in the water column (Cooke et al., 2004), consistent with olfactory recognition and homing to their natal river's mouth in preparation for freshwater entry. Photoperiod cues of behavioral selection were apparent for water depths where density gradients were the largest, in addition to a distinct diurnal (dusk and dawn) vertical migration behavior (Pearcy et al., 1984; Quinn and Adams, 1996). Adult fish of the first three stock timing groups mentioned above enter the Fraser River quickly upon reaching the river mouth, within a week or ten days of their mean passage time through adjacent marine areas. However, after reaching the river mouth, fish from the Late-run group historically have delayed for three to six weeks within or near the Fraser River plume and mouth prior to entering the mainstem Fraser River to continue their spawning migration (Cooke et al., 2004; Hinch, 2009).

5. Salmon population decline

An alarming decline of total run size and survival of Fraser River sockeye salmon began in adult return year 1995, with progeny returns resulting from contributing adult brood years significantly below replacement levels in return year 2009, judging from the performance of Chilko stock survival (Table 1, Fig. 2). No clear explanations of the causes of the recent decline in Fraser River sockeye salmon marine survival are readily apparent. Poor estuarine and ocean productivity are possibilities being consid-

Table 1
Fraser River sockeye total run size for recent years, Chilko stock smolt to age four marine survival and same data shifted two years earlier for smolt seawater entry timing (*source*: M. LaPointe, Pacific Salmon Commission).

Adult sockeye salmon return year	Total adult sockeye salmon run size ($\times 10^6$)	Chilko stock marine survival	Chilko stock marine survival shifted −2 years
1989	18.62	5.52%	18.59%
1990	21.99	23.37%	14.26%
1991	12.41	18.59%	ND
1992	6.44	14.26%	7.06%
1993	23.63	ND	2.91%
1994	17.28	7.06%	13.78%
1995	3.90	2.91%	12.40%
1996	4.52	13.78%	7.85%
1997	16.36	12.40%	2.62%
1998	10.87	7.85%	6.29%
1999	3.64	2.62%	3.04%
2000	5.20	6.29%	3.82%
2001	7.21	3.04%	7.15%
2002	15.14	3.82%	2.14%
2003	4.87	7.15%	2.80%
2004	4.12	2.14%	5.70%
2005	7.08	2.80%	1.38%
2006	12.95	5.70%	3.61%
2007	1.35	1.38%	0.30%
2008	1.75	3.61%	[a]
2009	1.51	0.30%	[a]

[a] Adult fish not returned as of this writing.

ered. Fifty percent of the adult fish sampled far north near the Queen Charlotte Islands in recent years had genomic indications of disease, viral infections or parasite infestations associated with stress responses, suggesting at least some of the fish become ill or susceptible to disease after entering seawater (Miller, 2009). This scenario would not exclude earlier challenges to juvenile fish migrating in the Salish Sea.

Management responses to the declining returns have been reductions in the fraction of fish allowed for harvest. U.S. and Canadian fisheries for Fraser River sockeye in 2006–2009 were severely limited in response to extremely low return levels. The run size was so small in 2009 that nearly the entire adult return was required for brood stock to sustain future returns, and almost no fishing was allowed. In contrast to the robust sockeye salmon harvest levels observed over much of the previous four decades, total harvests have fallen to a 2005–2009 annual average of 1.5 million fish (range 74,000 to 5.3 million, PSC, 2009), with an annual fishery value that is a small fraction of that recorded prior to the mid-1990s. The recent failure of the Fraser River sockeye salmon run has resulted in extreme hardship for Canadian First Nations and U.S. tribal fishers. Due to their traditional, static fishing locations, they have no alternative ceremonial, subsistence, and commercial salmon fishing opportunities available.

6. Methods

6.1. *Heterosigma* data collection

We used B.C. Harmful Algae Monitoring Program (HAMP) monitoring data from four regions delineated within the B.C. inland marine waterway as a primary data source to estimate the potential effect of *Heterosigma* blooms on Fraser River sockeye. Weekly samples collected by B.C. aquaculture companies near fish farm sites and other areas are sent to HAMP for analysis. Other than this program, there has been no systematic quantitative monitoring of *Heterosigma* bloom extent and duration over broad areas of the Salish Sea for multiple years, although Puget Sound fish farmers routinely monitor algal populations from May through October each year with increasing intensity during elevated risk periods. HAMP data are from water bottle samples from 1, 5 and 10 m depth and preserved with Lugol's iodine solution. All HAB species are enumerated using a Sedgwick-Rafter counting slide and a standard transmitted light microscope. HAMP database regions include, from north to south: (A) Broughton Archipelago and Queen Charlotte Strait, (B) Johnstone Strait to Quadra Island areas, (C) Sechelt and Jervis Inlets and (D) Southern Strait (Fig. 1) Region D was sampled along western nearshore waters from Departure Bay to Saltspring Island. Sample collections in regions A, B and C were conducted by fish farmers both at fish farm sites and remote locations; Region D was sampled in Departure Bay at the Pacific Biological Station (PBS) and two other locations by N. Haigh, who has managed the program since it initiation, or others. We also rely on published and unpublished reports from Washington State waters by fish farmers and researchers that involve sample collection and cell counts at sentinel location and fish farm sites as well as visual observations from fixed wing aircraft. Because many major *Heterosigma* blooms are monospecific (i.e., few other algae present, Taylor and Haigh, 1993) experienced observers are able to identify bloom location visually from aircraft by the characteristic purplish-red color of *Heterosigma*. Small vessel based water sampling for algal cell counts and other measurements are then used for ground truthing the aerial observations in many cases. Sampling is biased to the regions surrounding the fish farms, but may extend to 50 km or greater during airplane and small boat surveys.

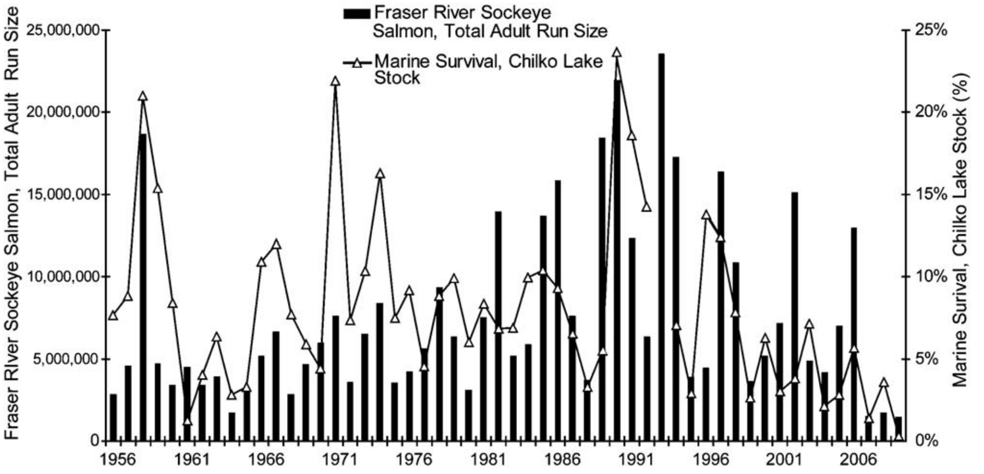


Fig. 2. Fraser River Sockeye Salmon total adult run size 1956–2009 and marine survival of Chilko Lake stock. *Data source*: Pacific Salmon Commission (2009).

There are currently eight continuously occupied commercial net pen fish farms in marine waters of Washington State. These farms are clustered in three widely distributed regions from Central to North Puget Sound and the Strait of Juan de Fuca. In North Puget Sound three farms are clustered near Cypress Island about 70 km south of the Fraser River mouth (Fig. 1c). In the much larger area of the Salish Sea waters of British Columbia, there are approximately an order of magnitude greater number of fish farms, but none currently in the Southern Strait (Fig. 1). Many fish farms were once located in Region C of British Columbia, approximately 100 km north of the Fraser River mouth, but recurring *Heterosigma* blooms resulted in removal or relocation of most of them. Presently, most B.C. fish farms are located farther north in Regions A and B or within inlets along the west coast of Vancouver Island.

Heterosigma cell counts from the HAMP database and were ranked by density as follows: 0 = no cells, 1 = low number of cells (i.e., not bloom levels, 0–10 cells mL^{-1}), 2 = moderate numbers of cells (possible to certain blooms, 11–999 cells mL^{-1}) and 3 = large numbers of cells (blooms of $>$1000 cells mL^{-1}). The concentration of cells causing salmon mortality is uncertain but is thought to occur in the level 2 range (Rensel and Whyte, 2003). A "bloom index" was constructed by summing different bloom rankings for known sockeye migration periods and regions. To indicate major blooms, level 2 and 3 rankings for each time period of interest were summed. Data from three annual periods (May through October, mid May through June for juvenile sockeye migration timing and July and August for adult sockeye migration timing) in the Salish Sea were compiled separately.

Sampling sites within regions were variable in number, averaging about 3 per year for Regions A and B and about 1.5 per year for Regions C and D. Fish farms in B.C. are relatively near shore, in water depths generally ranging from approximately 40–80 m. As such, these farm sampling sites are considered physically nearshore but not in any case biogeographically littoral (i.e., intertidal or nearshore subtidal).

