

Parent-offspring conflict over reproductive timing: ecological dynamics far away and at other times may explain spawning variability in Pacific herring

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Timing of reproduction may be of crucial importance for fitness, particularly in environments that vary seasonally in food availability or predation risk. However, for animals with spatially separated feeding and breeding habitats, optimal reproductive timing may differ between parents and their offspring, leading to parent-offspring conflict. We assume that offspring have highest survival and fitness if they are spawned around a fixed date, and use state-dependent life-history theory to explore whether variation in conditions affecting only parents (food availability and survival) may influence optimal timing of reproduction. We apply the model to Pacific herring (*Clupea palasii*) in Puget Sound, USA, where 20 subpopulations spawn at different times of the year. Our model suggests that relatively small differences in adult food availability can lead to altered prioritization in the trade-off between maternal fecundity and what from the offspring's perspective is the best time to be spawned. Our model also shows that observed among-population variability in reproductive timing may result from adults using different feeding grounds with divergent food dynamics, or from individual variation in condition caused by stochasticity at a single feeding ground. Identifying drivers of reproductive timing may improve predictions of recruitment, population dynamics, and responses to environmental change.

Keywords: climate change, *Clupea harengus*, match–mismatch, spatial ecology, spawning phenology, stochastic dynamic programming

Introduction

Many fish species do not provide care for offspring after birth, but parents can still play a major role for the success of their offspring by deciding where and when to spawn. Populations often return to the same areas year after year for reproduction, but there may be substantial variation in when spawning takes place, both between years and among subpopulations. To understand this variation and furthermore how reproductive timing may respond to climate change and other stressors, there is a need for evolutionary interpretations of

local variation in reproductive timing as the outcome of adaptive behaviour.

Consider this baffling example from Puget Sound, WA, USA (Figure 1a), where 20 different Pacific herring (*Clupea palasii*) subpopulations (stocks) spawn consistently but at different times of the year (between late January and June, Stick *et al.*, 2014; Figure 1b) even though all but two stocks show no discernible genetic variation (Small *et al.*, 2005). No known evidence exists that this variability in spawn timing is related to environmental conditions; though, at broader spatial scales, it is thought that annual

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temperature regimes regulate maturation and spawn timing (Hay, 1985). This raises the question of why these stocks display so much variation in reproductive timing. In addition, peak spawn date has been shifting for many of the Puget Sound herring stocks in recent years, but in different directions and magnitudes (Figure 1b). Local drivers of these changes have not yet been identified, and similar shifts have been observed but not yet explained for Pacific herring elsewhere along the west coast of North America (R. Bartling, pers. comm., S. Dressel and K. Hebert, pers. comm.). It seems clear that some underlying process is affecting the spawning time of each stock, while allowing large between-stock variation.

In fisheries science reproductive timing has been a hot topic for over 100 years, ever since Johan Hjort presented his famous “critical period” hypothesis (Hjort, 1914) to explain variability in recruitment. Hjort (1914) hypothesized that recruitment was determined as early as the time of first feeding, since starvation during this early larval phase could substantially reduce offspring survival. This idea was expanded on by Cushing, who proposed the “match–mismatch” hypothesis (Cushing, 1973, 1990). Cushing acknowledged that starvation of first-feeding larvae could contribute to variability in larval mortality, but built his argument on the observation that mortality declines with size (McGurk, 1986; Gislason *et al.*, 2010; Brodziak *et al.*, 2011). In Cushing’s view, poorly fed larvae grow slowly and are therefore more susceptible to predation. Accordingly, the central assumption of the “match–mismatch” hypothesis is that timing of spawning is adapted to seasonal plankton production blooms in the larval distributional area. In its original formulation, the hypothesis also assumed that fish populations in temperate waters spawn at fixed times and thus that mismatches arise due to variable plankton phenology (Cushing, 1969, 1973). However, many temperate fish populations demonstrate larger inter-annual variability in spawning time than can be explained from food availability for early life stages (e.g. see Wright and Trippel, 2009). For example, significant intra-specific variation (ranging 65–100 days) over three decades was reported for three Northwest Atlantic cod (*Gadus morhua*) populations (Hutchings and Myers, 1994). There is also large variation in timing of spawning among populations of the same species [e.g. Atlantic herring (*Clupea harengus*), Sinclair and Tremblay, 1984; haddock (*Melanogrammus aeglefinus*), Page and Frank, 1989; cod, Brander and Hurley, 1992; Myers *et al.*, 1993; sardine (*Sardina pilchardus*), Stratoudakis *et al.*, 2007]. While Atlantic herring populations spawn over the entire year, Pacific herring spawning can span over several months, and some populations spawn at different times of the year on the same spawning grounds (Sinclair and Tremblay, 1984).

Since the introduction of the “critical period” (Hjort, 1914) and “match–mismatch” (Cushing, 1973, 1990) hypotheses, much research has been devoted to explaining recruitment variability in fish populations (see Houde, 2008; Wright and Trippel, 2009). Most of this research relies on the assumption that fish spawning times have evolved so offspring encounter conditions that promote their survival, while any effects on the reproductive success of individual parents have been ignored (Wright and Trippel, 2009). Thus, it seems fair to say that our current understanding of the selective factors operating on timing of spawning is incomplete, which in turn implies that we lack a mechanistic understanding of the underlying drivers of recruitment variation (Munch *et al.*, 2005a, b).

A better understanding of spawning phenology is also of interest for climate change research, since climate warming is generally expected to shift reproductive activities earlier in spring or later in autumn (Stenseth and Mysterud, 2002; Parmesan and Yohe, 2003; Visser and Both, 2005; Both *et al.*, 2009). For over a decade, Cushing’s “match–mismatch” hypothesis has formed a main basis for studies on the effects of climate change on trophic interactions and their consequences for population dynamics (Durant *et al.*, 2007; Parmesan, 2007; Thackeray *et al.*, 2010). Some of these studies show declines in population fitness as a consequence of asynchrony between offspring food demand and availability (e.g. Both *et al.*, 2006; Visser *et al.*, 2006).

However, environmental variability influences more than the early life stages, it also impacts the success and survival of adults. A key insight and the driver of our model is that when resources and predation risk vary over the annual cycle, an adult may not be able to reproduce at the optimal time for its offspring if this timing conflicts with other priorities for adult survival or reproduction (e.g. Reznick *et al.*, 2006; Varpe *et al.*, 2007). In short, what is good for the offspring may not be good for the parent, and evolutionary thinking allows us to study this trade-off. For example, a parent may increase lifetime reproductive success by breeding later than the optimal timing of birth for its offspring, so that the parent can have more time to acquire additional energy in preparation for spawning, and thus eventually produce more offspring (Rowe *et al.*, 1994; Drent and Daan, 2002). In other cases, it can be better to reproduce earlier than optimal for the offspring, so that the parent can have returned to the feeding grounds in time for peak food availability. In addition to foraging considerations, variable predation risk can similarly influence adult reproductive decisions (Lima, 2009). In the case of Puget Sound herring, variable spawning times may thus come about not because of mismatch between early life stages and benign environmental conditions, but because parents are attracted to foraging opportunities or avoid predation risk in ways that are more decisive for their fitness.

To incorporate these considerations, we use the theory of parent–offspring conflict to model spawning time as a compromise between the mother’s expected survival and fecundity on the one hand, and accumulated reproductive success through the survival of her offspring on the other (Reznick *et al.*, 2006; Varpe *et al.*, 2007). This follows the logic of Trivers (1974), who showed that sexual reproduction can cause a conflict between parents and their offspring when the current reproductive investment of the parent has a negative effect on its future fitness. The prerequisites for such a conflict are that the optimal levels of parental investment differ between a parent and its young, and that investing more in the offspring can benefit the offspring but at a cost to the parent (Roitberg and Mangel, 1993). This leads to joint evolution of parental and offspring traits, and the outcome can either be evolutionarily stable or result in a continuing arms race (see Kilner and Hinde, 2012, and references therein). A spawning time that diverges from the optimal timing from an offspring’s perspective may thus result from stronger selection on related traits in parents, which may constrain offspring fitness although it maximizes parental fitness.

