Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

Relative effects of biotic and abiotic factors during early life history on recruitment dynamics: A case study

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0155.R1
Manuscript Type:	Article
Date Submitted by the Author:	30-Aug-2016
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Keyword:	RECRUITMENT < General, ENVIRONMENTAL EFFECTS < General, TROPHIC RELATIONSHIPS < General, PERCID SPECIES < Organisms, INLAND FISHERIES < General

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1 Relative effects of biotic and abiotic factors during early life history on
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Abstract

The relative effects of biotic and abiotic factors, and the life-history stages upon which they act to affect fish recruitment, vary among species and ecosystems. We compared the effects of spawning stock biomass, and factors operating at early-term (encompassing the egg, yolk-sac larval and first few days of swim-up larval stages), middle-term (including the swim-up larval and pelagic juvenile stages) and late-term (over the benthic juvenile stage) on recruitment by yellow perch (*Perca flavescens*) in the western basin of Lake Erie between 1999 and 2013. Variation of recruitment was mainly driven by middle-term effects. Then, abiotic factors, such as warming rate and wind speed, more strongly affected recruitment than did biotic factors. Among middle-term biotic factors, the top-down effect of yearling walleye abundance was stronger than the bottom-up effect of zooplankton abundance. Similar to marine species, physical processes appear to strongly affect recruitment dynamics of Lake Erie yellow perch over its pelagic larval and juvenile stages, demonstrating the importance of physical and biological processes in understanding fish population dynamics in large lakes.

Keywords: recruitment mechanism, trophic interaction, physical process, yellow perch, Lake Erie

Introduction

Recruitment to adult fish populations is determined by complex ecological processes acting on multiple early life-history stages (Houde 2008; Pepin 2015). The life-history stage during which year-class strength is established varies by species and ecosystems, but typically occurs during the first year after spawning, including egg, larval (encompassing the yolk-sac and swim-up larval stages) and early-juvenile life-history stages (Bradford 1992; Houde 1994). Recruitment theories emphasize alternative views about the relative importance of different ecological processes that act on different life-history stages to determine year-class strength. The “stock-recruitment” hypothesis emphasizes density-dependent effects of spawning stock size on subsequent recruitment (Myers and Barrowman 1996). The “critical period” and “match-mismatch” hypotheses emphasize feeding success during the larval stage, as affected by prey availability during the first few days of the swim-up larval stage, *i.e.* the first-feeding period (Hjort 1914), or the match, or lack thereof, between the timing of plankton production with fish reproduction (Cushing 1975). Alternatively, the “aberrant drift”, “stable ocean”, and “optimal window” hypotheses emphasize the effects of hydrodynamic conditions on larval and juvenile stages, whereby recruitment is determined by retention on, or transport to, favorable nursery areas (Hjort 1914; Begg and Marteinsdottir 2002) or favorable hydrological conditions for foraging (Lasker 1975; Cury and Roy 1989). Finally, the “growth-mortality” and “stage-duration” hypotheses emphasize the importance of rapid growth during larval and juvenile stages, which can limit cumulative mortality through greater starvation tolerance and predator evasion or shortened critical stage durations for larger individuals (Anderson 1988; Pepin and Myers 1991).

No single recruitment hypothesis universally explains fish recruitment dynamics, which indicates a need for an integrative approach that focuses on comparing and linking multiple hypotheses (Houde 2008; Hare 2014). The realization of ecosystem regime shifts (DeYoung et al. 2004; Lees et al. 2006) further implies that the relative importance of different ecological processes, as well as the life-history stages upon which they act, may change over time even for a single species in a given ecosystem (Bailey et al. 2005). It has become difficult to develop general theories about specific ecological processes which act on early life-history stages to drive fish recruitment. The context-specific nature of fish recruitment mechanisms argues for an integrative approach to evaluate evidence for multiple hypotheses for specific populations (Hare 2014).

Yellow perch (*Perca flavescens*) resemble many marine species with respect to their high fecundity, small egg size, and long pelagic larval stage (Pritt et al. 2014). Further, the hydrological conditions of large freshwater lakes approach those of marine environments, prompting the question: To what extent are factors influencing recruitment of freshwater yellow perch similar to factors known to be driving recruitment of marine fish species (Janssen et al. 2014; Ludsin et al. 2014)? Also, the geographic setting of the Laurentian Great Lakes ecosystem provides advantages over marine ecosystems, such as a relatively tractable spatial scale, accessibility for survey vessels and a semi-enclosed system, for systematic studies of fish recruitment (Ludsin et al. 2014; Pritt et al. 2014).