Up to eleven years of HAMP data (1999–2009) were available in Regions A, B and C. As there have been no active fish farms in Region D (South Strait) since 2003, and few there historically, annual data collection was more intermittent in this region with 8 of the 11 years having complete or partial records. Prior to the HAMP program and during the 1990s, biologists at the Fisheries and Oceans Canada PBS were involved in HAB research, recorded cell counts and hydrographic conditions in the vicinity and reported details of major blooms (Pacific Biological Station, 1999). Similarly, major bloom records from North and Central Puget Sound were used to evaluate what may have happened in the South Strait of Georgia during the three years when HAB data were not collected out of the entire 21-year period between 1989 and 2009.

6.2. Sockeye salmon survival

A primary metric to estimate the possible interaction of *Heterosigma* blooms with Fraser River sockeye was the annual marine survival data for the Chilko Lake stock, provided by the Pacific Salmon Commission (PSC). Marine survival is defined as number of returning adults divided by the number of smolts counted at weirs during migration from Chilko Lake, where adults are the total age-four adult run of the parental stock that includes the total fishery catch plus the observed spawning escapement plus the estimated freshwater adult en route loss (i.e., fish that entered the river and were counted in the lower river by hydroacoustic methods but died before spawning). Recruit per spawner estimates for the Fraser River sockeye salmon aggregate or individual stocks result from the combination of both freshwater and marine mortality, which are not separable. We therefore rely on the Chilko Lake stock marine survival data. Chilko Lake sockeye are considered a "summer run" timing stock (i.e., adult fish return to the river mouth in midsummer) and are therefore somewhat of a median representative of many of the other Fraser River stocks in terms of probable timing of adult migration through nearshore coastal waters. Stock-specific juvenile sockeye migration data are mostly not available from marine waters. We estimated the approximate temporal distribution of the bulk of outmigrating juvenile Chilko stock and most other sockeye juveniles relative to the HAMP sampling regions by utilizing the three-year study results of Groot and Cooke (1987). The period of mid-May through the end of June was selected as representative of the time that juvenile fish would be sequentially migrating into and through Regions D, B and A, from south to north, with a one week lag for Region A. The published literature provides no specific differentiation for Region A, We varied the timing plus or minus a week to find no significant change in the results reported below.

Some juvenile fish begin to migrate out of the river earlier than mid May, as early as late April, but the river mouth is remote from the HAMP sampling regions and some of the fish may remain near the river mouth and estuarine plume before migrating. Sockeye smolt migration in this most northerly subarea was not studied by Groot and Cooke (1987). We assumed that juvenile sockeye migration in the most northerly region (A) was approximately one week later relative to the southerly regions to account for additional travel time to reach this area. Recent acoustic tagging studies of Cultus Lake stock sockeye smolts (Welch et al., 2009) indicated most fish during the 2004–2007 study period moved rapidly northwards through Johnstone Strait to the Pacific Ocean with just a small percentage moving southward through the Strait of Juan de Fuca. Except for Welch et al. (2009) and Trudel et al. (2010), there are no juvenile sockeye migration timing data for Queen Charlotte Strait and Broughton Archipelago, as discussed above.

For returning adult Chilko stock sockeye, we estimated the bulk of the annual migration passes through Regions A, B and D in July and August, based on the literature previously discussed and PSC unpublished data (M. Lapointe, pers. comm. 2009). Table 1 includes total Fraser River run size (catch plus escapement), and marine survival of Chilko stock expressed as juvenile seawater entry and adult return year.

Statistical associations, using Pearson's correlations, were tested between the sum of annual bloom index levels 2 and 3 for juvenile or adult migration periods and the Chilko sockeye salmon marine survival rate estimates. Daily Fraser river discharge during the juvenile migration period was compared between bloom and non-bloom years using Student-t tests. Level 1 bloom index was only included in assessments to indicate *Heterosigma* presence or absence, as it represents low concentration of cells, below the probable level required to induce fish mortality.

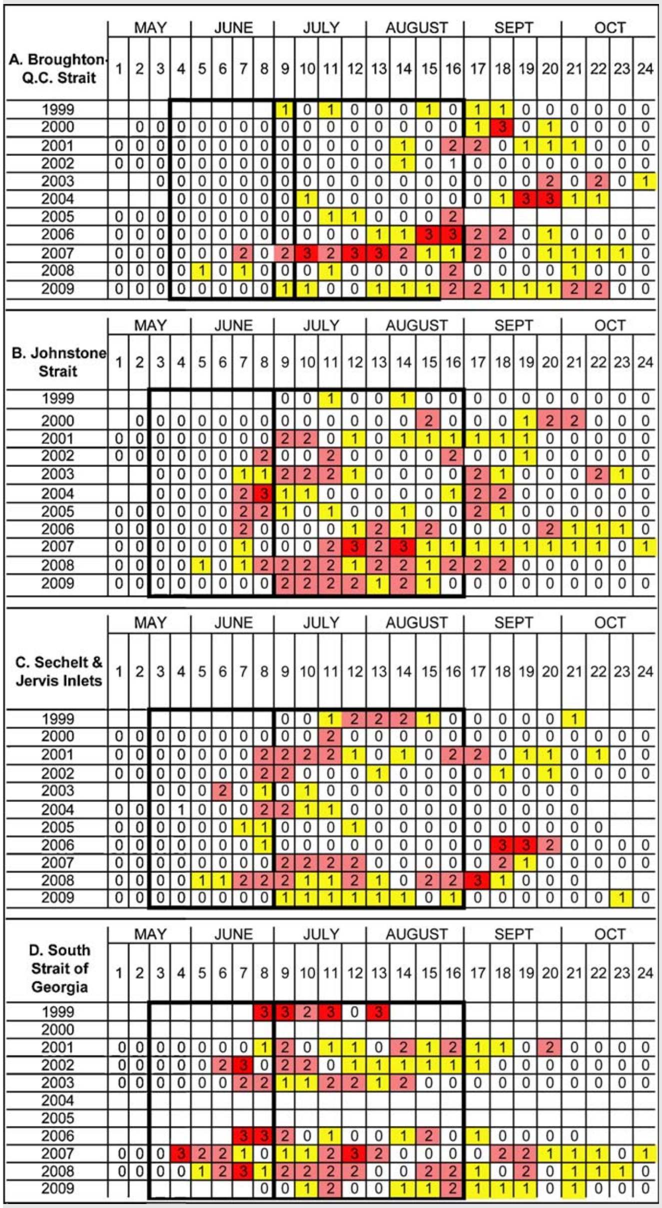
7. Results

7.1. Heterosigma database

Heterosigma blooms in sampled regions of British Columbia waters were remarkably frequent, particularly during the mid-June through October period in many years (Tables 2 and 3). The largest frequency of detection occurred in the South Strait region where 48% of the samples collected throughout the May through October period tested positive for *Heterosigma* (Table 3). Region B, Johnstone Strait to Quadra Island, averaged 35% cell detection, followed by Regions A and C with 29% and 24% occurrence respectively.

For estimated juvenile sockeye migration timing in years with complete weekly data (Table 3), mean annual level 2 + 3 bloom index increased from north (Region A) to south (Region D); 40% of

Table 2
Harmful Algal Monitoring Program results for *Heterosigma akashiwo* abundance by week, May through October, 1999 through 2009. Numbers indicate relative density of cells as explained in the text and are color coded to indicate patterns. Blanks indicate no data collection. Dark outline within each year indicates potential overlap with juvenile (left side) or adult (right side) sockeye salmon. 0 = No cells, 1 = low number of cells (i.e., not bloom levels, <10 cells mL^{-1}), 2 = moderate numbers of cells (possible to certain major blooms, 11–999 cells mL^{-1}) and 3 = large numbers of cells (major blooms of >1000 cells mL^{-1}).



	MAY				JUNE				JULY				AUGUST				SEPT				OCT			
A. Broughton-Q.C. Strait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1999									1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0
2000		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	0	1	0	0	0	0
2001	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	2	0	1	1	1	0	0	0
2002	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
2003			0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	1
2004				0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	3	3	1	1		
2005	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2								
2006	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	3	2	2	0	1	0	0	0	0
2007	0	0	0	0	0	0	2	0	2	3	2	3	3	2	1	1	2	0	0	1	1	1	1	0
2008	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	2	0	0	0	0	1	0	0	0
2009	0	0	0	0	0	0	0	0	1	1	0	0	1	1	1	2	2	1	1	1	2	2	0	0

	MAY				JUNE				JULY				AUGUST				SEPT				OCT			
B. Johnstone Strait	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1999									0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
2000		0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	2	2	0	0	0
2001	0	0	0	0	0	0	0	0	2	2	0	1	0	1	1	1	1	1	1	0	0	0	0	0
2002	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	2	0	0	1	0	0	0	0	0
2003			0	0	0	0	1	1	2	2	2	1	0	0	0	0	2	1	0	0	0	2	1	0
2004			0	0	0	0	2	3	1	1	0	0	0	0	0	1	2	2	0	0	0	0	0	0
2005	0	0	0	0	0	0	2	2	1	0	1	0	0	1	0	0	2	1	0	0	0	0	0	0
2006	0	0	0	0	0	0	2	0	0	0	0	1	2	1	2	0	0	0	0	2	1	1	1	0
2007	0	0	0	0	0	0	1	0	0	0	2	3	2	3	1	1	1	1	1	1	1	1	0	1
2008	0	0	0	0	1	0	1	2	2	2	2	1	2	2	1	2	2	2	0	0	0	0	0	
2009	0	0	0	0	0	0	0	0	2	2	2	2	1	2	1	0	0	0	0	0	0	0	0	0