Since timing of reproduction is an emergent property of the overall selection on parental timing and offspring survival (Trivers, 1974; Varpe *et al.*, 2007; McNamara and Houston, 2008), explaining variation in this trait requires incorporation of a full life cycle perspective (i.e. both offspring and parents). In this study we include the parental view and adopt a simplified

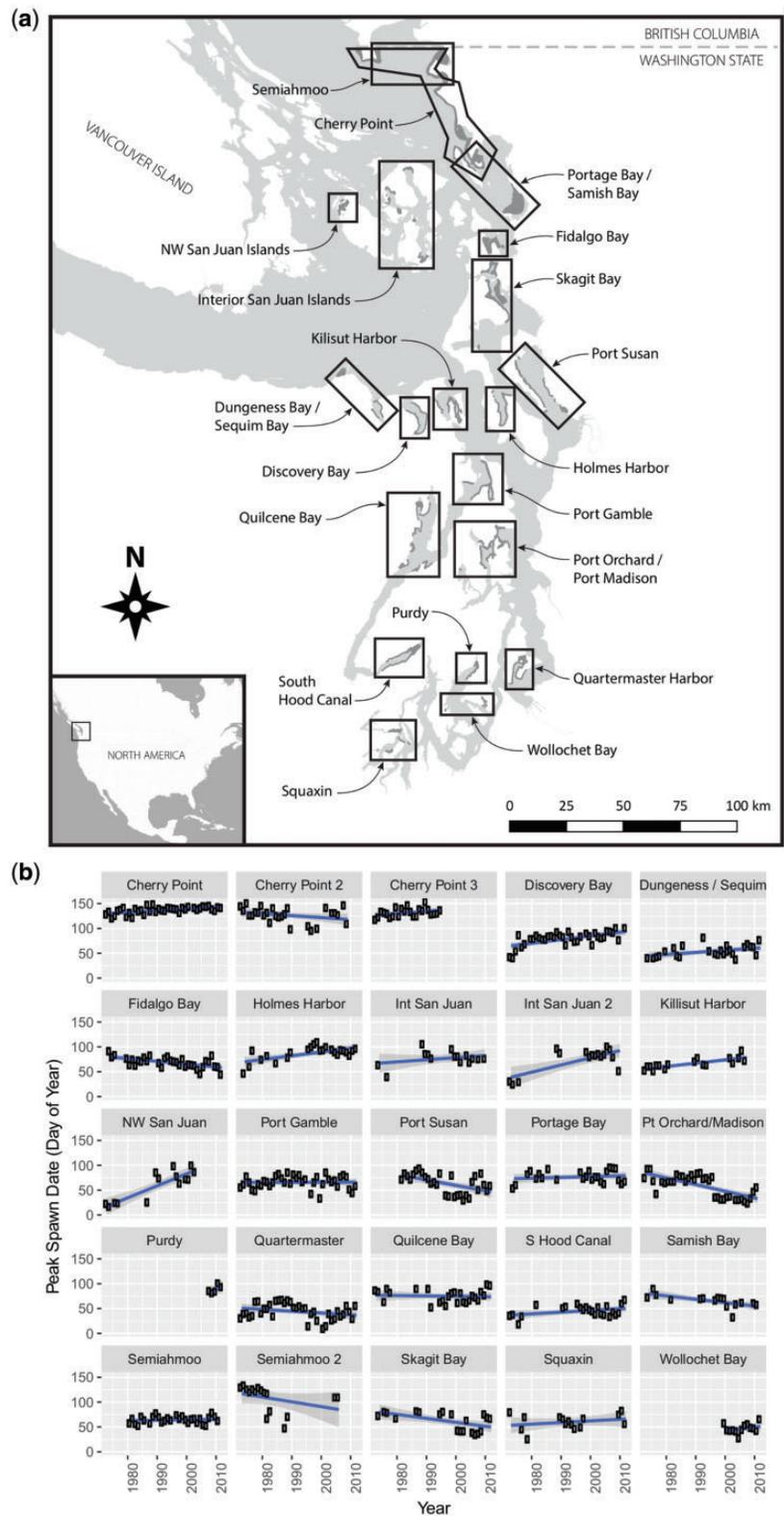


Figure 1. (a) Puget Sound herring are managed by the Washington State Department of Fish and Wildlife (WDFW) as 20 separate spawning populations (inset shows location in the northeast Pacific, WA, USA). (b) Time series of peak spawn dates (with linear smoother and 95% confidence interval) for Pacific herring spawning sites in Puget Sound. Peak spawn date is defined as the survey date on which the cumulative observed egg abundance (based on WDFW rake surveys) exceeded 80% of the total egg abundance observed for that year. Note that some of the stocks recognized by WDFW (Figure 1a, 20 in total) spawn in adjacent bays and have somewhat different peak spawn times, and have therefore been separated in the graphs showing spawning times (Figure 1b, 25 in total). Int San Juan 2 = Lopez Island; Cherry Point 2 = Birch Point; Semiahmoo 2 = Point Roberts; Cherry Point 3 = Hale Passage.

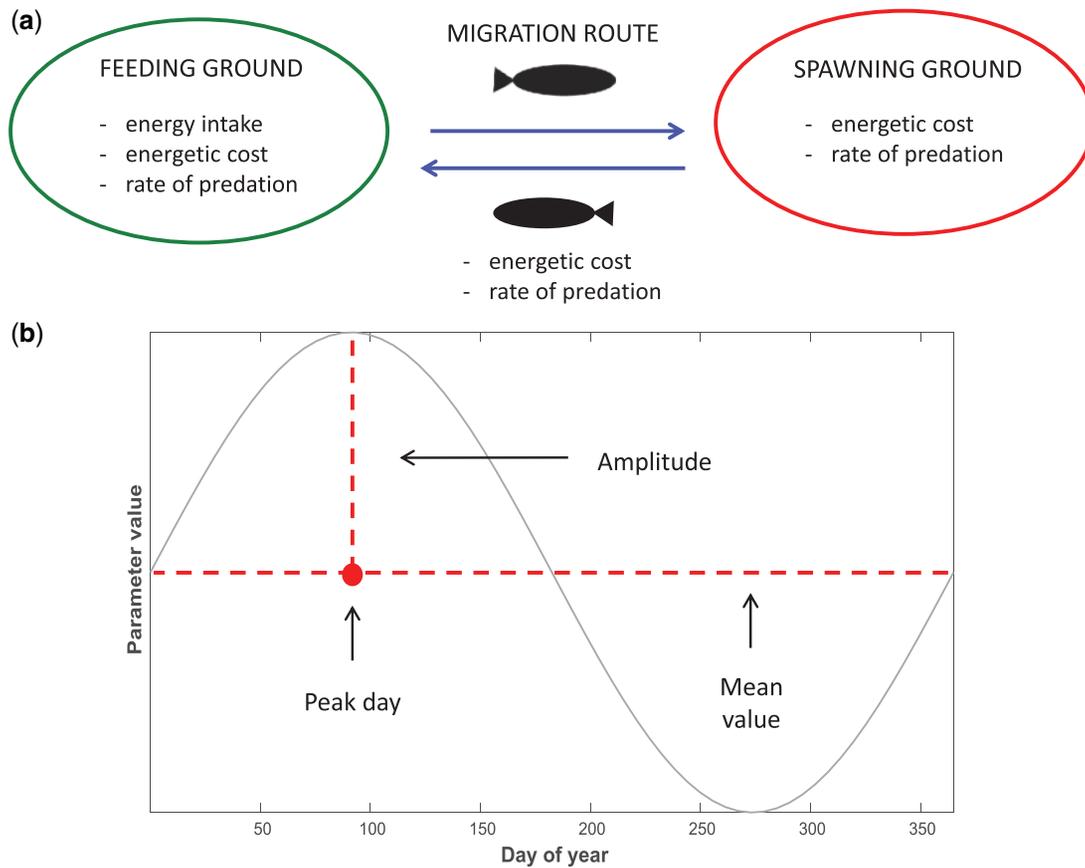


Figure 2. (a) Schematic illustration of the model. Individuals can either be at the feeding ground foraging and building reserves for spawning, at the spawning ground to reproduce, or migrating in between. Key variables are given in lowercase letters. (b) Seasonal variability of parameter values. When the environment varies seasonally, the annual sine curves are characterized by their peak day, mean value, and amplitude.