The availability of data from intensive surveys of biotic and abiotic conditions, together with abundant fisheries-dependent and -independent data about yellow perch in the western basin of Lake Erie, provides an opportunity to test among multiple recruitment hypotheses. We evaluated the weight of evidence among several potential mechanisms driving

recruitment by yellow perch in the western basin of Lake Erie in four operationally defined time periods based on yellow perch life history and the timing of data collection: 1) spawning, between late-April and early-May; 2) the period from spawning through May, including the egg, yolk-sac larval and the first few days of the swim-up larval stage (early-term); 3) the period from June through August, mainly encompassing the swim-up larval and pelagic juvenile stages (middle-term); and 4) the final benthic juvenile stage before maturing at age 2 (late-term) (Fig. 1). Specifically, we evaluated whether variation in recruitment by yellow perch was driven by 1) spawning stock biomass (SSB) during spawning period; 2) prey abundance, water temperature, wind speed and dissolved oxygen during the early-term; 3) predator and prey abundances, water temperature, spring warming rate, wind speed and dissolved oxygen during the middle-term; and/or 4) ecological processes acting during the late-term.

Methods

Study area

Lake Erie is the shallowest of the five Laurentian Great Lakes, with a mean depth of 19m and surface area over 25,000km² (Belore et al. 2014). The lake is surrounded by the province of Ontario and multiple U.S. states including Michigan, Ohio, Pennsylvania and New York. The high human population density and intensive agriculture in these regions makes Lake Erie the most heavily human influenced lake among the Great Lakes, and the lake has experienced substantial ecosystem changes due to eutrophication, phosphorus reduction, invasive species, *e.g.*, Dreissenid mussels and round goby (*Neogobius melanostomus*), and fishing (Griffiths et al. 1991; Tyson and Knight 2001). As the most productive of the Great Lakes, Lake Erie supports several important fisheries, with yellow perch and walleye (*Sander*

vitreus) being the largest (Belore et al. 2014; Wills et al. 2014). Lake Erie comprises eastern, central and western basins; the western basin is the most shallow (Fig. 2). The yellow perch fishery is assessed and managed on the basis of data collected across four management units (MUs), of which one is the western basin (Belore et al. 2014).

Yellow perch spawning stock size, recruitment, age-0 and age-1 juvenile densities

Since 1975, the Yellow Perch Task Group (YPTG) has generated age-specific estimates of yellow perch abundance and biomass in the western basin of Lake Erie using statistical catch-at-age (SCAA) models for age classes 2- 6 (Belore et al. 2014). The fishery-dependent data from commercial gillnet fishery and fishery-independent data from gillnet and trawling surveys were fit to the SCAA models for parameter estimation (Belore et al. 2014). We indexed recruitment as the abundance of age-2 fish in year t from Belore et al. (2014), whereas parental stock size was indexed as the abundance of mature fish (age-2 and older) in year $t-2$ from Belore et al. (2014). In Lake Erie, female yellow perch typically mature at age-2 to -4 (Sztramko and Teleki 1977). Therefore, we estimated annual percentages of mature age-2 and -3 females using the Ontario Partnership Index Gillnet Survey co-conducted by Ontario Ministry of Natural Resources and Forestry (OMNRF) and Ontario Commercial Fisheries' Association (OCFA); females age-4 and older were assumed to be 100% mature (D. Gislason, *unpubl. data*). SSB was estimated as:

$$SSB_t = \sum_{a=2}^n B_{a,t} * m_{a,t} * 0.5$$

where, SSB_t is the SSB in year t , n is the number of age classes, $B_{a,t}$ is the biomass of age- a fish in year t , $m_{a,t}$ is the proportion of mature fish of age- a in year t , and 0.5 is the constant used to calculate the proportion of females assuming a 1:1 sex ratio for all age classes.

An Interagency Index Trawling Survey (IITS), co-conducted by Ontario Ministry of Natural Resources and Forestry (OMNRF), Ohio Department of Natural Resources (ODNR) and United States Geological Survey (USGS), has been undertaken in the western basin of Lake Erie each August since 1988 (Thomas et al. 2014). The IITS conducted about 74 trawls per year between 1988 and 2014; sampling effort varied little among years. The age-0 and age-1 yellow perch juvenile densities ($\text{No.} \cdot \text{ha}^{-1}$) were estimated based on average catch-per-unit-effort (CPUE) during each annual survey.