	MAY				JUNE				JULY				AUGUST				SEPT				OCT			
C. Sechelt & Jervis Inlets	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1999									0	0	1	2	2	2	1	0	0	0	0	0	1			
2000	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
2001	0	0	0	0	0	0	0	2	2	2	2	1	0	1	0	2	2	0	1	1	0	1	0	0
2002	0	0	0	0	0	0	0	2	2	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0
2003			0	0	0	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0			
2004	0	0	0	1	0	0	0	2	2	1	1	0	0	0	0	0	0	0	0	0	0			
2005	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0		
2006	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	3	2	0	0	0	0
2007	0	0	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	2	1	0	0	0	0	0
2008	0	0	0	0	1	1	2	2	2	1	1	2	1	0	2	2	3	1	0	0	0			
2009	0	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	0	0	0	0	0	0	1	0

	MAY				JUNE				JULY				AUGUST				SEPT				OCT			
D. South Strait of Georgia	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
1999								3	3	2	3	0	3											
2000																								
2001	0	0	0	0	0	0	0	1	2	0	1	1	0	2	1	2	1	1	0	2	0	0	0	0
2002	0	0	0	0	0	2	3	0	2	2	0	1	1	1	1	1	1	0	0	0	0	0	0	0
2003	0	0	0	0	0	0	2	2	1	1	2	2	1	2	0	0	0	0	0	0	0	0	0	0
2004																								
2005																								
2006							3	3	2	0	1	0	0	1	2	0	1	0	0	0	0			
2007	0	0	0	3	2	2	1	0	1	1	2	3	2	0	0	0	0	2	2	1	1	1	0	1
2008	0	0	0	0	1	2	3	1	2	2	2	2	0	0	2	2	1	0	2	0	1	1	1	0
2009								0	0	1	2	0	0	1	1	2	1	1	1	0	1	0	0	0

the sampled weeks in Region D, South Strait, for the mid May through June period were ranked as bloom levels 2 or 3. Other regions were ranked much lower, not exceeding 18% occurrence (Regions B and C) and very low for Region A (3%). When ranked by potentially fish-killing *Heterosigma* bloom levels 2 and 3 during adult sockeye salmon timing the South Strait was also highest; 30% of the sampled weeks were observed to be bloom levels 2 or 3, followed by 24% occurrence in Region B. A correlation matrix (not shown) was used to assess the possibility that the bloom index for the entire mid May through August sockeye migration time period in the HAMP database was similar between any of the pairs of regions. Only Regions B and C were significantly correlated ($r = 0.63$, $p = 0.04$). These regions are adjacent and sampling sites are a mixture of channel and bay locations. Within regions other timing and bloom density differences become apparent.

Table 3
Percent detection of *Heterosigma* cells by migration timing category and region for May through October (entire database time period, all bloom index levels 1, 2 and 3), juvenile migration period and adult migration period in Salish Sea waters (only bloom levels 2 and 3 combined).

Migration timing, bloom level	Region	Detection
May thru October, bloom levels 1 + 2 + 3	A	29%
	B	35%
	C	24%
	D	48%
Juvenile timing, bloom levels 2 + 3	A	3%
	B	18%
	C	18%
	D	40%
Adult timing, bloom levels 2 + 3	A	13%
	B	24%
	C	15%
	D	30%

7.1.1. Region A: Queen Charlotte Strait and Broughton Archipelago

Heterosigma blooms occurred every year but 1999 and 2002 in this region, typically in mid August through mid October (Table 2). This timing was later than other regions reported here with no detections in the estimated juvenile sockeye migration period until one level 2 occurrence in 2007 and two level 1 occurrences in 2008. Only two level 2 or 3 blooms occurred during the July through August adult sockeye migration period until 2006, when two weeks of major blooms occurred in late August. Bloom activity clearly increased later in the time series, particularly when adult sockeye were migrating. Blooms during 2007 were very prevalent with continual levels 2 and 3 blooms occurring from the beginning of July until the last two weeks of August, but lower level 1 cell occurrences continued through that period too. Earlier *Heterosigma* cell occurrences continued in 2008 and 2009 but only as level 1 blooms in both cases and not early compared to Region D, discussed below.

7.1.2. Region B: Johnstone Strait to Quadra Island

Fewer major blooms (index level 2 + 3 events) occurred in this region, with only three level 3 weekly blooms observed. Blooms began in mid to late June in five of ten years and bloom activity during the July through August adult migration period was more pronounced in later years 2007–2009 than earlier years 1999–2006. Blooms during the juvenile sockeye migration period in this subarea were most pronounced in 2004–2006, but with only one level 3 bloom. When adult sockeye were migrating in 2008, 6 out of 8 weeks had level 2 blooms recorded. In 2009 there were 5 level 2 blooms in the same period.

7.1.3. Region C: Sechelt and Jervis Inlets

In Sechelt and Jervis Inlets, *Heterosigma* bloom level 2 activity centered in the late June and early July period. No level 3 blooms occurred throughout either the estimated juvenile or adult sockeye migration periods in this region, but three were reported in September during 2006 and 2008.

7.1.4. Region D: South Strait of Georgia

Level 2 or 3 *Heterosigma* blooms occurred in every sampled year, a frequency that was not observed in any other region. This

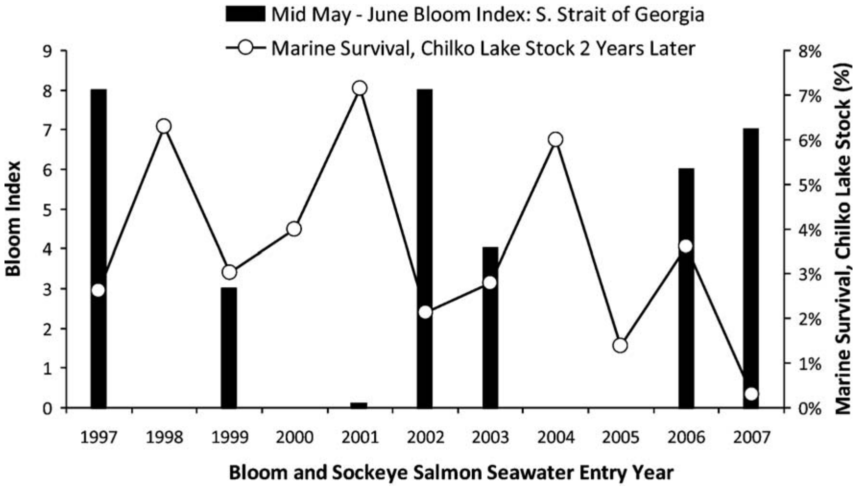


Fig. 3. Comparison of mid-May through June bloom index for the South Strait of Georgia (Region D) versus Chilko stock sockeye salmon marine survival as adults two years later. 2001 bloom index was zero.

region also had the most extensive late spring and early summer *Heterosigma* activity. Prior to 2007, bloom index level 1 through 3 occurrences commenced in the second to fourth week of June and all but one bloom index level 2 or greater blooms were completed by the end of August. In 2007 and 2008, however, major blooms (index levels 2 or 3) began in the last week of May and first week of June, respectively, a unique aspect of blooms in this region compared to other regions. A level 2 bloom occurred for the first two weeks of June 2008, intensified to level 3 in the third week of June and continued until the end of July at level 2.

7.2. Bloom occurrence during fish migration

Bloom index level 2 and 3 occurrences were summed for each year's estimated juvenile or adult sockeye migration period by region and compared to the sockeye salmon marine survival data presented in Table 1 and Fig. 3. Table 4 summarizes the Pearson's correlation coefficients (r) and alpha levels of these comparisons. For juvenile fish, there was a significant inverse correlation between South Strait *Heterosigma* bloom index in smolt year and Chilko stock marine survival to adult return two years later with a coefficient of -0.83 ($p = 0.04$).

A moderately strong inverse correlation between the same factors is shown for Region A, Broughton Archipelago and Queen Charlotte Strait ($r = -0.57$, Table 4). However this and other correlations except Region D juvenile timing were not statistically significant. To increase sample size we utilized weekly data collected in the 1997 by the Pacific Biological Station in the Southern Strait (Pacific Biological Station, 1999). Data were also available for 1993, but not for the entire juvenile sockeye migration period; other years in the 1990s were apparently non-bloom or minor bloom years or without useful weekly records of timing or sockeye survival data (e.g.,1989 and 1991, respectively, Table 5). Adding 1997 data to the correlation analysis described above and using only years with no missing juvenile migration weekly data ($N = 5$), we found a correlation coefficient of -0.88 ($p = 0.05$) between level 2 + 3 bloom index and Chilko stock marine survival. Finally, we reconfigured the same data into four bloom levels by splitting bloom level 2 in two (11–499 and 500–999 cells mL^{-1}) and for complete data years in the Strait found the correlation to improve (Pearson's $r = -0.91$, $p = 0.03$). Correlations between survival of sockeye to returning adult stage and bloom index varied from moderately weak ($r = -0.31$ for Region C) to weak ($r = -0.09$ for Region D, Table 4) and none were statistically significant.