annual routines approach to capture trade-offs resulting from life in a seasonal environment (Barta *et al.*, 2008; Feró *et al.*, 2008). To explore how variation in conditions (food availability and mortality rate) that only affect parents influences optimal reproductive timing, while accounting for seasonality in offspring recruitment probability, we use a state-dependent life-history model. We focus on migratory Pacific herring spawning in Puget Sound as it exemplifies a system in which the conditions that affect adults for most of the year are separated by migration from those that determine survival of early life stages. Although our focus is on migratory pelagic fish populations, the mechanisms and relationships are general and could be applied to explore reproductive decisions of other migratory organisms as well.

Our aims are: (i) point to possible drivers of evolved patterns in spawning time in fish populations and assess the potential magnitude of their effects on spawning time variability; and (ii) expand match–mismatch thinking by parent–offspring conflict as basis for a richer explanation of shifts in reproductive phenology associated with environmental change.

Material and methods

Overview of the model

We will now provide verbal summaries of the model; the relevant equations are given in appropriate detail in [Supplementary Material S1](#).

To explore how variation in food availability and mortality rate at the feeding grounds of adults affects their optimal reproductive timing, while taking seasonality in offspring recruitment probability into account, we used state-dependent life-history theory in which optimal life-histories are found by stochastic dynamic programming (Houston and McNamara, 1999; Clark and Mangel, 2000). The central assumption of our model is that there are three seasonally fluctuating relationships that influence reproductive success: (i) food availability and (ii) predation risk at the feeding grounds, affecting only adults, and (iii) probability of recruitment for offspring hatched on a certain day of the year (referred to as offspring fitness). We used the model to predict when it was optimal for parents to reproduce and how much energy they invest in current reproduction; both these decisions were conditional on the energy reserves of the parent, its location, and the day of the year. The model maximized expected lifetime reproductive output, accounting for current and future reproductive events. Thus, in this study decisions represent strategies and behaviours that have evolved by natural selection, and not decisions due to cognitive choice. We parameterized the model for Pacific herring in Puget Sound. After determining the optimal decisions for each state and time as they were constrained by physiology (bioenergetics) and ecology (food availability and mortality of adults and offspring), we used forward Monte

Table 1. Parameters and variables (italics) used in the three analyses.

Location	Parameter	Puget sound	Food availability analysis	Mortality analysis	Units	
Feeding ground (f)	Energy intake $-Y(t)$					
	Mean	10 11 12	10, 11, 12	10, 11, 12	kJ/day	
	Amplitude	10 11 12	1.375, 2.75, 4.125	0	kJ/day	
	Peak day	Every 50 days(30, 80, 130, 180, 230, 280, 330)	Every 50 days(30, 80, 130, 180, 230, 280, 330)	[constant]	Day of year	
	Energetic cost $a_f(t)$					
	Mean	6.7	6.7	6.7	kJ/day	
	Amplitude	1.8	0	0	kJ/day	
	Peak day	212	[constant]	[constant]	Day of year	
	Rate of mortality $m_f(t)$					
	Mean	0.5	0.1, 0.3, 0.5	0.2, 0.4, 0.6	Year ⁻¹	
Migration route (m)	Energetic cost $a_m(t)$					
	Mean	9.13	9.15	9.15	kJ/day	
	Amplitude	1.8	0	0	kJ/day	
	Peak day	212	[constant]	[constant]	Day of year	
	$m_m(t) = m_f(t)$		$= m_f(t)$	$= m_f(t)$	Year ⁻¹	
	Spawning ground (s)	$a_s(t) = a_f(t)$		$= a_f(t)$	$= a_f(t)$	kJ/day
		$m_s(t) = m_f(t)$		0.2	0.2	Year ⁻¹
		Offspring fitness $F_{\text{offspring}}(t)$				
		Mean	0.4	0.4	0.4	
		Amplitude	0.4	0.4	0.4	
	Peak day	91	91	91	Day of year	

Carlo simulation to predict individual lifetime trajectories. Differences across individuals thus arose from stochastic energy gain, and by summing across many individuals we obtained population-level distributions of key traits and behaviours. We have strived to present results as quantities that can be measured in the field.

Optimal decisions, state variables, the environment, and reproductive success

We consider three locations: a feeding ground; a migration route; and a spawning ground (see Figure 2a for a schematic illustration of the model).

We only consider females, assuming that males are sufficiently abundant that all eggs are fertilized. When a female is on the feeding ground, her possible behaviours are “stay” or “migrate”; when on the spawning ground, they are “wait,” “spawn a proportion of available reserves and migrate back to feeding grounds,” or “spawn all available reserves and die.” The latter option is not necessarily semelparity because it may be preceded by spawning events in which not all resources were used. It is thus better described as terminal spawning, and can occur at any time if conditions dictate so (Duffield et al., 2017). The reproductive output of an individual that spawns on a particular day of the year is obtained by multiplying the energy allocated to reproduction by a recruitment probability for offspring spawned on that day. We thus assume a seasonal curve for offspring fitness, and use the identical curve across all simulations so all variation in spawning time predicted in this study stems from environmental effects on adults. We assume that natural selection has acted on these behaviours to maximize accumulated reproductive output (expected number of recruited offspring a parent produces, i.e. offspring that survive to join the adult population).

The model characterizes the female by the physiological state variable energy reserves, which on day t has the value x , measured in joules (J). The feeding ground is characterized by three environmental parameters: food availability (energy intake, i.e. consumed energy minus losses due to digestion and waste; $J \text{ day}^{-1}$); energetic cost (temperature-dependent standard metabolism; $J \text{ day}^{-1}$); and rate of mortality (day^{-1}). Depending on the specific analysis (see Analyses section), we treat these either as constant or following seasonal patterns, given by sinusoidal functions with an annual period. The annual sine curves are characterized by a mean value, peak day, and amplitude (see Figure 2b, Table 1). We model energy intake as stochastic and autocorrelated between days, and let the environmental state variable $Y(t)$ ($J \text{ day}^{-1}$) represent the actual energetic intake on day t of the year. We assume that no feeding takes place during migration, or at the spawning ground, thus, these two locations are only characterized by an energetic cost and a rate of mortality. Hence, the state-dependent life-history model explicitly accounts for the trade-off between current and future reproductive output, within the constraint of the energy budget. See Supplementary Material S1 for equations and other details of numerical solution.

Analyses

Sources of environmental variability that could alter the cost/benefit ratio and thus timing of spawning are seasonal variation in resource availability and predation risk, because these potentially lead to feeding and survival opportunities lost to adults while they are away spawning. To systematically explore the effects of annual fluctuations in food availability and mortality rate at the adult feeding ground on optimal spawning time, we used three different analyses that vary these environmental variables within reasonable limits. First, we investigated the relative roles of energy

intake (“Food availability analysis”) and mortality rate (“Mortality analysis”) in driving variation in reproductive timing, then we explored dynamics with the model parameterized to Puget Sound (“Puget Sound analysis”). See Table 1 for parameters investigated in these analyses.

