Evolutionary perspectives on thiamine supplementation of managed Pacific salmonid populations

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Article impact statement

Thiamine deficiency represents a significant threat to Pacific salmonid populations' genetic health and may require active management.

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Abstract

Thiamine deficiency complex (TDC) in fishes has been identified in an ever-expanding list of species and populations. In many documented occurrences of TDC in fishes, rates of juvenile mortality have reached 90% at the population level, with many females producing no surviving offspring. Such sweeping demographic losses and concomitant decreases in genetic diversity due to TDC can be prevented by treating pre-spawn females or fertilized eggs with supplemental thiamine. However, some fisheries managers are hesitant to widely apply thiamine treatments due to the potential for unforeseen evolutionary consequences. Specifically, these hesitations are due in part to apprehension that thiamine supplementation may impede genetic adaptation to low-thiamine conditions or may give hatchery fish an advantage over wild-origin fish. With these concerns in mind, we first review the existing data regarding genetic adaptation to low-thiamine conditions and provide perspectives on evolution-informed treatment strategies with specific population examples. We also provide practical treatment information, consider the potential logistical constraints of thiamine supplementation, and explore the consequences of deciding against supplementation. Until new evidence bolsters or refutes the genetic adaptation hypothesis, we suggest that TDC mitigation strategies should be designed to support maximum population genetic diversity through thiamine supplementation. Furthermore, we offer guidelines on when the adaptation strategy may be applicable to certain populations.

Introduction

Thiamine (vitamin B_1) is required by all living organisms as an essential coenzyme in both anabolic and catabolic carbon metabolism (Whitfield et al. 2018). Yet despite being necessary for life, very few multicellular organisms can synthesize thiamine *de novo*, and most species must obtain it through diet or absorption from exogenous sources or partial synthesis from thiamine-related precursors (Kraft & Angert 2017; Tylicki et al. 2018; Whitfield et al. 2018). Thiamine deficiency in animals causes debilitating morbidities and neurological disorders and has even been linked to early life-stage mortality in taxa as diverse as foxes (Lee 1948), mink (Ender & Helgebostad 1939; Swale 1941), marine mammals (Aulerich et al. 1995), sheep (Evans et al. 1975), humans (Whitfield et al. 2018), reptiles (Marshall 1993; Honeyfield et al. 2008), and fishes (reviewed in Harder et al. 2018). In recent years, thiamine deficiency has been identified as a contributing factor to steep population declines in varied wildlife species globally (Fig. 1A; Balk et al. 2016). Balk et al. (2016) collected data from 45 stations in 15 regions of the world, and concluded environmental thiamine deficiency is more widespread and severe than previously realized. In fact, the authors identified it as a top emerging threat to wildlife worldwide, concurring with growing research efforts on thiamine deficiency over time (Fig. 1B).

Thiamine deficiency complex (TDC; reviewed in Harder et al. 2018)—also known as early mortality syndrome in the Laurentian Great Lakes (EMS; Marcquenski 1996) and M74 in the Baltic Sea (Börjeson and Norrgren 1997)—has been mostly diagnosed and studied within populations of anadromous fishes, where it is considered an emerging threat to global salmonid fishery stability. TDC has affected salmonid populations in the Laurentian Great Lakes (Fitzsimons et al. 1999; Riley et al. 2011), the Baltic Sea (Amcoff et al. 1999; Engelhardt et al. 2020), and the New York Finger Lakes (Ketola et al. 2005). In many occurrences of TDC in fishes, clinical signs are first noted during early developmental stages and can include ataxia (often seen as spiral or side swimming); hydrocephalus; large yolk sacs with opacities, edema, hemorrhaging; and elevated mortality rates (Fisher et al. 1995; Fitzsimons et al. 2001). However, prominent clinical signs of thiamine deficiency can also present in adults as erratic swimming patterns, lethargy, decreased migratory capacity, and increased pre-spawn mortality (Brown et al. 2005b; Fitzsimons et al. 2005). These observed effects are directly related to thiamine's crucial roles in metabolism and production of neurotransmitters, myelin, antioxidants, and energy (Bettendorff 2013). The underlying causes of thiamine deficiency may vary across environments, but in salmonids, TDC has most commonly been tied to consumption of prey that contain thiaminase—a thiamine-degrading enzyme (Honeyfield et al. 2005; reviewed in Harder et al. 2018). Thiamine deficiency can be treated by the addition of exogenous thiamine to deficient fry or adult fish. Deficiency can also be prevented by providing thiamine to specifically support embryologic development via maternal supplementation or by a direct administration to freshly spawned eggs prior to development.