To further examine the effect of missing years in the above Region D juvenile sockeye timing analysis, data and observations from adjacent waters of Puget Sound, immediately south of the South Strait (Region D) were compared (Table 5). There were no observed fish kills or major blooms in Puget Sound during the years when algal data were not collected in Region D (years 2000, 2004 and 2005) and the reasons for not collecting data were not related to bloom presence or absence. Major blooms and fish kills in Puget Sound and the Strait were observed during 1989, 1993, 1997, 2006 and 2007 but not in both areas in 1991, 1999, 2002, 2003 and 2008. 1989 and 1991 were reportedly major *Heterosigma* blooms years in the general region (Taylor and Haigh, 1993) but the former was located mostly in Jervis Inlet, not the south Strait (Taylor and Haigh, 1993). Blooms in 1991 commenced in late May and covered

Table 4
Correlation coefficients for Chilko sockeye salmon stock marine survival and *Heterosigma* bloom index levels 2 + 3 during juvenile ($N - 2$ years) and adult fish migration timing (N years).

Region	Juvenile years	Juvenile correlation coefficient	Adult years	Adult correlation coefficient
(A) Broughton-Queen Charlotte Strait	2000–2007	−0.57	1999–2009	−0.29
(B) Johnstone Strait	2000–2007	+0.05	1999–2009	−0.19
(C) Sechelt and Jervis Inlets	2000–2007	+0.56	1999–2009	−0.31
(D) South Strait of Georgia	1999, 2001–2003 2006–2007	−0.83*, $p = 0.04$	1999, 2001–2003, 2006–2009	−0.09
(D) South Strait of Georgia (complete data years only)	1997, 2001, 2002, 2003, 2007	−0.88*, $p = 0.05$	NA	
(D) South Strait of Georgia (complete data years only, split level 2 bloom rank into two new ranks)	1997, 2001, 2002, 2003, 2007	−0.91*, $p = 0.03$	NA	

Table 5
Comparison of major *Heterosigma* bloom events and timing from South Strait of Georgia publications, HAMP Database (level 2 and 3 blooms) and Puget Sound records during juvenile and adult Fraser River sockeye migration periods as defined herein. Timing shown in week number of year for HAMP database that begins with May 1 each year. Major blooms are those that were persistent in B.C. for several weeks or killed extensive numbers of farmed fish in Puget Sound during the Fraser River juvenile sockeye Strait of Georgia migration period.

Year	South Strait of Georgia bloom occurrence or timing	Puget Sound bloom occurrence or timing	Major blooms in both areas	Bloom in Puget Sound, not in Strait of Georgia	Data source
1989	Bloom occurred, timing uncertain	Early September	Yes	NA	Taylor and Haigh (1993), Pacific Biological Station (1999), Rensel (1995, 2007)
1990	Unknown	9	unknown	NA	Harrell (1990), Rensel (1995, 2007)
1991	~4–12	None observed	No	No	Taylor and Haigh (1993), Pacific Biological Station (1999), but no sockeye data
1993	8–16	10	Yes	No	Pacific Biological Station (1999), Rensel (1995)
1997	8–16	11	Yes	No	Pacific Biological Station (1999), Connell and Jacobs (1999)
1999	8–11, 13	None observed	No	No	HAMP; Rensel (2007)
2000	Unknown	None observed	No	NA	Rensel (2007)
2002	6–10	None observed	No	No	HAMP; Rensel (2007)
2003	7–8	None observed	No	No	HAMP, low cell counts
2004	Unknown	None observed	No	NA	Rensel (2007)
2005	Unknown	None observed	No	NA	Rensel (2007)
2006	7–9, 15	8–9, 13	Yes	No	HAMP; Rensel (2007)
2007	4–6, 11–13	4, 12	Yes	No	HAMP; Rensel (2007)
2008	6–7, 9–12, 15–16	None observed	No	No	HAMP; Rensel (2007)

a large area of the entire Strait by late June but no marine survival data were available for Fraser River sockeye from that seawater entry cohort. Two level 2 blooms were recorded in 2003, but no level 3 blooms, so that year qualified as a major bloom year according to the bloom index but was possibly borderline. Overall, major blooms during sockeye migration periods occurred in the Strait but not in Puget Sound during five of the ten comparable years, or 50% of the comparable observations (Table 5). This qualitative evaluation indicates a 50% probability of a major bloom in Region D during the unsampled algal years of 2000, 2004 and 2005. One of these, year 2005, yielded one of the lowest Chilko stock marine survival rates (1.4%) in recent records. The only lower marine survival in recent years was 0.3%, from the 2007 seawater entry juvenile cohort that returned as adults in 2009. This probability analysis indicates that at least one major *Heterosigma* bloom may have occurred in the Strait during the missing data years but there are no means to retrospectively investigate.

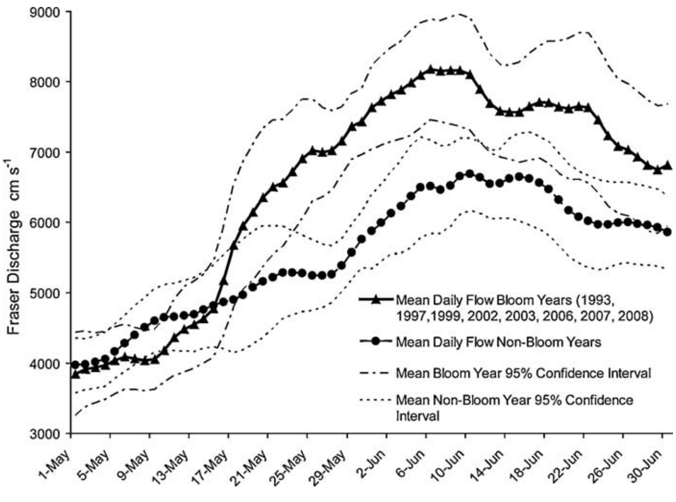


Fig. 4. Mean and 95% confidence interval of daily Fraser River discharge at Hope, B.C. during May and June period for bloom years (1993, 1997, 1999, 2002, 2006, 2007 and 2008) versus other years in the period 1989–2009.

7.3. Fraser River discharge and bloom occurrence

To evaluate possible effects of varying Fraser River discharge volume and timing on *Heterosigma* blooms during the juvenile sockeye salmon migration period, we plotted river discharge from years of known major blooms versus non-bloom years in Region D for the 1989 through 2009 period discussed above. Mean and confidence interval discharge plots (Fig. 4) and a Student's *t*-test of two sets of data indicate significantly greater river discharge ($p = 0.001$) in the May–June period of major *Heterosigma* bloom years versus other years. From 1989 through 1998, there were extremely large and early flows in major bloom years 1993 and 1997 that exceeded normal flows by up to 90% in the latter year. During the 1999–2009 period a similar trend was seen for bloom years. Rapid divergence of mean flow for the bloom versus non-bloom years began in mid May, coinciding with the bulk of the juvenile sockeye outmigration. The categories remained distinctly different throughout the remainder of the time series. Given past associations of *Heterosigma* blooms with brackish water conditions, these data suggest a probable linkage between May–June *Heterosigma* blooms and larger as well as earlier-than-normal peaking river discharge. The significance of statistical difference increases if only discharge between mid-May and June is considered, encompassing the period when most Fraser River juvenile sockeye migration occurs in the South Strait.

8. Discussion

We have presented correlative evidence of a link between Fraser River sockeye decline and the concurrent onset of large, frequent and possibly earlier than normal *Heterosigma* blooms in the South Strait of Georgia. In recent years these blooms have more fully coincided with seawater entry and outmigration of the juvenile sockeye salmon. If mortality of sockeye smolts was occurring in the Strait during bloom years, resident fish that inhabit near-surface water may also be expected to be affected. We examined young-of-the-year (YOY) September herring survey catch data published by Schweigert et al. (2009) extending from 1992 to 2007 (1991 purposely excluded for method differences, 2008 data point provided by J. Schweigert, personal communica-

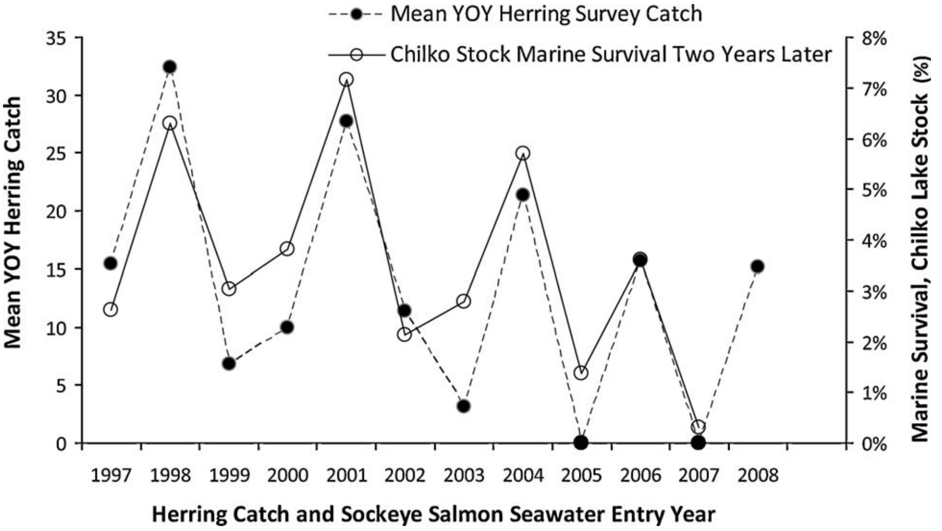


Fig. 5. Strait of Georgia herring survey mean catch (Schweigert et al., 2009) and Chilko sockeye stock marine survival as adults two years later.