Effects of SSB and late-term ecological factors

To identify key life-history stages potentially influencing yellow perch year-class strength, a Paulik diagram was used to test three step-wise correlations among log-transformed estimates of SSB in year t , age-0 juvenile density in August in year t , age-1 juvenile density in August in year $t+1$, and estimates of age-2 recruitment in year $t+2$, between 1999 and 2013 (Nash 1998). The Pearson correlation coefficient was calculated to test the correlation significance. The coefficient of variation (CV) was used to summarize relative annual variations in SSB, age-0 and age-1 juvenile densities, and recruitment. All statistical calculations were implemented using version 2.15.0 R software (R Development Core Team 2012).

If recruitment dynamics were strongly affected by SSB, all three pair-wise correlations should be significant. If variation of recruitment was mainly affected by late-term factors, the correlation between SSB and age-0 juvenile density should be strong, while either of the two other correlations should be weak. If the correlation between SSB and age-0 juvenile density was the weakest among the three correlations, we inferred that variation of recruitment was predominantly influenced by early-term and/or middle-term factors.

Effects of early-term and middle-term factors

In the western basin of Lake Erie, adult yellow perch (age-2 and older) typically spawn in the near shore area between mid-April and early-June, depending on water temperature and photoperiod (Farmer et al. 2015), but the peak usually occurs between late-April and early-May (Henderson et al. 2000). The duration of the egg period is two to three weeks, with about three days between hatching and first-feeding, *i.e.* yolk-sac larval stage (Rose et al. 1999). Swim-up larvae start pelagic feeding by late-May, and transform to pelagic juveniles sometime in June. These juveniles shift from pelagic to benthic feeding sometime in July (most individuals will begin benthic feeding by August) depending on zooplankton availability and individual body size (Wu and Culver 1992). Physical factors, *e.g.*, water temperature, warming rate, wind speed and dissolved oxygen, strongly influenced yellow perch survival during early life-history stages (Clady 1976; Henderson 1985; Farmer et al. 2015); biotic factors, *e.g.*, predator and prey abundance, were also important factors affecting yellow perch year-class strength (Hartman and Margraf 1993; Dettmers et al. 2003).

We used average bottom water temperature, dissolved oxygen, wind speed and zooplankton density in May to indicate early-term effects of physical environment and prey availability. Average bottom water temperature, dissolved oxygen and wind speed from June through August were used to indicate effects of middle-term abiotic factors. The warming rate was measured by regressing bottom temperature on Julian date from April to June (Henderson and Nepszy 1988). Monthly average zooplankton density from June through August was used to represent a middle-term, bottom-up effect of prey abundance. Walleye and alewife (*Alosa pseudoharengus*) are two important predators of yellow perch in the Laurentian Great Lakes (Hartman and Margraf 1993; Mason and Brandt 1996; Shroyer and McComish 2000), so the

middle-term, top-down effects of both walleye and alewife densities in August were also included.

The Lower Trophic Level Assessment (LTLA) program in Lake Erie, initiated by the Forage Task Group (FTG) of the Lake Erie Committee, has, annually since 1999, collected data about water temperature (°C), dissolved oxygen concentration (mg•L⁻¹), wind speed (km•h⁻¹), and zooplankton density (No.•L⁻¹), biweekly from April through September (Thomas et al. 2014). Four stations were located in the western basin, and the mean values of bottom water temperature, dissolved oxygen, wind speed, and zooplankton density were calculated across stations and samples within each month between 1999 and 2013. Walleye and alewife densities were estimated based on average catch-per-unit-effort (CPUE) during each annual survey of IITS between 1999 and 2013 (Thomas et al. 2014); CVs of these early- and middle-term factors were also calculated (Table 1).