Food availability analysis

In this analysis, we used three mean levels of the annual sine curve in energy intake over three different amplitudes, and with three constant levels of feeding ground mortality to investigate the effects of variation in food availability on optimal spawning time. To isolate the effects of variation in energy intake, we kept the energetic costs constant. Keeping all other parameters constant, we ran forward Monte Carlo simulations over three levels of energy intake (low, medium, high), for several different peak days of this variable), to represent feeding grounds of different quality and timing. To reduce the number of combinations of parameters to explore, we kept mortality rates constant and equal at all three locations.

Mortality analysis

In this analysis, we investigated the effects of variation in mortality rate on optimal spawning time. We simulated three mean levels of the annual sine curve in feeding ground mortality rate over three amplitudes, and three constant levels of energy intake. To isolate the effects of variation in mortality rate, we kept the energetic costs constant. Keeping all other parameters constant, we ran forward Monte Carlo simulations for several different peak days in mortality rate.

Puget Sound analysis

In this analysis, we explored the seasonal dynamics of herring spawning in Puget Sound. Food availability and energetic costs were characterized by annual sine curves, with parameter values representative of Puget Sound herring. Although the model is conceptual and parameters are coarse, it shows the potential range of spawning times that could be brought about by environmental fluctuations that affect only parents at the feeding grounds. Keeping all other parameters constant, we ran forward Monte Carlo simulations for several different peak days in energy intake.

Optimization and simulations

We used state-dependent behavioural and life-history theory by stochastic dynamic programming (Houston and McNamara, 1999; Clark and Mangel, 2000) to find optimal life-history strategies by iterating backwards from a final point in time, constantly assuming that an individual acts optimally at every future decision point. Our model runs by daily time steps and finds the optimal strategy for when to move between feeding grounds and spawning grounds for each combination of the state variable and time. The optimization criterion is accumulated lifetime reproductive output, i.e. the sum of the energy spawned at each reproductive event discounted by survival probability to that event, and multiplied with offspring fitness (recruitment to the population) for that day of year. Thus, the predicted strategies are evolutionary optima for the specific parameter set used to describe the ecology of the system. To allow for investigation and visualization of individual and population level patterns emerging from the

interaction between the optimal strategy and the environment, we simulated 10 000 individuals that followed the optimal strategy in a stochastic food environment.

Parameterization

The parameter values used in the model were chosen to represent Pacific herring spawning in Puget Sound (Supplementary Table S1). The majority of the parameter estimates was obtained from a model study on Pacific herring in an adjacent area, the west coast of Vancouver Island, British Columbia, Canada (Megrey *et al.*, 2007).

We used the Wisconsin bioenergetics framework (Hewett and Johnson, 1992) to model energy intake (see Supplementary Material S2.1 for equations, and Supplementary Material S2.2 for parameter values and references). Briefly, we estimated the daily energy intake [consumption – (specific dynamic action + excretion + egestion)]; J day^{-1}) and energetic cost due to respiration (J day^{-1}), for the highest (14°C , day 212) and lowest seasonal (7°C , only used for respiration cost) water temperature in the Puget Sound region (Megrey *et al.*, 2007). Depending on the analysis, particularly whether the environment was modelled as seasonal or constant, we used the estimated values to set the limits for the corresponding annual sine curve, or their mean value. Parameters for daily consumption rates are commonly derived from lab experiments conducted at the optimum temperature under *ad lib* feeding conditions. Thus, the estimated value for energy intake at the highest seasonal water temperature is the theoretical upper limit for this parameter, and we assumed a lower value to reflect realized intake. Puget Sound herring weigh ~ 100 g at the start of their feeding season and gain typically 30 g, sometimes up to 40 g, over the season (Schweigert *et al.*, 2002). We assumed that all this weight gain is fat, so that length and non-reproductive mass are constant over the feeding season, and parameterized the bioenergetics for an adult herring of average size (115 g).

The annual sine curve for offspring recruitment probability (offspring fitness) was set to depend on prey availability for newly hatched larvae, assuming that its combined effect on starvation (Hjort, 1926; McGurk, 1984; Huwer *et al.*, 2011) and predation mortality (McGurk, 1986; Bailey and Houde, 1989; Litvak and Leggett, 1992; Takasuka *et al.*, 2003; Jørgensen *et al.*, 2014) dictates the likelihood that offspring survive until recruitment. Hence, our offspring fitness curve represents the probability that individuals spawned on different days of the year survive from that day until recruitment, considering all factors acting on their survival during that time. The peak day in offspring fitness was set in early April, because this is the typical period of max abundance of nauplii larvae, which are prime food for herring larvae and produced by adult copepods during the spring phytoplankton bloom. The exact dates of peak food abundance for larvae vs. adults in Puget Sound are of less importance in this study since we do not aim to precisely fit the model to data, but rather to use the Puget Sound case for motivation and a general sense of what needs to be explained. Depending on the analysis, adult mortality rates were set to different levels within an ecologically appropriate range. Natural mortality rates for adult herring of $0.2\text{--}0.4 \text{ yr}^{-1}$ are considered typical for herring worldwide, and similar values were reported for Puget Sound herring up until the late 1970s (Stick *et al.*, 2014). Since then, mortality has increased. A mortality rate of 0.8 yr^{-1} was reported for the years 1973–1990 (Siple *et al.*, 2017) and the current rate is thought to be around 1.2 yr^{-1} (Stick *et al.*, 2014; Siple *et al.*, 2017). In the “Puget Sound analysis,” we