tion). Beginning in 1997 and extending to 2007 there was a highly significant correlation between YOY herring catch and Chilko sockeye salmon marine survival ($r = 0.90$, $p = 0.0001$, Fig. 5). Including earlier years (1992–1994) in the analysis resulted in a non-significant correlation (e.g., $r = 0.26$ for 1992–2007, $p = 0.36$). Using data for the period 1995–2007, the correlation coefficient increased to 0.66 ($p = 0.02$), and increased further to 0.93 ($p = 0.0001$) for the 1998–2007 period. Strait of Georgia herring hatch in early spring and most sockeye enter seawater beginning in late spring. Chilko stock sockeye apparently leave the Strait within about six weeks, although other stocks may have different timings. YOY herring remain in the Strait through summer and are systematically surveyed in September. The two species are affected by the same environmental conditions during the six week period but, because of size differences, likely consume different prey or life stages of the same prey species. Herring survey catch was highly correlated ($r = 0.93$, $N = 5$) with *Heterosigma* bloom index in the Southern Strait from mid May through June in complete data years described above, but at a lower alpha level ($p = 0.07$). The concept of significant early marine mortality of sockeye salmon is not new (e.g., Furnell and Brett, 1986). However, these data are remarkably strong, supporting the hypothesis that two-year-long marine survival rates of the sockeye salmon are principally determined within the Strait of Georgia. This occurs within the first six weeks of sockeye seawater rearing during the recent period of declining sockeye survival (since the mid 1990s) and appears linked to *Heterosigma* bloom occurrence.

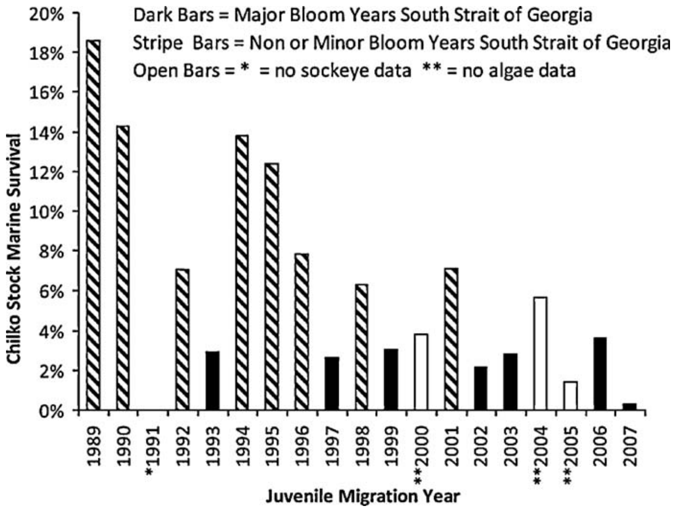


Fig. 6. Chilko Stock Fraser River sockeye marine survival and occurrence of major *Heterosigma* blooms during juvenile sockeye salmon years in the South Strait as measured through the HAMP database (1999–2009), Department of Fisheries and Oceans observations at the Pacific Biological Station (1993–1999), and inferred from major bloom records from Puget Sound (1989–2009). Missing years in fish or algae database indicated with asterisks.

Fig. 6 is a qualitative summary of the HAMP (1999–2007) and other prior data (PBS, 1989; Taylor and Haigh, 1993, period 1989–1998) assembled in one illustration and considering the data qualifications discussed above. Prolonged and intense blooms of *Heterosigma* were documented in 1993 and 1997 at the Pacific Biological Station (Pacific Biological Station, 1999). Chilko stock juvenile sockeye salmon entering the sea during these years produced the two lowest marine survivals for the 1989–1999 period (2.9% and 2.6%, respectively) two years later. For comparison, 12.3% average marine survival occurred during non-bloom or minor bloom years of the same time period. During the 19 year period of 1989–2007 marine survival of Chilko Stock averaged 10.9% in non-bloom or minor bloom years versus 2.7% in major bloom years indicated in Fig. 6. We suggest that the observed correlation is not coincidence, but rather that the alga is responsible for acute or chronic toxicity of the salmon, food web and prey impoverishment, or some combination of these factors.

A variety of factors such as predation, food web limitations, competition and disease are known to contribute to early marine mortality of salmon and reduced stock productivity (Ricker, 1976; Pearcy, 1992; Peterman, 1984; Beamish et al., 1997; Kent et al., 1998; McKinnell, 2008). Harmful algal blooms cause significant losses of wild fish in other coastal seas as noted above, but previously have not been considered as a factor in the Salish Sea or for salmon runs elsewhere in the world. Here we examine known factors that could be promoting increased *Heterosigma* abundance or timing shifts, present a conceptual model of sockeye salmon loss from direct or chronic exposure, and food web perturbation. Measures to further investigate and mitigate the potential problem complete the discussion.

8.1. Oceanographic effects, weather and climate

Fraser River discharge volume vastly exceeds all other rivers flowing into the Salish Sea with average annual discharge of

$3600\ m^3\ s^{-1}$, typically peaking in late June (Environment Canada, 2010). The river has profound effects on biological and physical processes throughout the area and especially in the Strait. Reduced sockeye salmon marine survival was linked to earlier than normal and larger Fraser River discharge peaks in every known major *Heterosigma* bloom year since 1993. The vertically stratifying effects of the Fraser River in the Strait result in a proximal "river plume" and a more distant "estuarine plume" (Yin et al., 1997) with warm, brackish conditions in the latter, which are ideal for *Heterosigma*. Margalef's phytoplankton model "Mandala" (Margalef, 1997), and subsequent species succession models (e.g. Smayda and Reynolds, 2001) predict a shift in phytoplankton morphotypes from diatoms (r species) to flagellates (K species) as mixing and nutrient availability decrease in the upper water column. Microflagellates and dinoflagellates dominate the algal community as mixing and nutrient flux decrease and vertical migration ability is required to sequester subsurface nutrients. In an area like the Strait the situation remains static until a wind or tidal-induced mixing event of sufficient energy occurs to shift the system back to increased r species prevalence.

Several factors may account for increased incidence and earlier timing shift of *Heterosigma* blooms in the South Strait. Earlier than normal and prolonged peaking of Fraser River flows, which provide the physical setting for bloom embellishment, is strongly correlated with major blooms in May and June. Water temperature is a key factor in cyst germination, with repeated empirical observations in the past showing a 15 °C threshold of bloom initiation in English Bay adjacent to the South Strait (Taylor and Haigh, 1993). However these same authors report, and we concur, that blooms may continue to occur at lower temperature (N. Haigh, J. Rensel, separate unpublished data from B.C. and Puget Sound, respectively). Other observations point to a multi-decade trend of increasing water temperature in the Strait, both in surface to bottom waters along deepwater transects (Masson and Cummins, 2007) and of deepwater in seven marginal inlets (D. Stucchi, DFO unpublished data). Prior to 2007, there is no record of any extensive Strait or Puget Sound *Heterosigma* blooms in May although minor blooms have been seen early in the spring in other areas (Sechelt Inlet, Taylor et al., 1994). Winter and spring air temperatures in British Columbia have risen more rapidly than summer and fall temperatures in the period 1950–1998 (Zhang et al., 2000) and more recently (B.C. Ministry of Environment, 2006). Warmer springtime air temperatures would reduce cooling or embellish warming of surface waters of shallow inlet or bay waters where *Heterosigma* blooms are thought to originate. Modeled climate-change effects of warmer water and lower food availability predicted smaller-sized Fraser River sockeye and reduced adult fish recruitment (Hinch et al., 1995). In their study, warmer water was assumed not to be a direct effect on sockeye physiology but rather a surrogate for increased levels of predation, decreased food supply or other processes causing interannual patterns of abundance.

Climate variability or change may contribute to variation of early marine mortality of salmon as it has been linked with overall productivity of aggregate stocks of salmon over broad regions (Beamish et al., 1999). In the past it has taken a profound change, such as the 1976/1977 Northeast Pacific climate shift, to produce a sufficiently clear change in trends of Fraser River sockeye productivity (Beamish et al., 1997) that could be discerned, but not necessarily understood in terms of food web change. Evidence of increasing harmful algal prevalence and range extensions in other seas due to global warming trends is accumulating (e.g., Hallegraeff, 1993; Peperzak, 2003; Hays et al., 2005; Anderson, 2007). There is scant evidence of such shifts in the Salish Sea, but there has been an apparent increase since the 1950s in the frequency, magnitude, and geographical scope of paralytic shellfish poisoning in Puget Sound (Trainer et al., 2003) although not in the period 1993–2007 (Moore et al., 2009).