Recently, TDC was identified and documented for the first time in Pacific populations of Oregonian steelhead trout (*Oncorhynchus mykiss*; Reed et al. 2023) and federally endangered Chinook salmon (*Oncorhynchus tshawytscha*) (Mantua et al. 2021), joining the expanding the list of ecosystems known to have TDC-impacted populations (Fig. 1A; Appendix S1). These recent descriptions of TDC, alongside earlier data collected from Western Alaskan Chinook salmon (Honeyfield et al. 2016), have raised the alarm among fisheries researchers and managers in the Pacific Northwest who previously considered TDC to be unlikely to emerge in the region. For stocks already on the brink of collapse, an additional stressor such as thiamine deficiency could be the breaking point. For example, California's Central Valley Chinook salmon have been experiencing precipitous declines since the early 1980s (Fisher 1994), which have only worsened with recent unfavorable marine conditions (2005-2006) and frequent drought conditions in years since (Williams et al. 2016). Additional demographic losses due to TDC could further suppress reproductive success and recruitment. In such cases, supplementing with thiamine is prudent because it is likely to help and there are no known disadvantages. But even in stocks with moderate population sizes, the stochasticity introduced by TDC-related mortality could be enough to drive cohorts to extirpation (Ivan et al. 2018; Vuorinen et al. 2021). In response to clinical signs of TDC identified in conjunction with low egg thiamine concentrations, fish management teams in California and Oregon have begun supplementing some stocks on a routine basis each year. Fish management teams in Alaska, Idaho, Colorado, Utah, and Washington are also investigating or implementing thiamine supplementation.

Thiamine supplementation to prevent TDC in managed fish populations is relatively inexpensive and effective. The two most commonly applied thiamine treatment strategies are (i) injecting mature females with supplemental thiamine prior to spawning and (ii) immersing eggs in a pH-balanced thiamine bath at the time of fertilization, both with the objective of increasing egg thiamine and, subsequently, yolk sac thiamine concentrations to support individual development until initiation of exogenous feeding (Brown et al. 2005a; Fitzsimons et al. 2005; Reed et al. 2023). However, there is growing concern that thiamine supplementation may impede natural selection on the ability to tolerate low thiamine availability, or that providing supplemental thiamine will give supplemented hatchery fish an advantage over non-supplemented wild-origin fish by increasing the health and survival of adults to spawn as well as fry during early development. The confusion around whether to supplement with thiamine is not surprising given the very recent discoveries of occurrences of TDC in the Pacific Northwest

(Mantua et al. 2021, Reed et al. 2023), a lack of understanding of thiamine dynamics in the eastern Pacific ecosystem, and the paucity of information on the potential for fish to genetically adapt to low-thiamine conditions (Harder et al. 2020). We explored the prevalence of TDC research on fishes by searching ISI Web of Science Search for articles on thiamine deficiency published between 1985 and 2022 using the search methodology of Bernhardt et al. (2010). First, we searched all fields for "thiamin* deficien*" OR "early mortality syndrome" OR "M74" (TDC, n = 2,611) to estimate the number of papers published to-date on thiamine deficiency. Next, we searched for publications addressing fish by adding "fish OR teleost OR salmon*" (TDC + fish; n = 245). Finally, to find papers that addressed evolutionary considerations, we next added "Evolution* OR Evo* OR gene*" (TDC + fish + evolution; n = 78). Despite increasing observations of TDC globally (Fig. 1A; Appendix S1), few publications address TDC in fishes (Fig. 1B). Of ~2,600 publications examining thiamine deficiency since 1985, only 9% of those included consideration of fishes, and a mere 78 papers have discussed TDC in conjunction with evolution in fishes.

Essentially there are two options in the face of TDC: wait and see if the population can adapt to low thiamine conditions or intervene with thiamine treatment. Until more conclusive evidence is found of the adaptive benefit of not supplementing, we suggest that supplementation be considered as a management option to ensure population persistence. We first review the existing data regarding genetic adaptation to low-thiamine conditions and provide perspectives on evolution-informed treatment strategies with specific population examples. Finally, we provide practical treatment information, consider the potential logistical constraints of thiamine supplementation, and explore the consequences of deciding against supplementation.