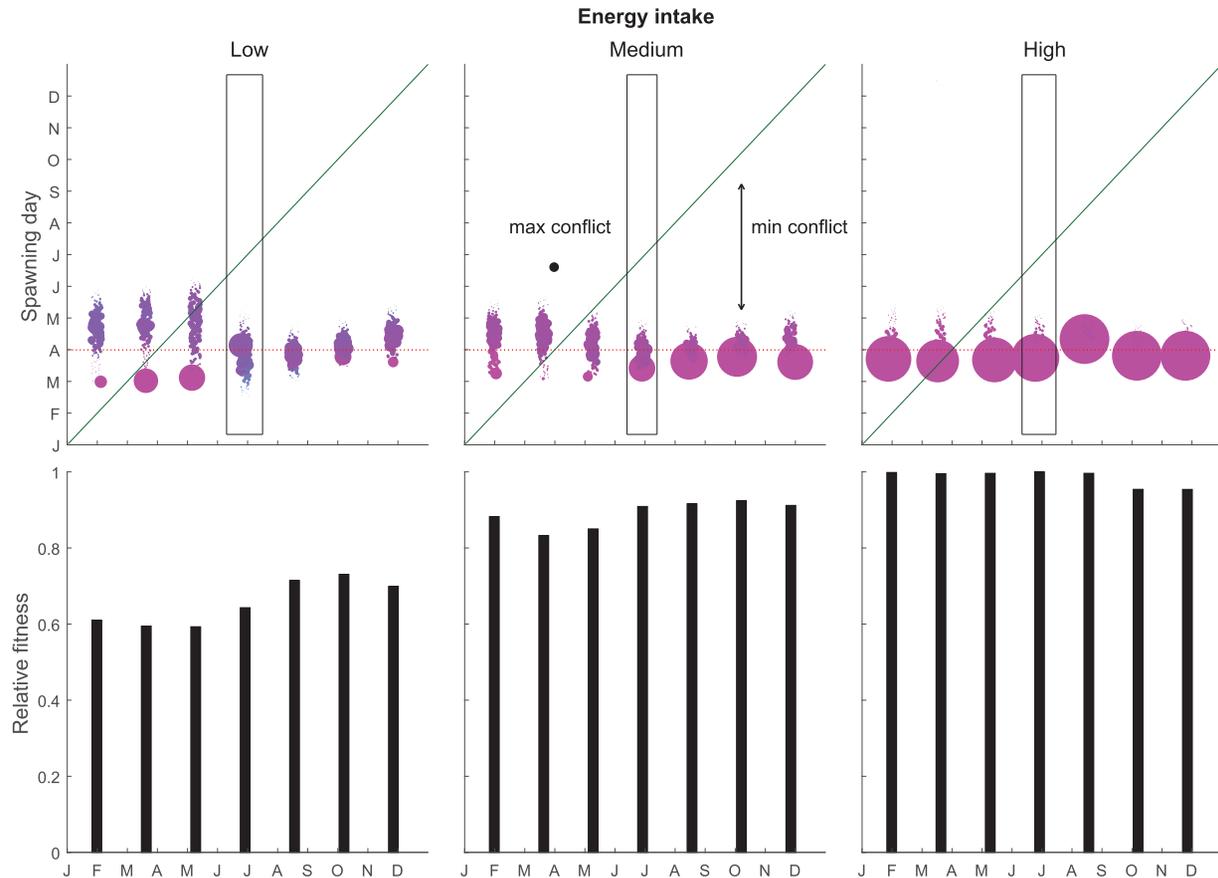


Figure 3. The top panel shows the predicted spawning days for 10 000 individuals following the optimal strategies for the reference case in the “Food availability analysis,” showing the effects of variation in food availability. Dots represent predicted spawning days for different peak days and three mean levels of energy intake under a medium feeding ground mortality rate. The size of the dot indicates the frequency of spawning events predicted for that day and the colour the energy spawned as a proportion of the maximum predicted spawning energy for that peak day (blue to pink = less to more). The dotted red horizontal line shows the peak day in offspring fitness and the green diagonal line the peak day in energy intake. Rectangle indicates the case explored in Figure 3. The bottom panel shows the relative fitness value of each peak day in food availability (energy spawned on each predicted spawning day multiplied with offspring fitness for that day, summed across all individuals simulated and for all days, and divided by the number of individual-years simulated).

used an intermediate mortality rate of 0.5 yr^{-1} , assuming that herring life-histories in this area are undergoing adaptation to the new and higher natural mortality, but have not yet fully adapted to this new selection regime. Results for a mortality rate of 0.8 yr^{-1} are qualitatively similar and shown in Supplementary Figure S7.

Results

A common feature of our results is that food dynamics at the feeding grounds of adults influenced optimal timing of spawning (both mean and variance), and that lower food availability lead to a wider spread in timing of spawning.

Food availability analysis

Food availability was a major driver of optimal spawning time, and spawning dates were more variable when there was little food (Figure 3). From Figure 3, the isolated effect of different food levels can be read by comparing the location and size of the predictions for the same peak day in energy intake across the three levels of energy intake. Similarly, the effects of different amplitudes in energy intake, and for the three levels of mortality, can

be read by comparing with Supplementary Figures S1–S3. Of particular interest is the comparisons between simulations that differ in the strength of the parent-offspring conflict. Where the red dotted and solid green lines cross on Figures 3 and 5, food availability peaks at the date of maximum offspring fitness, thus implying maximum conflict between parental feeding and the fitness return from each egg spawned. This conflict is minimal where the red dotted and solid green lines are half a year apart, i.e. around October in Figures 3 and 5. In addition to at low food levels, spawning dates were more variable when this conflict was large, while less conflict allowed for better timing from an offspring perspective. This resulted in lower relative fitness at higher than at lower levels of conflict.

In Figure 4, we show individual trajectories in detail, assuming a peak day in zooplankton abundance ~ 1 st July (see boxes in Figure 3). Spawning times were more variable at low food levels. Further, individuals spawned earlier if they had acquired little energy for reproduction, so that they were away for spawning closer to the trough of the annual food curve. This strategy allowed them more time to forage for the subsequent spawning event, and more of that time was around the food peak. At medium and high food levels, individuals spawned more consistently around

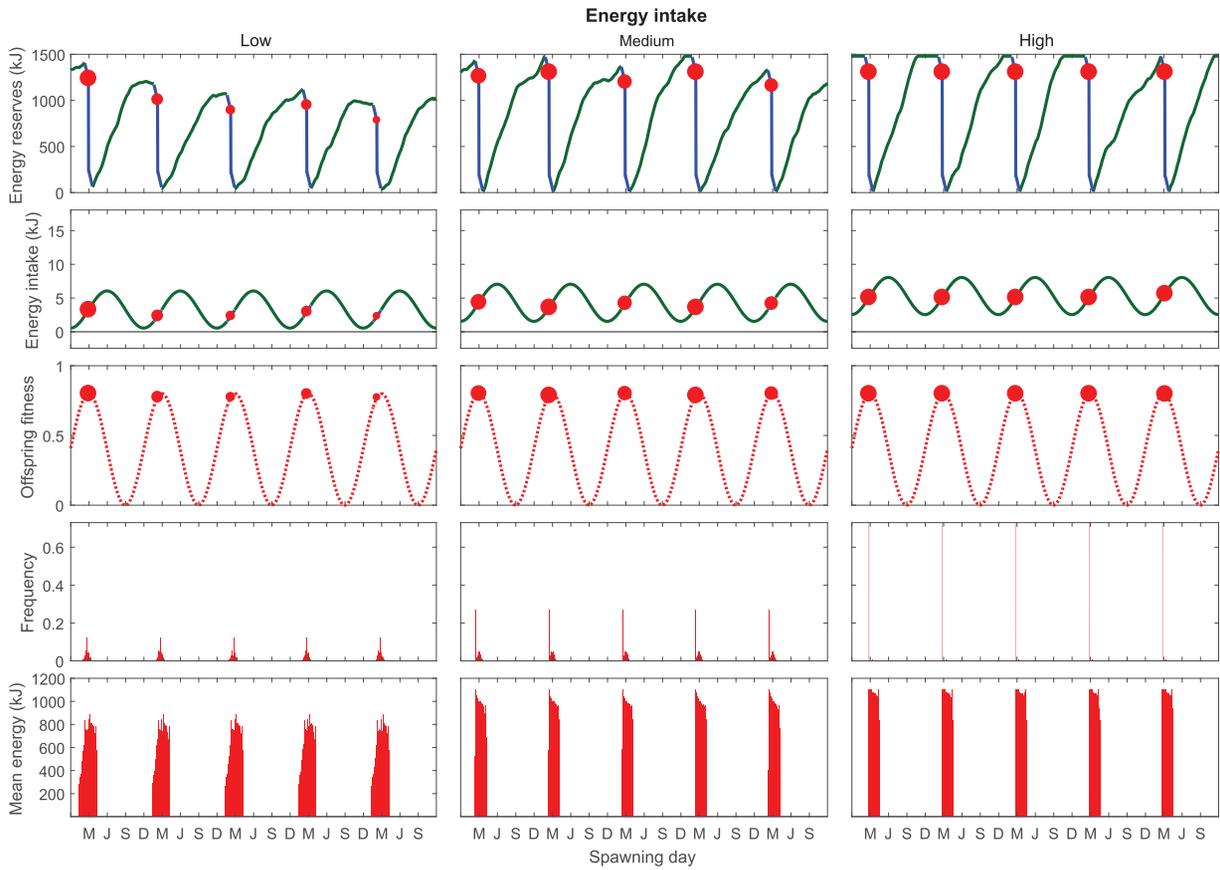


Figure 4. Detailed results for an individual following the optimal strategies, assuming a peak day in zooplankton abundance \sim 1st July and the three levels of food availability in the “Food availability analysis” over five years. First row: the energy reserves of the individual, green line indicates that the individual is on the feeding ground and blue line that it is migrating. The red dot represents a spawning event and its size the amount of energy spawned (proportion of maximum amount of energy spawned). Second row: the energy that an individual can acquire if on the feeding ground. Third row: offspring fitness. Fourth and fifth rows: frequency of spawning and mean energy allocated to reproduction, respectively, for each day of the year for 10 000 individuals. Note that individuals may spawn considerable energy at spawning dates when very few fish spawn.

the peak of the offspring fitness curve, indicating that the trade-off between this and next year’s fecundity was less severe. More figures related to this analysis are available in [Supplementary Material S3.1](#).