8.2. Acute and chronic fish mortality due to Heterosigma exposure

It is established that *Heterosigma* can kill many species of marine fish and salmonids and that blooms have apparently been more prevalent in recent years, but if this is the case, why are observations of wild fish kills in the Salish Sea not more prevalent? A conceptual model of wild fish loss to *Heterosigma* blooms illustrates how large numbers of juvenile sockeye could have been injured or killed in Salish Sea waters without being detected. Salmonids are physostomous fishes, i.e., they must imbibe air into their swim bladder by gulping air at the surface to maintain neutral buoyancy. Is it possible that Fraser River sockeye affected by *Heterosigma* over moderate to deep water areas could thus disappear without human notice? First, we know that moribund and dead salmonids tend to sink in the temperate waters of the Salish Sea, as they do within net-pen fish farms during a harmful algal bloom. Only a very small fraction (far less than 1%) of farmed fish exposed to the alga are typically seen floating at the surface of net pens during a fish kill caused by *Heterosigma*. Sinking versus floating of moribund or dead fish has not been studied for wild salmonids in marine waters of the subject regions, but was experimentally addressed by Patterson et al. (2007) for adult Fraser River sockeye in freshwater tanks. In their study, all dead fish sank, and the time for a carcass to resurface was inversely related to water temperature, ranging from 1 to 3 days at 20 °C to 12 to 18 days at 6 °C. The authors suggested that predators or scavengers or physical damage in the natural environment could prevent resurfacing of dead fish through violation of the peritoneum and release of decomposition gases. A separate study of net-pen farmed salmon in B.C. found that dying fish release gas from their swim bladders and become negatively buoyant and sink (Stephen and Ribble, 1995).

Once a fish sinks to the sea bottom, its fate is determined by water temperature, the carcass location relative to shore, habitat type and density of predators and scavengers. The littoral zone of the Strait is replete with pelagic and epibenthic predators and scavengers including schools of Pacific spiny dogfish (*Squalus acanthias*) and Dungeness crab (*Cancer magister*) that are both highly adept at locating and consuming fish carcasses. If the fish sink through the warmer surface layer into the much cooler deep layer, time to resurface increases greatly or may prevented entirely. Even if a fish is not wholly consumed at this point, if the peritoneal cavity is severed by a predator or mechanically damaged, a fish may never resurface. If the dead sockeye salmon were not scavenged or physically damaged during the time on the bottom, eventually some could float up to the surface, while being transported by tides and currents and be subject to predation by scavenging fish species. At the surface, a variety of seabirds such as gulls may also feed on the carcasses. In this manner, large numbers of juvenile fish could be lost due to harmful algae, die over a broad area and be assimilated by various types of predators and scavengers without being overtly noticeable to casual observers.

Observations of *Heterosigma* related fish kills at net-pen fish farms have shown that not all salmon are killed simultaneously and rates of dying appear to be different among pens, stocks and ages of fish. This could be due to patchiness of the bloom in terms of density of all cells or density of more virulent clones or to differing sensitivity of individual fish. Some fish typically survive, some are obviously affected and some die later, usually within a few days.

Given the variable rates of salmon death observed at fish farms during *Heterosigma* exposure, and the possibility of sublethal effects, we could reasonably expect *Heterosigma*-exposed sockeye salmon juveniles to react similarly, and thus would not expect to see their carcasses concentrated at some single point. With blooms occurring over large areas of the Strait (Haigh and Taylor, 1990; Taylor and Haigh, 1993), repeated exposure and mortality of migrating fish is therefore possible over a wide area that reduces the chance of detection by human observers. In the only Strait area-wide bloom-mapping event, sampling was restricted to 2 m depth only (Taylor and Haigh, 1993), which could over state or understate the concentration that migrating sockeye may encounter, and points to the need to understand the vertical distribution of *Heterosigma* cells relative to depths that the juvenile or adult sockeye salmon utilize.

Further evidence for *Heterosigma* impacts on wild fish is that in every major *Heterosigma* bloom in North Puget Sound since 1989, fish farm staff, sports fishermen or others have seen scattered carcasses of dead or distressed wild fish including juvenile salmonids during the blooms that killed farmed fish (Rensel, 2007; K. Bright, Icicle Seafoods Inc., pers. comm. 2009). In British Columbia, reports of dead salmon have been made during *Heterosigma* blooms, but the coastal area is huge and sparsely populated in most areas except the lower mainland and southeast Vancouver Island. In August 2009, numerous dead adult chum and pink salmon were seen during a widespread and intense *Heterosigma* bloom near Klemtu (coastal fjord area north of Vancouver Island) that also killed farmed fish. The observer, an experienced fish farm manager, noted that the fish appeared to be pre-spawning mortalities (A. Haslam, pers. comm. to N. Haigh, 2010).

An unknown number of dead wild fish of mixed species including salmonids have periodically been observed in Case Inlet, a shallow, distal water body of South Puget Sound, during *Heterosigma* blooms as reported by Hershberger et al. (1997) and observed by others in subsequent years including 2009 (T. King, Washington Sea Grant, B.D. Bill, NOAA, NWFSC Seattle, pers. comm. 2009). It is apparent that water temperatures throughout the shallow, inner inlet are high (>20 °C) during these blooms compared to conditions during blooms in the main basins of Puget Sound. In the main basins and deeper bays and inlets, surface water temperatures are also typically high but variable (ca. 14–18 °C) during *Heterosigma* blooms. But deep layer temperatures, to which dead and dying fish may sink, remain much cooler, resulting in longer time to resurface and increased probability of not resurfacing due to predation and scavenging as discussed above. The Case Inlet situation may be interpreted to suggest that dead fish resulting from *Heterosigma* blooms would be more commonly seen if subsurface water temperatures in the main basins were higher during blooms.

Lack of interest in the potential risks to wild fish associated with *Heterosigma* blooms in the Salish Sea may be due in part to the opinion that either the blooms are never concentrated enough to kill free-swimming fish, or that fish have behavioral avoidance adaptations that allow them to swim around or under surface blooms (e.g. Taylor and Harrison, 2002), but there are no data to support this conjecture. *Heterosigma* blooms do concentrate very near the surface at times, such as during daylight hours with quiescent wind conditions in Sechelt Inlet (Taylor et al., 1994), but at other times and locations in B.C. they may be mixed throughout the upper water column (Gaines and Taylor, 1986) or the cells may vertically migrate to the nutricline at night. Rensel (2007) found in North Puget Sound channels that the 2006 *Heterosigma* bloom extended from the surface to many tens of meters deep and killed farmed fish reared in water that was mechanically airlifted from 20 m depth or more, similar to blooms in other years (R. Horner and J. Rensel unpublished cell count data from Central and Northern Puget Sound, 1990 and 2007, respectively). Haigh and Taylor (1990), in their study of the North Strait of Georgia, suggest that *Heterosigma* cells prefer the top 10 m of the water column, a depth range that corresponds with the reported primary distribution of juvenile sockeye salmon throughout the Strait (Groot and Cooke, 1987). If the algal cells are mixed or vertically migrate throughout the upper water column, given the natural behavior of many juvenile fish, including salmonids which are shallow-water oriented, swimming under or around a bloom may not be an effective bloom-avoidance strategy.

8.3. Food web perturbation

Heterosigma is well known to adversely affect diversity and abundance of other algae, often excluding many other or all phytoplankton species. It also may cause mortality or feeding inhibition of some secondary trophic level zooplankton grazers (Clough and Strom, 2005). The prolonged occurrence of blooms in the South Strait of Georgia, up to four months of the algal growing season in some years, may therefore result in an impoverished food web and lack of suitable phytoplankton prey for zooplankton that support juvenile sockeye salmon on their migration through the Strait. This view is supported by recent workshop findings that noted the problem of reduced productivity, most noticeable in the 2009 sockeye salmon returns, occurred after the juvenile fish began their migration towards the sea and that the food web may be involved (Simon Fraser University, 2009).

Heterosigma blooms are often unialgal in the Salish Sea and it is probably the most allelopathic HAB species known, being inhibitory to all classes of organisms, from bacteria to fish (Smayda, 2006). In other regions, *Heterosigma* may co-occur with and be grazed by other harmful raphidophytes such as *Chattonella subsalsa* (Demir et al., 2008), dinoflagellates (Jeong et al., 2005) and *Noctiluca scintillans* (Nakamura, 1998). Bloom index data from 1999 to 2009 indicated potentially elevated concentrations of *Heterosigma* in the South Strait during 40% of the observations in all sampled years. This may be sufficiently frequent to compromise zooplankton prey of the fish in the otherwise usually productive surface layer, as well as benevolent phytoplankton species that form the base of the pelagic marine food web. There have been, however, no targeted studies of the aquatic food web structure along the pathways of the migrating juvenile salmon during HAB blooms, nor any studies of diel vertical migration by harmful algae in the Strait. Many prior studies in the region used chlorophyll measurements of phytoplankton abundance that provide no species composition information, obtainable from traditional cell count methods or possibly with HPLC phytoplankton pigment analysis (Claustre et al., 2004). Few studies anywhere in the Salish Sea have comprehensively addressed phytoplankton species composition and secondary production. The few that have, such as Harrison et al. (1991), were limited in duration, in this case 10 days at the end of July 1987 and in mid channel areas of the Strait affected by the Fraser River plume, but no *Heterosigma* cells were recorded. The authors recommended further short and longer term studies in the Strait in order to understand how variation of riverine discharge affects nutrients and plankton dynamics. The eight day study of Yin et al. (1997) and studies by Masson and Peña (2009) began to address these needs, but did not examine phytoplankton species composition or Strait margins where juvenile sockeye salmon migrate.