Relative importance of early-term factors on year-class strength

We evaluated the relative importance of early-term ecological factors based on stepwise contrasts among variants of the Ricker model (Zwolinski and Demer 2014), with age-0 juvenile density in August used as an index of yellow perch year-class strength (Farmer et al. 2015),

$$J_t = \alpha S_t e^{-\beta S_t + \sum (\gamma_i E_{i,t}) + \varepsilon} \text{ (Ricker-J)}$$

where J_t is the age-0 yellow perch juvenile density in year t , S_t is the spawning stock biomass in year t , $E_{i,t}$ is the i th early-term ecological factor in year t , α is the productivity parameter, β

is the density-dependent parameter, γ_i is the effect parameter for the i th factor, and ε is a random error following a normal distribution with mean of 0 and standard deviation of σ . First, just one early-term factor was included in the Ricker-J model at a time (Table 2), and their relative importance was inferred from the Akaike weights of their corresponding models (Johnson and Omland 2004),

$$\Delta_i = AIC_i - AIC_{min}$$

$$W_i = \frac{e^{-1/2\Delta_i}}{\sum_{j=1}^R e^{-1/2\Delta_j}}$$

where, AIC_i is the AIC of the i th model, AIC_{min} is the AIC of the model with the lowest AIC, W_i is the Akaike weight of the i th model, R is the number of models. An early-term factor was considered to be candidate if its corresponding Ricker-J model had greater Akaike weight than the basic Ricker-J model without any ecological factors (Table 2). Second, different combinations of the candidate early-term ecological factors were incorporated into the Ricker-J model. The Akaike Information Criteria corrected for small samples (AICc) was used to select the best model representing early-term effects (Burnham and Anderson 2002).

$$AICc = AIC + \frac{2k(k+1)}{N-k-1}$$

where, N is the sample size, and k is the number of parameters in the model. All data were fitted to generalized linear models using version 2.15.0 R software (R Development Core Team 2012). The early-term factors in the best model were considered as the important factors representing early-term effects.

Relative importance of middle-term ecological factors on year-class strength

The same approach was used to compare the relative importance of middle-term ecological factors, and the candidate factors were selected based on the Akaike weights of their corresponding models (Table 3). Different combinations of the candidate middle-term ecological factors were incorporated into the Ricker-J model to infer the important factors representing middle-term effects (Table 4).

Relative effects of SSB, early-term and middle-term factors on age-2 recruitment dynamics

Finally, to infer the relative importance of early-term factors on age-2 recruitment dynamics, the important early-term factors were incorporated into a variant of Ricker model, with age-2 recruitment as the response variable,

$$R_{t+2} = \alpha S_t e^{-\beta S_t + \sum(\gamma_i E_{i,t}) + \varepsilon} \text{ (Ricker-R)}$$

where, R_t is the age-2 yellow perch recruitment in year t , S_t is the spawning stock biomass in year t , $\sum(\gamma_i E_{i,t})$ is the linear combination of the important early-term factors in year t , α is the productivity parameter, β is the density-dependent parameter, γ is the effect parameter for the i th factor, and ε is a random error following a normal distribution with standard deviation of σ . The same approach was used to incorporate the important middle-term factors to the Ricker-R

model. Then, the Akaike weights of those two models, and the basic Ricker-R model (with no ecological factors), were calculated to rank the relative importance of SSB, early-term, and middle-term ecological factors on age-2 recruitment dynamics (Table 5).

Results

Variation in yellow perch recruitment was mainly influenced by early- and/or middle-term factors, rather than by SSB or late-term factors. The temporal variability for age-0 (CV=1.34) and age-1 juvenile densities (CV=1.18), and age-2 recruitment (CV=0.86) were much greater than for SSB (CV=0.26) (Fig. 3), consistent with the idea that, within the range of the available data, variation in factors during early life-history stages largely generates recruitment variation, in addition to that which may be caused by variation in SSB. Among the three step-wise correlations, the SSB was not significantly correlated with age-0 juvenile density, though there were significant correlations between age-0 juvenile density in year t and age-1 juvenile density in year $t+1$, as well as between age-1 juvenile density in year $t+1$ and age-2 recruitment in year $t+2$ (Fig. 4).

Wind speed in May positively affected yellow perch year-class strength and was ranked the most important among the early-term factors (Table 2), from which we inferred that wind speed more likely affected yellow perch year-class strength than the other early-term factors, *i.e.*, dissolved oxygen, bottom water temperature and zooplankton density, for which we had data. As the only candidate early-term factor, it was the only early-term factor selected to represent early-term effects in contrasts among the effects of SSB, early- and middle-term factors on age-2 recruitment dynamics (Table 5).