Mortality analysis

Varying mean level, peak day, and amplitude of mortality rate at the feeding ground had only negligible effects on spawning time ([Supplementary Figures S5–S7](#)). In agreement with the results of the “Food availability analysis,” the spread in predicted spawning days was higher at low levels of food availability and decreased with higher food levels, regardless of the seasonality in feeding ground mortality.

Puget sound analysis

When using parameters representative of Puget Sound, the model predicted variable spawning dates, generally within the broad range observed from February to June ([Figure 5](#)). A major reason there is more variation in spawning time within the “Puget Sound analysis” is the long period of negative food intake, typically in winter in the wild but in the simulations we vary its timing. The model predicts that the degree of parent-offspring

conflict (approximated by the distance between actual spawning day and the peak day in offspring fitness) differs depending on food level. This means that, even with fixed environmental effects on early life stages, certain adult feeding conditions can bring about variation in spawning times comparable to that observed in Puget Sound. Further, at the metapopulation level, different sub-stocks of herring may utilize food resources that differ in their abundance or timing, so that spawning in Puget Sound as a whole may be assembled by different spawning components sampled across the three panels in [Figure 5](#).

For a peak day in adult energy intake that corresponds to the approximate current peak in zooplankton abundance in the Puget Sound region (\sim 1st July, [Moore *et al.*, 2016](#); see boxes in [Figure 5](#)), we predicted a range in spawning time of approximately four months across the three food levels (early February to late May). We consider a peak day in adult zooplankton abundance between November and February unlikely for Puget Sound and hence do not include these results in our interpretation and discussion. They could however be relevant for other systems, so the results are reported on the figures for theoretical completeness.

We explored the current case (peak day in energy intake \sim 1st July; see boxes in [Figure 5](#)) further by forward simulating a

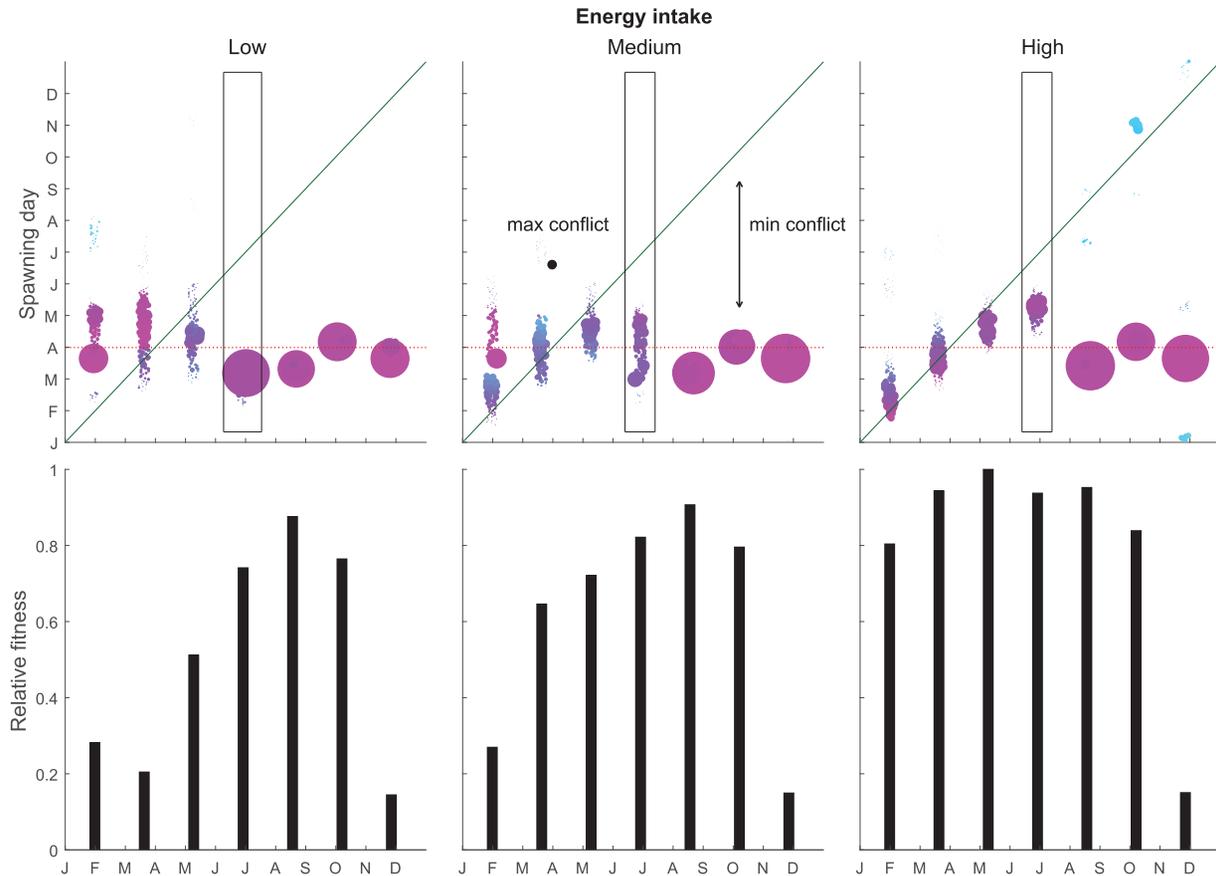


Figure 5. The top panel shows predicted spawning days for 10 000 individuals following the optimal strategies with parameters representative of Pacific herring in Puget Sound (“Puget Sound analysis”). Dots represent predicted spawning days for different peak days and three levels of energy intake. The size of the dot indicates the frequency of spawning events predicted for that peak day and the colour of the dot indicates the energy spawned as a proportion of the maximum predicted spawning energy for that peak day (blue to pink = less to more). The dotted red horizontal line shows the peak day in offspring fitness and the green diagonal line the peak day in energy intake. Rectangle indicates the case explored in Figure 6, representing the approximate current peak day in zooplankton abundance in Puget Sound (~1st July). The bottom panel shows the relative fitness value of each peak day in food availability (energy spawned on each predicted spawning day multiplied with offspring fitness for that day, summed across all individuals simulated and for all days, and divided by the number of individual-years simulated).

population of individuals following the optimal strategies, for three levels of food availability (Figure 6). These results suggest that the diverse spawning times displayed in Figure 5 can be driven by different prioritization in the trade-off between feeding to ensure high fecundity vs. hitting the peak in offspring fitness. At low food levels, spawning often took place slightly before the optimal spawning time, as there was not enough food in spring for adults to substantially increase fecundity. Sometimes it was seen that individuals stayed behind at the feeding grounds and spawned later than the optimum, this happened when current feeding conditions were particularly good. At intermediate and high food levels, adults feed more consistently in spring, thus increasing fecundity, but they also spawned slightly after the fitness peak. These differences in prioritization are illustrated in the individual as well as the frequency plots in Figure 6. For example, at the low food level, the frequency of spawning events peaked before the peak offspring fitness, whereas at the medium and high food levels the frequency was distributed around and after the peak. More figures related to this analysis are available in Supplementary Material S3.3.