Food web perturbations may extend well beyond the Salish Sea to affect Fraser River sockeye salmon. Irvine et al. (2010) found a positive correlation between Queen Charlotte Sound (north of Vancouver Island) satellite-derived chlorophyll *a* concentration and marine survival of Chilko Lake sockeye in their ocean entry year. Productivity data were from 30 March and 22 April of 1998–2007, time periods appropriate for measuring the spring bloom of diatoms that fuels the temporally lagging secondary production of zooplankton that the sockeye rely upon for prey. The lowest average chlorophyll *a* concentration and salmon survival both occurred in 2007 but in none of the years did the highest chlorophyll values exceed 2.0 μg/L. Queen Charlotte Sound is an exposed continental shelf area located just north of the Salish Sea and, compared to the Strait, is an unlikely location for frequent *Heterosigma* blooms. Low primary productivity such as occurred in early spring 2007 in Queen Charlotte Sound was followed by extensive blooms of *Heterosigma* in the South Strait in late May and June, as reported herein, but not in other HAMP subareas at that time. It is therefore probable that the sockeye smolts encountered reduced availability and quality of prey throughout their early marine migration in the South Strait, as shown above with the juvenile herring data, and in Queen Charlotte Sound thereafter, which could have contributed to the extremely poor survival and return of adult sockeye in 2009.

8.4. Sublethal effects and disease

Sublethal effects of fish or shellfish exposed to harmful algae are known to occur in some cases (e.g., Deeds et al., 2006) but in most cases are not well described. Often the gills of fish are adversely affected by harmful algae but observed gill histopathology is not diagnostic as to causative algal species. North Puget Sound fish farmers have observed that surviving pens of salmon did not return to normal feeding and growth rates in comparison to cohorts not exposed to a *Heterosigma* bloom, suggesting some sublethal physiological damage or stress (K. Bright, Icicle Seafoods Inc. 2006 fish growth data analysis). In shellfish, adverse digestive system effects have been found for eastern oyster (*Crassostrea virginica*) exposed to *Heterosigma* (Keppler et al., 2005).

Fish disease is another possible cause of salmon mortality in marine waters, directly, or indirectly through weakened condition leading to predation. Fish are subject to cumulative stress and injury from multiple sources, including harmful algae, which can adversely affect fish health and the propensity for disease epizootics. One cosmopolitan diatom, *Chaetoceros* (subgenus *Phaeoceros* including *Ch. convoltus*), has long been implicated in Salish Sea wild and farmed fish kills even at very low, non-bloom concentrations (Bell, 1961; Albright et al., 1993; Rensel, 1993). These species form long chains and have spiny setae that lodge in the gills of salmon, causing excessive gill mucus production, and cellular damage that leads to blood hypoxia and subsequent mortality. Secondary infection by bacteria that gain entry through gill epidermal cells damaged by the alga has also been implicated in some cases. Understanding the effects of diseases and parasites of coastal and ocean-migrating fish is difficult because in the past affected fish could not be tracked. Fish may die and disappear without detection (Bakke and Harris, 1998; McVicar, 1997), but some data exist for British Columbia (e.g. Kent et al., 1998).

A follow-up report (Welch, 2010) on recent hydroacoustic tagging studies (Welch et al., 2009) from two returning adult Fraser River sockeye salmon used incremental spatial survival calculations to demonstrate that a major mortality event occurred after the tagged Fraser River (Cultus Lake Stock) juvenile sockeye passed through Queen Charlotte Strait northbound, not earlier in the Strait. It is apparent that these tagged fish largely escaped acute mortality in the Strait due to *Heterosigma* blooms or other causes in 2007. Chilko Lake stock marine survival and total Fraser River sockeye return was extremely poor from 2007 outmigrating smolt production returning as adults in 2009. Acoustic tagged juvenile sockeye were released below Cultus Lake on 16 May 2007 and exited the river in less than 6 days, but it is impossible to determine if these fish avoided the large and earlier-than-normal occurring *Heterosigma* bloom that was detected in the South Strait beginning at the end of the final week of May; there is not enough spatial fish and alga data to be certain. Alternatively, the bloom could have been concentrated on the surface both day and night, for example if there was no need for the alga to migrate to depth for nutrients at night, allowing the fish to pass through without adverse effect. The possibility of sublethal effects and the well-known allelopathic effects of the alga, however, are not inconsistent with both sets of authors' findings. Sockeye salmon weakened for over a month by inadequate supply or quality of prey in the Strait and the physiological stress of blood hypoxia that accompanies gill damage from many types of HABs, including *Heterosigma*, would not be expected to survive the rigors of oceanic migration for long. A fundamental of fish health science is that cumulative stressors, including environmental contaminants, inappropriate basic water quality conditions and ostensibly sublethal exposure to harmful algae including *Heterosigma,* may predispose fish to infection or infestation from fish diseases and parasites. In the absence of companion field or experimental data, the above postulate regarding sublethal effects of *Heterosigma* remains a potentially useful but unproven concept.

8.5. Adult fish and HAMP sampling locations

Although our data indicates that juvenile sockeye may be the primary life stage affected by *Heterosigma* blooms, we emphasize that our data collection stations more closely represent the juvenile fish pathways, and not those of the adult sockeye salmon, which tend to migrate in large schools over greater depths. Samples were collected at fish farm sites and reference areas that were typically 40–80 m deep overall. Nevertheless, adult fish may be increasingly affected by the alga as they migrate to the Fraser River. The annual proportion of the total Fraser sockeye run returning through the northerly route (Johnstone Strait and southward via waters east of Vancouver Island versus the Strait of Juan de Fuca) has been consistently elevated since the mid 1990s and run timing through the Strait of Georgia coincides with July and August *Heterosigma* blooms, particularly in Regions A and D (Table 2). In several recent years the Pacific Salmon Commission has estimated large abundances of sockeye adults passing through Johnstone Strait, based on test CPUE and historic run size models. The fish should have entered the Strait and later ascended the river but many never arrived, raising the specter of adult en route loss in the Strait during *Heterosigma* bloom season.

Additionally, since 1995, late run adult sockeye have not delayed their migration into the Fraser River by staging for weeks in the Southern Strait near the river mouth commencing in late August and September, as was their normal behavior in previous years, but have entered the river directly or after only a few days (Cooke et al., 2004). Occurring for unknown reasons and continuing through 2009, this early river entry behavior has been associated with abnormally high mortality during upstream migration. Pre-spawning freshwater mortality has exceeded 90% of the late-run sockeye stock, leaving significantly fewer adult fish than entered the river to spawn (Lapointe, 2009). This behavior may suggest that marine water factors, perhaps associated with exposure to *Heterosigma* either near the river mouth or previously, were agonistic to the adult fish, driving them to enter the river prematurely. Water sampling for harmful algae has not been conducted near the mouth of the river at times when late-run stock sockeye salmon arrive and once milled prior to 1995. The early entry behavior could also be a delayed effect of prior en route exposure in August or September for fish returning from the northern regions (Tables 2 and 3).

8.6. Nutrients

Heterosigma blooms in some other locations worldwide have been linked to cultural eutrophication, a prime example being the Seto Inland Sea of Japan (Honjo, 1993). Smayda (1998, 2006) suggested a number of factors that may explain the wide distribution and apparent adaptability of *Heterosigma,* including its use of moderate or highly eutrophic environments, and moderate to highly vertically stratified water bodies with riverine influence and variable salinity. Anthropogenic effects on Salish Sea *Heterosigma* blooms are possible in nutrient sensitive subareas, such as some poorly flushed bays and inlets. However, in most B.C. waters of the Salish Sea the available evidence points to physical factors such as water temperature (for cyst germination) and water column vertical stratification (from river discharge) as paramount factors promoting *Heterosigma* blooms. The region with the most frequent and intense blooms is the Strait of Georgia, which is also the major B.C population center and devoid of commercial net pen fish farms. Evidence from the past suggests that in at least some years *Heterosigma* blooms originated in this region near the Fraser River and spread northward in the Strait (Taylor and Haigh, 1993). Blooms in the Broughton Archipelago and Queen Charlotte Strait (Region A) occur significantly later than in the South Strait (Region D) but it is likely that there are other bays or inlets throughout all regions that provide suitable cyst germination habitat and that not all blooms originate from one bay or inlet.