Among middle-term factors, warming rate negatively, and wind speed positively, related to yellow perch year-class strength (Table 3). Models incorporating warming rate,

wind speed, or yearling walleye density had greater Akaike weights than the basic Ricker model, while models incorporating dissolved oxygen, bottom water temperature, and zooplankton and alewife density were weighted much less. Among different combinations of the three candidate middle-term ecological factors, warming rate and wind speed more likely affected yellow perch year-class strength than other middle-term factors, *i.e.*, bottom water temperature, dissolved oxygen, zooplankton, yearling walleye and alewife densities (Table 4); warming rate and wind speed thus represented middle-term factors in contrasts among the effects of SSB, early-term and middle-term effects on age-2 recruitment (Table 5).

Overall, variation of age-2 recruitment was more strongly affected by middle-term factors than by early-term factors or SSB (Fig. 5). The model representing middle-term effects had greater Akaike weight and R^2 than the models representing effects of SSB and early-term factors, and was about 2-fold more likely than the basic Ricker model (Table 5).

Discussion

Stock-recruitment hypothesis

A strong effect of SSB on recruitment dynamics is assumed for most stock-recruitment models adopted for fisheries management, including the classic Ricker and Beverton-Holt models (Ricker 1954; Beverton and Holt 1957). Despite that, often, any strong relationships between SSB and recruitment are undetected (Koslow 1992), the importance of stock-recruitment relationship for linking consecutive outputs from stock assessment (*e.g.*, statistical catch-at-age models), and to a need to provide management reference points, preserve its popularity among fisheries managers (Subbey et al. 2014). An effect of SSB on recruitment may be detected if there is a sufficiently wide range of variation in SSB (Myers and Barrowman 1996), and we expect recruitment would be reduced under extremely low

spawning stock biomass (at the extreme case, there will be no recruitment if SSB is zero). However, the actual variation of SSB in a fishery may not be great enough to pose a strong effect on recruitment, and the effects of other ecological factors may drive recruitment dynamics in a way that is independent with variation in SSB (Vert-pre et al. 2013). We did not find strong effects of SSB on yellow perch recruitment in the western basin of Lake Erie (Table 5), nor a clear stock-recruitment relationship (Fig. 6), consistent with previous work which did not detect any strong effects of SSB and spawning stock age structure on yellow perch recruitment across three basins of Lake Erie (Zhang et al. 2015). Collectively, this evidence is consistent with the idea that yellow perch recruitment was mainly driven by other ecological factors acting on early life-history stages.

Late-term effects and establishment of recruitment strength

In contrast to the stock-recruitment hypothesis, other recruitment hypotheses focussed on the ecological factors acting on early life-history stages (Houde 2008). The natural mortality rate typically decreases over early life-history stages, and variation in mortality during the fragile and vulnerable egg and larval stages may strongly affect subsequent recruitment (Koslow 1992). Recruitment strength (*i.e.*, the relative size of recruitment to adult population) is generally determined at larval stages for marine fish species and at the juvenile stage for freshwater species (Bradford 1992; Houde 1994). As such, juvenile index surveys may be used to make short-term recruitment predictions for freshwater species, an approach that is currently applied in assessments of yellow perch and walleye fisheries in Lake Erie (Belore et al. 2014; Wills et al. 2014). We did not find strong late-term effects on yellow perch recruitment in the western basin of Lake Erie, suggesting that the recruitment strength was established within the first four months after spawning (*i.e.*, during early- and/or middle-term).

Our results are consistent with Janetski et al. (2013), who showed that yellow perch recruitment strength in Lake Muskegon was established within the first few months after spawning. However, yellow perch recruitment in Lake Huron was not established until age-1 (Ivan et al. 2011), and strong correlations between age-0 and age-1 yellow perch were not observed in Lake St. Clair (Henderson and Nepszy 1988). Therefore, the relative importance of late-term effects and the determination time of recruitment strength should be evaluated from a context-dependent perspective.

Early-term effects

Fish mortality from starvation during transition from endogenous to exogenous feeding (first few days of swim-up larval stage) was found to be critical to recruitment strength for Atlantic herring in Norway, leading to the “critical period” hypothesis (Hjort 1914). Similarly, the “match-mismatch” hypothesis considered that prey availability around spawning time was key for successful recruitment (Cushing 1975). We did not detect strong effects of early-term factors on recruitment of Lake Erie yellow perch. Further, among those early-term factors, the bottom-up effect of zooplankton density was weaker than the physical effects of wind speed, dissolved oxygen and bottom water temperature on yellow perch year-class strength. Therefore, the “critical period” and “match-mismatch” hypotheses, which focus on early-term effects, were not supported.