Genetic adaptation to low-thiamine conditions

Estimates of the amount of thiamine required to support development in eggs and juveniles are typically based on measurements of egg thiamine concentrations, which can then be used to predict approximate TDC severity once a species or population baseline is established. However, the amount of thiamine required to support development in early life stages and metabolic functions in adults is known to vary across species of salmonids and across populations of the same species (Harder et al. 2018). Within one population of Atlantic salmon (*Salmo salar*), variation in survival rate has even been observed among the offspring of thiamine-deficient females, with offspring survival not predicted by the amount of thiamine allocated to each developing embryo (Harder et al. 2020). Individual genetic variation in how thiamine is acquired, used, or retained may underlie these differences. If there is genetic variation associated with differential survival under low-thiamine conditions, selection on adaptive loci could allow for a population to genetically adapt to low thiamine availability. Over time, individuals with these adaptive genetic variants would increase in frequency in the population via increased relative survival and reproduction, increasing the population's overall resilience to TDC.

Given thiamine's ubiquitous roles in cellular metabolic functions, any adaptive genetic mechanisms would likely be complex and polygenic, involving interactions among variants in coding or regulatory regions for dozens or hundreds of genes (Harder et al. 2020). Such complicated genetic architecture would preclude development and implementation of marker-assisted selection methods (*i.e.*, selective breeding based on genetic profiling) in hatchery-supplemented populations affected by TDC. Furthermore, even if adaptive genetic variants can be identified in one population, the genetic variation underlying adaptation could differ across populations of the same species, making it difficult to predict adaptive responses in newly affected populations. Experimental results in Atlantic salmon are consistent with genetic adaptation to low-thiamine conditions, with one study demonstrating population-level differences in liver thiamine concentrations in response to consumption of thiaminase (Houde et al. 2015) and another describing putatively adaptive differences in gene expression underlying differential survival of TDC across families within a single population (Harder et al. 2020). Findings in lake trout (*Salvelinus namaycush*) specifically suggest that genetic variation in thiamine utilization rates may underlie adaptive differences among stocks with different histories of co-occurrence with alewife (*Alosa pseudoharengus*), a thiaminase-containing prey species (Fitzsimons et al. 2021). However, additional data are needed to definitively support the adaptation hypothesis; specifically, individual genetic and fitness data from a single population experiencing low thiamine availability must be sampled at multiple developmental stages and across multiple spawning years to explicitly link differential fitness and specific genetic loci. Until new evidence bolsters or refutes the genetic adaptation hypothesis, we suggest that TDC mitigation strategies should be designed to support maximum population genetic diversity and to facilitate adaptation when reasonable.

Treatment strategies that consider genetic diversity

Population genetic diversity tends to be correlated with adaptive potential—the ability of a population to genetically respond to future environmental changes (DeWoody et al. 2021; Kardos et al. 2021). Demographic losses experienced by a TDC-affected population can translate into losses of unique genetic variants, thereby increasing the likelihood of population extirpation in response to future challenges. In documented occurrences of TDC in fishes, rates of juvenile mortality have reached 90% at the population level, with many females producing no surviving offspring (Marcquenski & Brown 1997; Ketola et al. 2000; Harder et al. 2020). Such sweeping demographic losses and concomitant decreases in genetic diversity can largely be avoided with supplemental thiamine.

Treating as many individuals as possible with supplemental thiamine would remove low thiamine as a selective pressure and prevent selection on susceptibility to TDC. Until more conclusive evidence is found that adaptation to low thiamine levels is a successful and feasible strategy, supplemental thiamine would conserve overall population genetic diversity by minimizing demographic losses. Furthermore, if it is found that adaptation as a management strategy is not possible, forgoing supplemental thiamine in favor of allowing natural responses to TDC could lead to catastrophic demographic and genetic diversity losses in the affected population.

Population size further complicates potential outcomes of treatment decisions. For threatened or endangered populations, we posit that thiamine supplementation could be used to support the successful reproduction of as many individuals as possible to minimize demographic and genetic losses. If adaptation is possible, it may only provide a reasonable solution for large populations, where selection on rare alleles is far more effective than in small populations where allele frequencies can be predominantly driven by genetic drift (*i.e.*, random chance) (Lynch & Gabriel 1990; Willi et al. 2007; Gossmann et al. 2012). For populations of sufficient size or appropriate conservation status, modified treatment schemes could facilitate selection while also maintaining genetic diversity, allowing managers to support individual animal welfare and population persistence under future environmental conditions (see discussion of Lake Champlain population below and overview of concepts in Fig. 2).