Model sensitivity

Most key parameters have been subject to analysis in the sections above, with additional results reported in the Supplementary Material. Another parameter of potentially influential role is the duration of migration, which when approaching zero would imply that breeding takes place in the feeding habitat and not a separate location. Results for each analysis of using migration durations of 10, 30, and 40 days (instead of the default value of 20 days) are reported in the Supplementary Material S4. Changing the parameter did not qualitatively alter model predictions, except for the Puget Sound scenario where reproduction became more frequent and almost continuous at the shortest migration duration (see Supplementary Material S4.2).

Discussion

To date, most research on reproductive phenology and recent shifts associated with climate change has focused on offspring (e.g. see reviews by Visser and Both, 2005; Durant *et al.*, 2007; Wright and Trippel, 2009). This is natural, since timing of birth

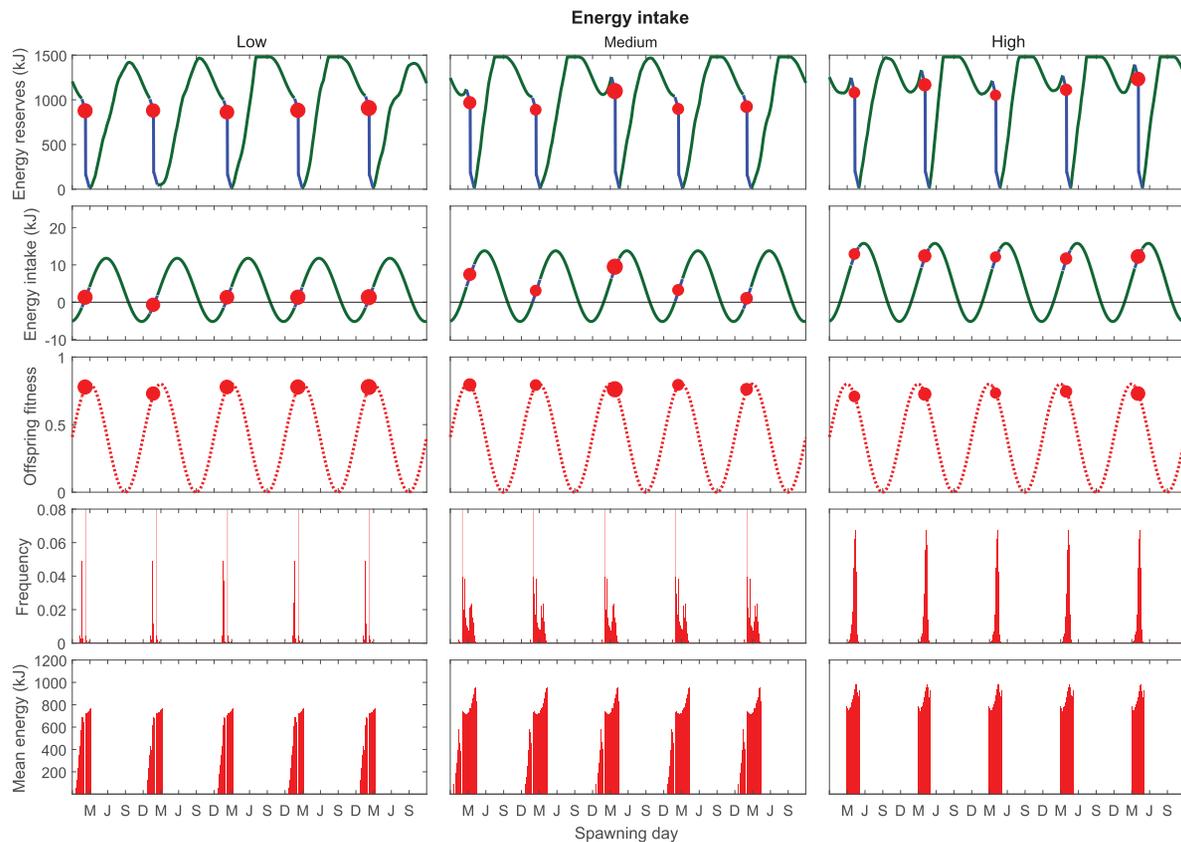


Figure 6. Detailed results for an individual following the optimal strategies for the approximate current peak day in zooplankton abundance in the Puget Sound region (~1st July) and the three levels of food availability in the “Puget Sound analysis” over five years. See legend for Figure 3. for description of plot specifications.

is of crucial importance for offspring fitness in many species, and particularly in seasonal environments (Price *et al.*, 1988; Olsson and Shine, 1997; Reznick *et al.*, 2006; Varpe *et al.*, 2007; Plard *et al.*, 2015). However, when food availability and predation risk vary over the year, life cycle constraints and trade-offs may cause a mismatch between optimal time of birth for offspring and the optimal time to give birth for parents, leading to a parent-offspring conflict (Trivers, 1974). The evolutionary outcome of such a conflict can have important implications for recruitment, since the optimal timing of offspring birth or parental spawning (or more likely both) may be compromised. Thus, incorporating the adult perspective into research on reproductive phenology will help advance our understanding of the causes and consequences of inter-annual and intra-specific variability, and of shifts associated with environmental change.

In this study, we explored how conditions that only affect parents influence optimal timing of reproduction by modelling the annual routine of a pelagic fish that migrates between spatially separated feeding and spawning grounds. Even though we kept environmental conditions for the offspring constant, we found that resource dynamics at the feeding grounds of adults influenced timing of reproduction. Variation in both the mean level and timing of peak food availability for adults affected when it was optimal to reproduce, how much variance there was in reproductive timing, and the degree of parent-offspring conflict.

Drivers of variability in reproductive timing and parent-offspring conflicts

In all oceans, primary production varies both spatially and temporally over the season due to a range of factors, including variation in light, temperature, and circulation patterns. If populations use different feeding grounds, it is thus likely that they experience divergent resource dynamics or predator regimes. How large do these differences have to be to produce alternative life-history strategies? The results of our model suggest that relatively small differences in resource availability can change optimal strategies, and lead to altered prioritization in the trade-off between optimal timing of reproduction (from an offspring’s perspective) and fecundity (maternal resources invested into reproduction).

Unexpectedly, parent-offspring conflicts were also pronounced when adults had a high food supply. This is best explained by focusing on a resource-poor environment: when the cost of investing into offspring is high (in terms of energy and starvation risk), it is important to get the maximum possible return for the investment and hence to time it right. However, when investing into young is not as costly, timing becomes less important and parental priorities may have stronger effects on reproductive timing. This was most pronounced in the Puget Sound scenario, where net intake was negative for substantial parts of the year and energetic trade-offs therefore more dominant. Furthermore, our

model suggests that low resource levels can lead to large annual and inter-annual variation in the duration and timing of spawning even within a single feeding ground. This is due to stochasticity in the food source, where individuals may experience different histories of environmental exposure, which in turn affect their energy reserves and lead to different behaviours (Houston and McNamara, 1999; Clark and Mangel, 2000).

Breeding schedules of migratory organisms are adapted to conditions at several locations, which may experience different patterns and rates of environmental change (e.g. Visser *et al.*, 2004). Circumstances on wintering grounds may thus be a poor predictor of changes in reproductive conditions, especially for long-distance migrants or if the cue used to trigger migration is independent of the change at the breeding site. Such mechanisms may be responsible for recent reproductive mistiming in several long-distance migratory birds (Both, 2010; Both *et al.*, 2010), and have been linked to the decline of some populations (Both *et al.*, 2006; Møller *et al.*, 2008). However, the specific cause of these declines is not clear (Knudsen *et al.*, 2011). Low food availability when parents are feeding their young can lead to low parental investment, with consequences for nestling growth and survival (Sanz *et al.*, 2003). A lack of food is also likely to increase parental risk taking, and has been shown to lead to foraging effort beyond optimal levels (Thomas *et al.*, 2001; Drent and Daan, 2002). Although post-breeding parental effects are not included in our model (Pacific herring do not provide parental care), the relative importance of these effects could be teased apart with an extended model based on the same template.