Wind speed might positively or negatively affect egg survival. On the one hand, low oxygen concentration is an important cause of egg mortality (Köster et al. 2003), and strong winds may facilitate oxygenation of the benthic eggs in the nearshore area. On the other hand, strong water currents generated by strong wind may cause egg destruction, and/or displacement from spawning sites to less favorable areas (Clady 1976). In our study, the

positive effects of wind speed and dissolved oxygen suggested that egg mortality controlled by oxygen availability might affect yellow perch survival. However, the effect of dissolved oxygen concentration on yellow perch egg and yolk-sac larvae survival is not as well studied, and may be a fruitful area for future research.

Middle-term effects

Contrasting with hypotheses about factors causing early-term mortality, is another school of thought about the importance of size related mortality during the larval and early-juvenile stages (middle-term) (Anderson 1988; Bailey and Houde 1989; Pepin and Myers 1991). Growth during early life-history stages may negatively affect cumulative mortality, because fast growing individuals usually have greater energy reserves which reduce starvation risk (Anderson 1988), larger body size and ability to better escape predation (Bailey and Houde 1989), and shorter duration of the fragile larval period (Pepin and Myers 1991). For Lake Erie yellow perch, variation in recruitment was mainly affected by middle-term factors. In particular, water warming rate in spring, which negatively affected yellow perch year-class strength, was the most important ecological factor.

Spring warming rate may affect yellow perch growth through three mechanisms. First, high rates of warming may disrupt spawning phenology, affecting prey availability during the growing season. Yellow perch spawning time was affected by both water temperature and photoperiod (Starzynski and Lauer 2015). In short winters when warming rate was high, the optimal spawning temperature was reached early in the year, but the photoperiod condition was not appropriate, leading to delayed spawning at sub-optimal water temperature (Farmer et al. 2015). On the other hand, the zooplankton cycle, better synchronized to changes in water temperature, may lead to a temporal mismatch between fish larvae and peak zooplankton

abundance (Cushing 1975). Second, warming rate may affect reproductive traits, further affecting growth rate during the larval stage. Egg size and size-at-hatch were smaller for yellow perch spawning in years with high warming rates and short winters in Lake Erie (Farmer et al. 2015), which may decrease larval growth rate and increase mortality (Berkeley et al. 2004a). Third, warming rate may affect larval growth via changes in hatching date. Following long winters with slow warming rates, spawning and hatch dates were usually late (Starzynski and Lauer 2015), and later-hatching yellow perch had greater growth rates and survival (Weber et al. 2011).

Regardless of the mechanisms affecting larval growth, the ultimate cause of mortality was either a bottom-up effect, via starvation, or a top-down effect, via predation. Both bottom-up and top-down effects on yellow perch recruitment have been detected in the Laurentian Great Lakes region (Janssen et al. 2014; Pritt et al. 2014). Zooplankton abundance was an important factor affecting yellow perch survival in Lake Michigan (Dettmers et al. 2003), and both walleye and alewife exerted strong top-down effects on yellow perch recruitment (Hartman and Margraf 1993; Mason and Brandt 1996; Redman et al. 2011). In our study, the effect of yearling walleye on yellow perch year-class strength was much greater than the effects of alewife or zooplankton. Other studies in the western basin of Lake Erie also found greater yellow perch larval survival in the Maumee river plume, likely due to reduced predation risk (Reichert et al. 2010; Carreon-Martinez et al. 2014). Therefore, the interaction between growth rate and predation during middle-term, which was linked with various biotic and abiotic factors, may strongly affect yellow perch recruitment in the western basin of Lake Erie.

Implications for fisheries management

Disentangling the effects of harvest and environment on fish population dynamics continues to substantially challenge fisheries science and management (Essington et al. 2015). For many fish species, population dynamics is strongly affected by recruitment variability (Caley et al. 1996). A major effect of harvest on a population is the removal of SSB. Therefore, evaluating the relative effect of SSB on recruitment dynamics provides insight with respect to the effect of harvest on population dynamics. A strong effect of SSB on recruitment means recruitment strength is sensitive to variation in SSB, suggesting, in turn, strong effects of harvest on population dynamics. On the other hand, if recruitment is largely insensitive to variation in SSB, it is implied that effect of harvest on recruitment dynamics through its effect on SSB is also weak. Nevertheless, fisheries managers need to remain cognizant of other potential effects of harvest, such as changes to population age structure and/or habitat (Auster and Langton 1999; Berkeley et al. 2004b).