Considering primarily conserving genetic diversity, we have provided a pathway to navigate decisions around supplementing salmonid populations with thiamine (Fig. 2). If the population is experiencing TDC or has the potential to experience low thiamine based on migratory patterns, high-thiaminase prey consumption, or confirmed low egg thiamine concentrations, and the population is threatened or endangered, treating with thiamine will preserve maximum genetic diversity. If the at-risk population is not endangered or threatened but is small, treating with thiamine will preserve maximum genetic diversity and prevent loss of genetic variation. If the population is large, there are multiple treatment options to consider: not treating any fish and allowing TDC to act as a potential selective pressure; only treating part of the population (i.e., managed fish from a larger run); or treating the entire population, which removes low-thiamine conditions as a selective pressure while preserving maximum genetic diversity. However, if the population is neither at risk nor has the potential to be at risk, a suggested approach would be to monitor population and ecological conditions and evaluate thiamine status of these populations on an annual or regular basis while continuing to collect data (i.e., clinical signs, egg thiamine values, ecological parameters, changes in prey consumption, and migratory alterations).

Population-specific considerations may affect choice of TDC mitigation strategy

For most populations, treatment strategy development will require consideration of potential demographic and genetic effects, logistical constraints imposed by treatment (see "Clinical and practical management of thiamine supplementation" below), relative effects on hatchery and wild fish population contributions, individual fish welfare, population conservation status, and other ecological challenges faced by the population. Two populations of salmonids affected by

TDC represent two divergent scenarios: Chinook salmon in California's Central Valley and Atlantic salmon in Lake Champlain. For Central Valley Chinook salmon, TDC was initially detected in 2020, and subsequent research identified a shift in their primary forage from prey with low thiaminase activity (e.g., krill, squid) toward Northern anchovy (*Engraulis mordax*)—a thiaminase-containing species—as the likely culprit of TDC emergence (Mantua et al. 2021). Given the precarious conservation statuses of these salmon populations, managers worked quickly with their veterinary team to develop and deploy thiamine supplementation strategies to minimize demographic and genetic losses by treating as many individuals as possible. In similar cases, we suggest maximum retention of population genetic diversity could be prioritized over specifically promoting genetic adaptation to low-thiamine conditions via partial thiamine treatment schemes. Central Valley Chinook are of conservation concern, and many populations are small; thus, treating with thiamine could help preserve maximum genetic diversity and avoid genetic drift or the chance that adaptive alleles are not present in the remaining population members (Fig 2).

In contrast, the Lake Champlain population of Atlantic salmon was entirely hatchery-supported as part of a reintroduction effort when TDC was first detected. Emergence of TDC in this system was also linked to consumption of alewife (*Alosa pseudoharengus*), which had been introduced to the lake in 2003 (Ketola et al. 2000)—long after Atlantic salmon had been extirpated from the system in the 1800s (Marsden & Langdon 2012). Many of the historically numerous Great Lakes native species in the lake (e.g., bloater [*Coregonus hoyi*], yellow perch [*Perca flavescens*], ninespine stickleback [*Pungitius pungitius*]) have low thiaminase activity relative to established exotic species like alewife and rainbow smelt (*Osmerus mordax*) (Tillitt et al. 2005). Because no natural reproduction had been detected in the lake prior to TDC occurrence (*i.e.*, the Lake Champlain population likely did not include an appreciable number of locally adapted, wild-origin individuals), experimental approaches to TDC mitigation via genetic adaptation were feasible. From 2016-2018 at White River National Fish Hatchery, batches of fertilized eggs were split into two groups, one receiving supplemental thiamine and one remaining untreated (Ardren et al. 2009). All of the treated offspring comprise the “maximum diversity” broodstock, with the goal of retaining genetic representation from as many individuals as possible. All untreated offspring that survive to exogenous feeding comprise the “low-thiamine tolerant” broodstock. If genetic adaptation is possible, it is presumed that this broodstock contains the adaptive genetic variants required to tolerate low-thiamine conditions. Over the next 10 years, data will be collected to compare the performance of these two broodstocks with respect to return rate, length at age, and reproductive success (personal communication, K.C. Heim). As such, the Lake Champlain population represents a valuable opportunity to empirically assess the potential for genetic adaptation to low-thiamine conditions and to inform development of modified treatment strategies for populations where such large-scale risks may not be reasonable. The Lake Champlain Atlantic salmon population was large and managed enough that additional flexibility in treatment for TDC could be considered (Fig 2).