There has been little study of *Heterosigma* nutrient dynamics and potential links to cultural eutrophication in the Salish Sea (Anderson et al., 2008), but some aspects of cultural eutrophication are known. Mackas and Harrison (1997) calculated rates of nitrogen flux in Salish Sea waters with regard to natural and anthropogenic sources of nitrogen to evaluate risks of cultural eutrophication. Influx of nitrogen from the ocean via estuarine circulation far surpassed that produced by anthropogenic and riverine sources, particularly in the Strait of Juan de Fuca and adjacent channels leading to the Strait of Georgia. Background nitrogen concentrations relative to half saturation rates of phytoplankton uptake or growth were also generally high, which meant that addition of nitrogen in those areas is unlikely to alter phytoplankton production rates. The authors concluded that for most of the Strait, except for poorly flushed marginal bays or inlets that had signs of potential fragility, the ecological effects of incremental nutrient loading were likely negligible. Rensel Associates and PTI Environmental Services (1991) ranked the nutrient sensitivity of main basins, channels, bays and inlets in Puget Sound using the Washington State Department of Ecology's monthly survey database of surface nitrogen concentration and deepwater dissolved oxygen data. Main channels and basins were ranked less sensitive or insensitive to nutrient additions compared to poorly flushed bays and inlets that become seasonally stratified, stripped of nutrients in the surface waters and sometimes subject to hypoxia in the deepwater. In Puget Sound, the brevity of *Heterosigma* blooms, a few days to at most a week in duration, the apparent dependency on warm weather periods, and strongly physical transport factors observed for North Puget Sound highlight the importance of naturally occurring physical forcing factors to bloom dynamics (Rensel, 2007; Anderson et al., 2008).

Masson and Peña (2009) studied the pattern of phytoplankton spatial and temporal variability including mixed layer depth and the near-surface layer of increased density stratification at numerous offshore locations in the Strait of Georgia/Juan de Fuca Strait system during cruises averaging 5 days duration in of each of the four seasons from 2001 through 2007. The authors found that nitrate nitrogen was abundant throughout the study region, except during summer near the surface of the Strait where concentrations in the top 10 m declined below 2 μM, a value approximately midway through the distribution of half saturation constants for many diatom and flagellate species (Bowie et al., 1985). *Heterosigma* has nitrogen half saturation constants (K_s) of 1.44, 1.47 and 0.42 μg-at N L^{-1} for NH_4^+, NO_3^- and urea, respectively, and any of these substrates could maintain a bloom (Herndon and Cochlan, 2007). However, because *Heterosigma* is able to vertically migrate at speeds of 1 m h^{-1} or more (Yamochi and Abe, 1984), and given the ~10 m depth nutricline in the Strait during the growing season (Taylor and Haigh, 1993), macronutrients are well within the achievable daily range of vertical migration. Thus nutrient supply and the potential issue of anthropogenic waste discharges may not be a major factor in the main body of the Strait for *Heterosigma* blooms. However, in nutrient-sensitive adjacent bays and inlets of British Columbia where *Heterosigma* cysts may germinate, there are no systematic, long-term data regarding nutrient concentrations or bloom dynamics to adequately judge the possibility of nutrient dynamics change and effects of human activities. Anthropogenic sources of nutrients in such bays may play an important role in aiding *Heterosigma* blooms to become further established, prior to moving into the Strait. Approximately 76% of the existing B.C. human population resides on the southwest coast, with the population of the Greater Vancouver area more than doubling in the period 1981-2009 to the present level of about 2.4 million people. Untreated combined sewer overflow and primary-only treated discharge are scheduled for eventual elimination but remain significant sources of nitrogen in addition to non-point-nutrient emissions (B.C. Ministry of Environment, 2007). The interaction of anthropogenic sources of nutrients and algal blooms including harmful algae remains an area of research needing more attention, particularly in the nutrient-sensitive portions of the Salish Sea.

8.7. Future direction, study and mitigation

In the short term, there is an immediate need to expand regular sampling of phytoplankton species composition in the Strait at least during juvenile and adult sockeye salmon migration periods. In particular, such studies need to address concurrent vertical distribution of both *Heterosigma* and sockeye smolts, the latter through applications of hydroacoustic tags (e.g., Welch et al., 2009) that are now available for smaller sockeye smolts. Release timing and location as well as size of acoustic-tagged fish are critical factors to account for in future studies.

Plankton monitoring effort may be prioritized by weekly weather conditions and fortnightly tidal conditions because *Heterosigma* blooms in the region prosper during clement weather and neap tides. At such times fixed-wing aircraft surveys, such as those used by Puget Sound fish farmers, are useful to document the extent of *Heterosigma* blooms. As noted previously, the alga presents a visually distinctive purplish-red color that a trained observer can discern by eye to track these blooms (Anderson et al., 2001; Rensel, 2007). Bioassays and analyses could be conducted to assess survival and behavior of acoustically tagged, seawater adapted sockeye smolts migrating through blooms of known dimensions or as part of ongoing Pacific Ocean Shelf Tracking Array work (Welch et al., 2009).

In the long term, automated molecular monitoring and remote sensing of *Heterosigma* is possible using specially designed buoys known as Environmental Sample Processors (ESP), which provide collection and analysis of water samples and molecular probes to identify HABs and their gene products while archiving samples (Scholin et al., 2008). Satellite chlorophyll tracking of surface blooms in the Strait is possible, although the variability of *Heterosigma* bloom depth, relative to sockeye salmon depth, is unaccountable with this method and interference from Fraser River discharge turbidity is high in the Strait of Georgia. Over time, probability estimates of *Heterosigma* depth distribution may be developed for specific locations linked to known forcing factors such as winds and tidal phase driven vertical mixing. As the propensity to vertically migrate more aggressively and be more surface oriented may vary among *Heterosigma* ecotypes, attention to the genetic components of the species may be required (Bearon et al., 2004; Fredrickson et al., in press).

This paper has focused on *Heterosigma* as the HAB species most likely to be involved in mortality of sockeye salmon in the Salish Sea. However, other species of harmful algae implicated in fish or invertebrate kills in the Salish Sea include *Chaetoceros* (subgenus *Phaeoceros*), *Cochlodinium fulvescens*, *Dictyocha* spp., *Chrysochromulina* spp., *Chattonella* sp., *Corethron criophilum* and *Alexandrium* spp. The HAMP database contains data for all these species throughout the Salish Sea and in four more regions along the outer coast of Vancouver Island where *Heterosigma* blooms are also frequent. Some of these species, especially *Chaetoceros* (Phaeoceros) and *Chattonella* sp. are very likely to contribute to mortality of wild fish. The former because of its frequency and virulence at low concentrations throughout the water column as well as occurrence in spring and summer/fall periods of salmon migration and the latter is associated with a high degree of fish toxicity and apparent worldwide expansion in range and severity of effects.

Further validating the sockeye salmon—*Heterosigma* interaction hypotheses could involve considerable effort and some may argue that if there is no solution to natural blooms, or if anthropogenic factors are not causing the blooms, it is not worth contemplating. However, if blooms originate from cysts germinating in Salish Sea shallow marginal inlets and bays, as expected, there are possible means of removing or mitigating blooms before they spread into the main basins. Spraying of certain types of clay slurries is known to be highly effective in removing *Heterosigma* cells from the water column (Sengco et al., 2001; Sengco and Anderson, 2005) and has been widely used in Korean coastal oceans with apparent success (Lee et al., 2008). Preliminary environmental-effects studies of *Heterosigma* mitigation with clay treatment have been conducted in Puget Sound indicating no adverse effects from occasional treatment (Rensel and Anderson, 2004). Because the alga apparently does not produce a stable toxin that accumulates, flocculation and removal to the sea bottom will not contaminate benthic communities with a toxin as is the case for fish-killing dinoflagellates such as *Karenia brevis* in Florida and elsewhere (Haubois et al., 2007). Other types of flocculants used for potable water treatment such as polyaluminum chloride (Zeng et al., 2007) are also being assessed for HAB control with (Sengco and Anderson, 2005) or without clay (Pan et al., personal communications). Other techniques also hold promise for *Heterosigma* removal including treatment with ozone (Honjo et al., 2004). Biological controls of harmful algae have long been studied but progress in practical applications has been slow. However, the heterotrophic dinoflagellate *Stoeckeria algicida* in Korea has been shown to efficiently feed and grow using *Heterosigma* as prey during field studies (Jeong et al., 2005) as has the prostomatid ciliate *Tiarina fusus* (Jeong et al., 2002), which is also common in the Salish Sea, suggesting that biological control may be possible in B.C. after further research. Other possible biological controls include naturally occurring viruses, widespread in sediments of the Strait (Lawrence et al., 2002), which cause lysis of *Heterosigma* cells. Research efforts are now underway to ascertain the physiological cause(s) of fish death due to *Heterosigma* exposure by a team centered at the NOAA Northwest Fisheries Science Center in Seattle. Resolving this issue will help development of mitigation techniques.

We have shown strong correlations between occurrence of major *Heterosigma* blooms in the South Strait of Georgia and reduced marine survival of Chilko stock Fraser River sockeye salmon. We also demonstrated a strong correlation between marine survival rates of these salmon and juvenile herring, indicating that survival of the salmon may be principally determined within the Strait of Georgia and likely within the first six weeks of sockeye seawater rearing. We do not know if the alga is causing significant acute mortality of the juvenile fish, sublethal effects or if fish survival is indirectly affected through food web impoverishment, or a combination of these factors. Moderate to extreme interannual variation of Fraser River sockeye marine survival will likely continue in the future as juvenile fish encounter *Heterosigma* blooms or not and are faced with other factors that control marine survival discussed herein. As this paper is being published in 2010, estimates of the total adult return from the 2008 juvenile sockeye seawater entry year are very large, stemming mostly from the late run timing stocks (PSC, 2010). Our findings point to the need for further attention to resolving the role of *Heterosigma* in survival of Fraser River sockeye salmon and other fish in the Salish Sea.

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