Variation in SSB appears to have had relatively smaller effects than environmental variation on yellow perch recruitment in the western basin of Lake Erie; neither does there appear to be positive effects of population age structure on recruitment (Zhang et al. 2015). Together, these results suggest that coupled physical and biological processes during middle-term may be most important factors affecting recruitment by yellow perch. Our results underscore the importance of physical-biological modelling to study freshwater fish recruitment in large lakes is recognized (Janssen et al. 2014; Ludsine et al. 2014).

Recruitment prediction

Recruitment predication has both excited and frustrated fishery scientists over many decades due to its importance to fisheries management, and the challenge it represents for fisheries modellers (Mertz and Myers 1995; Subbey et al. 2014). The availability of adequate

time series data raises the issue of whether complex models might be overfitted to sparse data, leading to poor predictive power (Ginzburg and Jensen 2004). Here, we were challenged by the need to constrain our data to 15 years, *i.e.*, the shortest of the time series available among the environmental variables we investigated. To reduce the risk of overfitting, we used the simple generalized linear regression model, restricted the majority of our models to two or three parameters, and used AICc for model comparisons among more complex models. Despite this, our “best” model may still have a relatively low predictive power.

In any case, instead of building a single “best” predictive model, we aimed to compare the relative importance of ecological factors acting at different early life-history stages to influence recruitment dynamics, which may help to determine future research priorities. Correlative recruitment models have been criticized for poor predictive power (Walters and Collie 1988; Myers 1998), and more mechanistic models, *e.g.*, individual-based model and spatial-explicit model, have gained popularity in fisheries research (Werner et al. 2001; Hedger et al. 2013; Persson et al. 2014). A conflict exists between the great data demand of these mechanistic models and the limited resources of research institutions and management agencies to collect those data. We systematically sifted among multiple alternative hypotheses about mechanisms driving recruitment, and found strong effects of physical-biological processes during the middle-term (June to August). This suggests that there is merit in collecting more middle-term ecological data to support development of spatially-explicit, individual-based models, to better understand and predict yellow perch recruitment in Lake Erie (Ludsin et al. 2014).

In summary, physical-biological factors operating over swim-up larval and pelagic juvenile stages primarily drove recruitment by Lake Erie yellow perch; effects of SSB, early-

term and late-term factors were less important. Physical environmental factors, such as spring warming rate and wind speed, had stronger effects than biological factors, such as walleye and zooplankton densities, on recruitment, confirming the importance of coupling physical and biological processes in understanding fish recruitment mechanisms in large lakes. The failure to detect a strong effect of SSB on recruitment suggests that the relative effect of harvest on yellow perch population dynamics may be weak during our study period. Nevertheless, the relative importance of different factors may change over time, due to changing interactions among ecological factors driven by ecosystem regime shifts (DeYoung et al. 2004; Brander 2005; Hare 2014).

Acknowledgements

This research was funded by a Natural Sciences and Engineering Research Council of Canada Strategic Networks grant to Canadian Fisheries Research Network and a grant-in-aid of research from the Ontario Commercial Fisheries' Association. We thank Robert McLaughlin (University of Guelph), Dan Gillis (University of Guelph), Jake Rice (Fisheries and Oceans Canada), Beren Robinson (University of Guelph), and two anonymous reviewers for comments that improved earlier drafts of this manuscript. We thank David Gislason (University of Guelph) for providing data on percentage maturation at age of Lake Erie yellow perch. We thank the Lake Erie Management Unit (Ontario Ministry of Natural Resources and Forestry) for providing biotic and abiotic data used for this study. Data for this research was provided to the authors under written agreement with the Lake Erie Committee.

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621 Table 1. The min, max, mean and coefficient of variation (CV) of early-term and middle-term
 622 factors in the western basin of Lake Erie between 1999 and 2013.