Clinical and practical management of thiamine supplementation

Thiamine is water soluble and has a very wide margin of safety demonstrated for many species, and it is used extensively in veterinary medicine to reverse thiamine deficiencies in mammals including dogs and cats, livestock and small ruminants, exotic birds, and reptiles (Rammell & Hill 1986; “Diagnosis | Thiamine deficiency” 2011; Markovich et al. 2013). For fish, thiamine supplementation has been readily applied by managers of hatchery-supported salmonid populations in ecosystems such as the Baltic Sea and the Laurentian Great Lakes (Fitzsimons 1995; Koski et al. 1999), and most recently to fish of the Pacific coast of North America (Reed et al. 2023).

Thiamine is highly sensitive to light (Carlucci et al. 1969) and unstable at physiological pH ranges (Maier & Metzler 1957), therefore application of thiamine as a drug has some nuance to avoid degradation. To treat TDC in juvenile fish, a bath of thiamine is administered at a balanced pH (~7), with a standard application of 1000 ppm for 1 hour (Fitzsimons 1995). Rescued fish can regain normal swimming functions within a few hours. Eggs can be treated with a 1000 ppm thiamine solution applied as an immersion treatment for one hour just after fertilization (Brown et al. 2005a). This strategy may lead to other managerial conflicts such as time constraints during a long day of spawning or availability of staff. Thiamine HCl injectable solution has been successfully administered to adult fish as a single injection both with (for intramuscular injections) and without (for intraperitoneal injections) additional pH buffering at 50 mg/kg. This single injection has been shown to successfully increase egg thiamine concentrations and prevent TDC in the progeny if given at least 2-3 weeks prior to spawning (Koski et al. 1999; Fitzsimons et al. 2005; Futia et al. 2017; Reed et al. 2023).

The administration of thiamine therapy to a managed fish population can be employed after considering the logistics of its application. For adult injections, a team must consider whether injected thiamine has adequate time to be delivered to the eggs, that is at least 2-3 weeks prior to spawning but can be successfully administered as long as 5-6 months prior to spawning and provide increases in egg thiamine concentrations. However, some hatcheries, fish traps, or adult processing facilities may not have the means to handle adults prior to spawn because of infrastructure or logistical constraints; more often, though, some adults are not handled, held, or collected prior to spawn with enough time to ensure supplemented thiamine reaches the eggs. In cases like these, a fish management team may consider supplementing thiamine to the eggs at spawning as an alternative to injecting adults.

Moving forward with supplementation

Risks associated with thiamine supplementation are negligible at an individual level, but treatment of large numbers of individuals may impose material and personnel costs or efforts that managers would prefer to avoid. Testing egg thiamine concentrations via current methods is time consuming (Brown et al. 1998), with results typically available in a few weeks at the earliest. An ideal solution might involve rapid assessment of tissue or egg thiamine concentrations in returning adult salmon and immediate translation of these results into a practical population treatment plan. Such rapid testing of thiamine concentrations is not likely to emerge given the significant financial investment that development of such a method would require, nor would results be available in time to make appropriate treatment decisions for most managed populations.

In certain populations, it may be possible to develop population-specific predictors of TDC occurrence or severity that could be analyzed prior to spawning season and applied to treatment plan development. For example, marine diet studies could be linked to subsequent collections of thiamine concentration data in returning adults to identify populations or population segments at risk of TDC-induced juvenile mortality. As any such solution will unequivocally require thiamine measurement data for returning adults, we suggest collection and analysis of egg samples distributed throughout each spawning run for affected populations. Sample collection could be continued even in years without apparent signs of TDC given the often cyclical nature of TDC occurrence within a population (*e.g.*, see Figure 1 in (Ladago et al. 2020). Collection of additional information, such as mortality data at the level of individual females or mate pairs in the absence of thiamine treatment, could also shed light on the potential for population genetic adaptation to low-thiamine conditions.

Ensuring the survival and success of managed fish populations in hatcheries is already a practice that State, Federal, and Tribal agencies not only support but actively implement. There are policies and procedures in place that aim to prevent morbidity and mortality by intervening: by administering drugs such as antibiotics, vaccines, and disinfection chemicals to combat infectious diseases; by providing optimally designed nutrition to prevent deficiencies and bolster the immune system; and even by altering water quality conditions or providing entirely artificial rearing environments all to promote fish survival and prevent losses (e.g., the United States Department of Agriculture’s National Aquaculture Health Plan and Standards (NAHP&S)). Ensuring the survival and conservation of managed fish populations has not only ethical but also financial implications; it is in these agencies’ best interest to have success of their programs, which often is measured as the survival and reproductive success of their product, the fish.