Spawning time in Puget Sound herring—proximate and ultimate causes

In Puget Sound, herring spawn between January and June, with the bulk of the subpopulations spawning between February and April (Stick *et al.*, 2014). There is no known evidence that this variation is associated with environmental gradients. In this study, we use our model to generate new hypotheses about potential ultimate causes of this pattern. Ultimate causes explain why strategies and behaviours have evolved under a set of environmental conditions while proximate explanations describe how these strategies and behaviours are expressed as a response to the immediate environment. The model suggests a wide span in timing among populations that breed in the same location could result from the use of different feeding grounds with divergent food dynamics, or act through individual variation in condition caused by high stochasticity at a single feeding ground.

Herring in this region have been observed to spend variable times in prespawning aggregations before maturation and spawning, and variation in spawn timing has been associated with maturation rate as estimated by the gonadosomatic index (GSI; Ware and Tanasichuk, 1989), a measure of reproductive condition and allocation. Furthermore, the GSI of herring in this region has been found to be affected by both body weight and temperature (Ware and Tanasichuk, 1989), indicating that maturation rate may be a proximate cause of their spawning time behaviour. As such, in addition to the ultimate explanations for spawning time variability explored in this study, variation in GSI due to the immediate environment could contribute to explaining both the duration of spawning within a stock at a given spawning site, and the variability across stocks in a broader geographic region.

Puget Sound herring are thought to consist of a mix of migratory and resident stocks (Penttila, 2007; Stick *et al.*, 2014), with the migratory stocks moving between spawning grounds inside the estuary and feeding grounds on the continental shelf outside Vancouver Island (see Figure 1a). Migratory and resident individuals within single stocks have also been proposed (Penttila, 1986), suggesting that partial migration with regards to feeding migrations may also be widely present. It is interesting to note that shorter migration duration led to even higher variation in spawning times for the Puget Sound scenario (Supplementary Figure S13). Whether migratory stocks and individuals use the same or different feeding grounds, migration routes and timings, is currently largely unknown. In addition, the stocks associated with spawning sites in the central Puget Sound are well mixed (Small *et al.*, 2005; West *et al.*, 2008), indicating diffuse migration strategies. Our results show that locating where and when different stocks feed, by tagging studies or molecular markers to determine stock structure, may potentially add new insights into why herring stocks spawn at such variable times in this area. Until this effort is made, current evidence may allow the spatio-temporal structure of the environment to be qualitatively compared with the quantitative output from this model to generate new hypotheses for more targeted field studies.

Here, we considered variation in spawn timing around the peak spawn date. Other potential metrics of spawn timing include onset of spawning activities, i.e. the date of first observed spawn, and duration of spawning activities, i.e. the time between first and last observed spawn. Future work could consider how behavioural tradeoffs and other factors influence these features of spawn timing. Peak spawn was selected for the present analysis in part because the existing herring spawn monitoring program in Puget Sound is not guaranteed to capture the exact first or last day of spawning; each spawn site is surveyed at most once per week. Thus, there is potential for error in estimating start/end day by 7+ days. In addition, because herring spawning activities occur at individual sites over a period of days to weeks, peak spawn measures a point in time by which the majority of spawn has occurred, or the point in time by which the majority of individuals returning to that site have done so. Also, it has been hypothesized and there is traditional knowledge that older individuals spawn before younger individuals at a given site (MacCall *et al.*, 2018). Because our model is not age-structured, using peak spawn avoids age-based bias that would not be accounted for in our model.

A meta-population perspective

In this study, we assume local adaptation and thus predict optimal life-history strategies under conditions at set feeding and spawning grounds. However, there could also be other mechanisms that are relevant for the dynamics seen in Puget Sound herring. One consequence of the wide variability in spawning times among stocks is that it provides a portfolio effect (Siple and Francis, 2016), by which subpopulation diversity can confer a stabilizing effect on the overall spawning population (Gillespie, 1974, 1977, Schindler *et al.*, 2010, 2015). In a strict sense, the portfolio effect cannot be the evolutionary mechanism acting on individuals to create diversity in spawning times, as that would presuppose a group selection type of argument. However, dispersal bet-hedging, through which risk is spread across space by decoupling the fates of individuals of the same genotype or lineage, could provide an evolutionary explanation for such an effect

(Starrfelt and Kokko, 2012; Schindler *et al.*, 2015). This could happen if females produce offspring that can take on a range of spawning strategies, which drift into different locations, and acquire the strategy of the individuals at that location. There is some evidence in Atlantic herring that younger fish learn migration patterns from older fish, whom they follow to spawning sites (the “adopted-migrant hypothesis”; McQuinn, 1997; Corten, 2001; Huse *et al.*, 2002, 2010; MacCall *et al.* in press). As such, bet-hedging could be an adaptation to unpredictable environmental variation that could play out as a stabilizing effect at the population level.

In recent years, spawn timing shifted significantly in half of the 25 Puget Sound subpopulations, with equal numbers spawning on average earlier and later (Figure 1b). These changes are occurring against a backdrop of wide variability, but no consistent trend, in the timing of the spring bloom (Moore *et al.*, 2016). There is little understanding about what factors are associated with these changes, though there is some evidence that local shifts may be associated with population age structure, with Puget Sound stocks having fewer older fish spawning later and stocks having more older fish spawning earlier (TF, unpublished data). An age structure dominated by younger individuals may, for example, influence spawn site selection according to the “adopted-migrant hypothesis” (McQuinn, 1997; Corten, 2001; Huse *et al.*, 2002, 2010; MacCall *et al.*, 2018). This mechanism could lead to delayed spawning for subpopulations dominated by younger fish, not familiar with migration routes, or waiting for social cues to begin spawning. Age may also affect the trade-off between timing and fecundity, since fecundity increases with age in many fishes. Another potential explanation for the inconsistent changes in spawning times observed in Puget Sound herring is replacement of extirpated local populations by individuals from other subpopulations. This mechanism has, for example, been suggested to be responsible for marked demographic and phenotypic changes in a North Sea cod population (Hutchinson *et al.*, 2003).

Implications for research on reproductive phenology

Puget Sound is not the only system in which migratory herring spawn at highly variable times. In the Pacific, there are both winter–spring and spring–summer spawning herring subpopulations (Haegle and Schweigert, 1985), and different Atlantic herring stocks spawn in all months of the year (Sinclair and Tremblay, 1984). Other species show similar dynamics. For example, in the northeast Atlantic, sardine (*S. pilchardus*) spawn all throughout the year (Stratoudakis *et al.*, 2007). Hence, our model findings suggest that research on spawning time and recruitment variability in several fish species could benefit from incorporating the parental perspective. The possibility that specific characteristics of seasonal food cycles in adult feeding areas can lead to differences in spawning time was already suggested by Iles in 1964 (Iles, 1964), in an attempt to explain variability among several Atlantic and North Sea herring populations. However, he discarded this hypothesis because it could not account for the full range of observed spawning times. This can be expected since timing of reproduction is a life-history trait that is shaped by selection on both parents and their offspring (Trivers, 1974). Thus, identifying the underlying mechanisms that form the annual routines of adults, while accounting for seasonality in offspring fitness, is a prerequisite for understanding the causes of reproductive variability.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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