Ultimately, the decision whether to apply supplemental thiamine treatments to a population experiencing TDC will depend on population characteristics and management objectives. Our findings suggest that managers making such determinations could consider: (i) supporting maximum population genetic diversity through thiamine supplementation whenever possible, (ii) facilitating potential genetic adaptation when reasonable (i.e., when the population is large and has potential for adaptation), and (iii) relying on diverse perspectives from population geneticists, fish health specialists and veterinarians, and evolutionary fish biologists to draw these distinctions.

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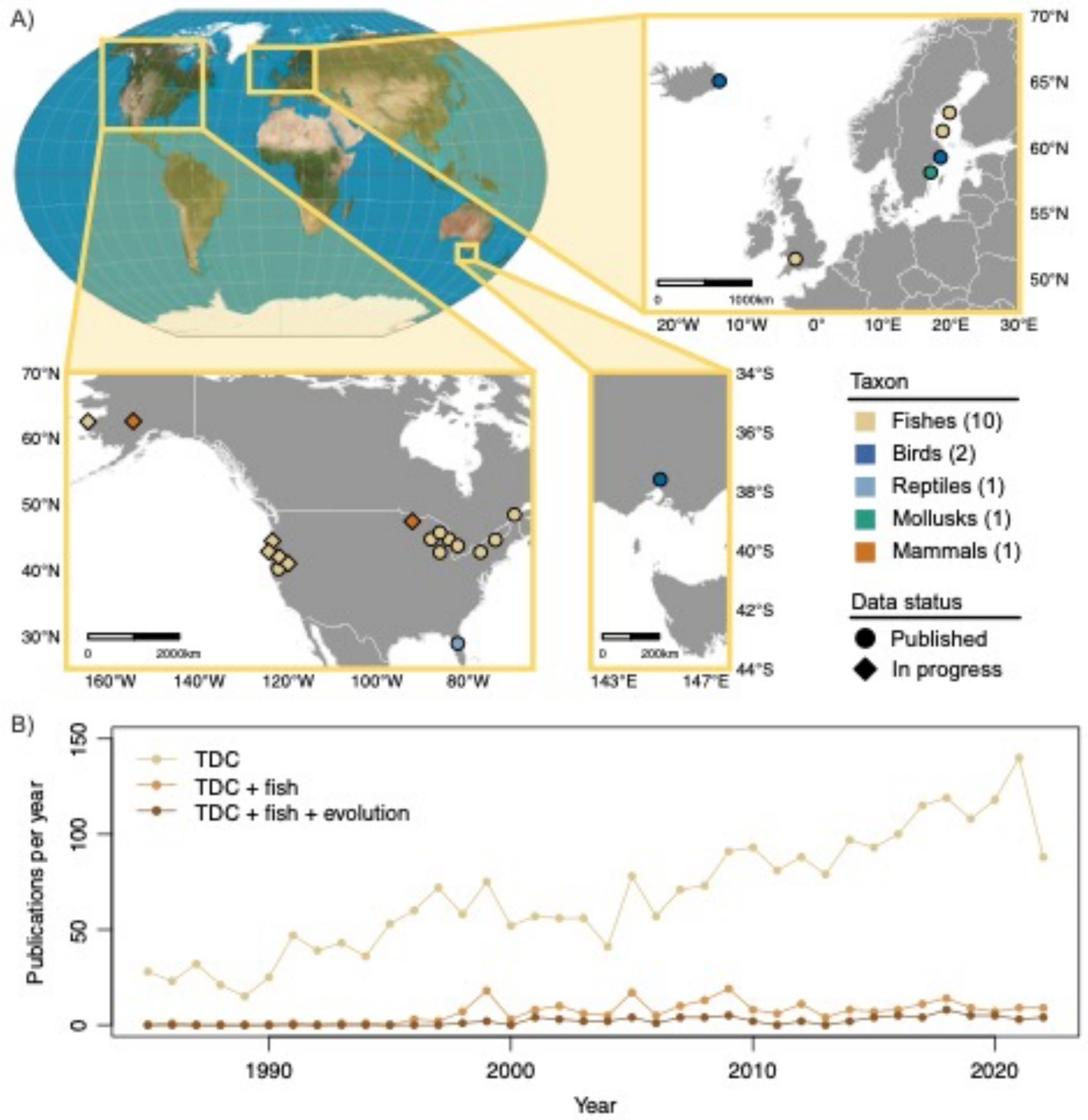

Figure 1. (A) Global occurrences of thiamine deficiency complex (TDC) across five taxa, with the number of unique species affected per taxon provided in parentheses in the figure key. Each point represents one species-level occurrence per watershed (*i.e.*, a single point may indicate multiple affected populations within the watershed). Point shape indicates whether the data supporting the detection of TDC (i) have been published as part of a peer-reviewed article or (ii) are studies in progress. Reference information for data points is available in Appendix S1. (B)

Results of an ISI Web of Science Search (Clarivate PLC) for articles on thiamine deficiency from 1985-2022 using the search methodology Bernhardt et al. (2010) used in their review of nanoparticles. First, we searched all fields for “thiamin* deficien*” OR “early mortality syndrome” OR “M74” (TDC, n = 2,611) to estimate number of papers published to-date on thiamine deficiency. Next, we searched for publications addressing fish by adding “fish OR teleost OR salmon*” (TDC + fish; n = 245). Finally, to find papers that addressed evolutionary considerations, we next added “Evolution* OR Evo* OR gene*” (TDC + fish + evolution; n = 78). Search conducted on 16 June 2023.

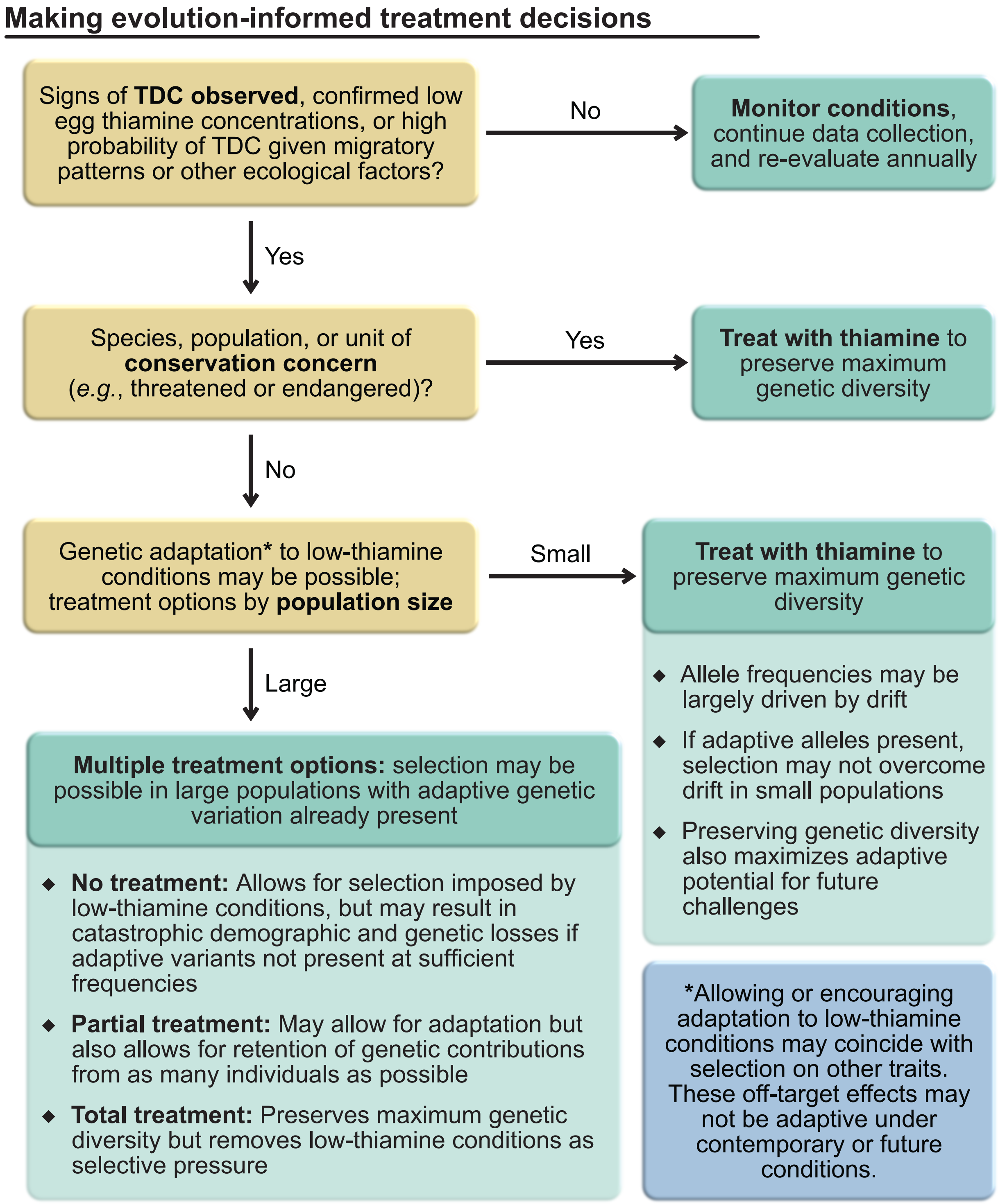

Figure 2. Overview of thiamine treatment considerations and options, given various population characteristics. While certainly not exhaustive, this diagram provides a summary of potential evolutionary outcomes of different treatment decisions, including the decision not to treat.

Determining where a population falls on the spectrum from small to large population size should include consideration of the population’s specific demographic and evolutionary history.

Appendix S1. Data supporting thiamine deficiency complex (TDC) occurrences presented in Fig. 1A. For many listed species and localities, TDC monitoring is ongoing.

Species	**Taxon**	**Locality**	**Data status**	**Reference**
Common eider (*Somateria mollissima*)	Birds	Eskifjörður, Iceland	Published	(Balk et al. 2016)
Common eider (*Somateria mollissima*)	Birds	Stockholm, Sweden	Published	(Balk et al. 2016)
Red wattlebird (*Anthochaera carunculata*)	Birds	Melbourne, Australia	Published	(Paton et al. 1983)
American eel (*Anguilla rostrata*)	Fishes	St. Lawrence River, Canada	Published	(Fitzsimons et al. 2013)
Atlantic salmon (*Salmo salar*)	Fishes	Finger Lakes, New York, U.S.	Published	(Fisher et al. 1996)
Atlantic salmon (*Salmo salar*)	Fishes	Baltic Sea, Sweden	Published	(Keinänen et al. 2012)
Atlantic salmon (*Salmo salar*)	Fishes	Lake Champlain, U.S.	Published	(Ladago et al. 2020)
Brown trout (*Salmo trutta*)	Fishes	Laurentian Great Lakes, U.S.	Published	(Marcquenski & Brown 1997)
Brown trout (*Salmo trutta*)	Fishes	Baltic Sea, Sweden	Published	(Amcoff et al. 1999)
Chinook salmon (*Oncorhynchus tshawytscha*)	Fishes	Central Valley, California, U.S.	Published	(Mantua et al. 2021)
Chinook salmon (*Oncorhynchus tshawytscha*)	Fishes	Laurentian Great Lakes, U.S.	Published	(Futia & Rinchard 2019)
Chinook salmon (*Oncorhynchus tshawytscha*)	Fishes	Yukon River, Alaska, U.S.	Published; In progress	(Honeyfield et al. 2016); (unpublished data, K. Howard)
Coho salmon (*Oncorhynchus kisutch*)	Fishes	Laurentian Great Lakes, U.S.	Published	(Futia & Rinchard 2019)
European eel (*Anguilla anguilla*)	Fishes	River Severn, England	Published	(Balk et al. 2016)

Lake trout (*Salvelinus namaycush*)	Fishes	Laurentian Great Lakes, U.S.	Published	(Fitzsimons et al. 2007)
Lost River sucker (*Deltistes luxatus*)	Fishes	Klamath Basin, Oregon, U.S.	In progress	(unpublished data, C. Nichols)
Shortnose sucker (*Chamistes brevirostris*)	Fishes	Klamath Basin, Oregon, U.S.	In progress	(unpublished data, C. Nichols)
Steelhead trout (*Oncorhynchus mykiss*)	Fishes	Alsea and Elk Rivers, Oregon, U.S.	Published	(Reed et al. 2023)
Steelhead trout (*Oncorhynchus mykiss*)	Fishes	Laurentian Great Lakes, U.S.	Published	(Futia et al. 2017)
Moose (*Alces alces*)	Mammals	Duluth, Minnesota, U.S.	In progress	(unpublished data, D. Tillitt)
Moose (*Alces alces*)	Mammals	Alaska, U.S.	In progress	(unpublished data, D. Tillitt)
Blue mussel (*Mytilus sp.*)	Mollusks	Herrhamra, Sweden	Published	(Balk et al. 2016)
American alligator (*Alligator mississippiensis*)	Reptiles	Lake Griffin, Florida, U.S.	Published	(Honeyfield et al. 2008)