Ecological factor	Min	Max	Mean	CV
Early-term				
Bottom water temperature	11.97	17.56	14.44	0.11
Wind speed	2.50	16.67	8.69	0.54
Dissolved oxygen	7.99	11.07	9.88	0.11
Zooplankton density	0.99	72.38	20.65	1.05
Middle-term				
Bottom water temperature	19.62	22.39	20.94	0.043
Wind speed	0	6.70	11.46	0.28
Dissolved oxygen	8.08	9.73	8.88	0.055
Zooplankton density	176.3	813.4	387	0.53
Warming rate	0.10	0.20	0.24	0.18
Yearling walleye density	0.11	45.50	5.03	2.29
Alewife density	0	291	44.76	2.23

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Table 2. Comparison of Ricker-J models incorporating early-term ecological factors through May in the western basin of Lake Erie between 1999 and 2013. * indicates the candidate early-term ecological factors, and the bolded model is the one selected to represent early-term effects.

Model	Ecological variables (effect direction)	Parameter	df	R ²	AIC	Scaled AIC	Akaike weight
Ricker- J(WR)	wind speed* (+)	3	12	0.16	49.58	0	0.32
Ricker-J	none	2	13	0.016	49.90	0.32	0.28
Ricker- J(DO)	dissolved oxygen (+)	3	12	0.080	50.88	1.30	0.13
Ricker- J(WT)	bottom water temperature (+)	3	12	0.044	51.46	1.88	0.17
Ricker- J(ZD)	zooplankton density (+)	3	12	0.017	51.88	2.30	0.10

631 Table 3. Comparison of Ricker models incorporating middle-term ecological factors from June
 632 through August in the western basin of Lake Erie between 1999 and 2013. * indicates the
 633 candidate middle-term ecological factors.

Model	Ecological variable (effect direction)	Parameter	df	R ²	AIC	Scaled AIC	Akaike weight
Ricker- J(WR)	warming rate* (-)	3	12	0.26	47.55	0	0.33
Ricker- J(WS)	wind speed* (+)	3	12	0.23	48.31	0.76	0.22
Ricker- J(WL)	yearling walleye density* (-)	3	12	0.18	49.10	1.55	0.15
Ricker-J	none	2	13	0.016	49.90	2.35	0.10
Ricker- J(DO)	dissolved oxygen (+)	3	12	0.071	51.03	3.48	0.058
Ricker- J(ZD)	zooplankton density (+)	3	12	0.050	51.37	3.82	0.049
Ricker- J(WT)	bottom water temperature (+)	3	12	0.043	51.48	3.93	0.046
Ricker- J(AL)	alewife density (-)	3	12	0.028	51.71	4.16	0.041

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Table 4. Comparison of Ricker models incorporating combinations of candidate middle-term ecological factors from June through August in the western basin of Lake Erie between 1999 and 2013. Bolded model is the one selected to represent middle-term ecological effects.

Model	Ecological variable	Parameter	df	R ²	AICc
Ricker-J(WR+WS)	warming rate, wind speed	4	11	0.56	45.8
Ricker-J(WR+WS+WL)	warming rate, wind speed, yearling walleye density	5	10	0.62	48.17
Ricker-J(WR)	warming rate	3	12	0.26	49.73
Ricker-J(WS)	wind speed	3	12	0.23	50.49
Ricker-J(WR+WL)	warming rate, yearling walleye density	4	11	0.37	51.24
Ricker-J(WS+WL)	wind speed, yearling walleye density	4	11	0.36	51.25
Ricker-J(WL)	yearling walleye density	3	12	0.18	51.28

640 Table 5. Comparison of Ricker models representing effects of SSB, early-term and middle-
 641 term ecological factors on yellow perch age-2 recruitment dynamic in the western basin of
 642 Lake Erie between 1999 and 2013.

Model	Meaning	R^2	AIC	Scaled AIC	Akaike weight
Ricker- R(WR+WS)	Middle-term effects	0.33	41.93	0	0.58
Ricker-R	Effects of SSB	-0.0019	43.17	1.24	0.31
Ricker-R(WS)	Early-term effects	-0.0018	45.17	3.24	0.11

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Figures

Fig. 1. Life history of yellow perch in the western basin of Lake Erie, and illustration of operationally-defined “early-term”, “middle-term”, and “late-term” periods encompassing different yellow perch early life-history stages.

Fig. 2. Study location in the western basin of Lake Erie.

Fig. 3. Temporal variation of spawning stock biomass (SSB), age-0 juvenile density, age-1 juvenile density and age-2 recruitment of yellow perch in the western basin of Lake Erie between 1999 and 2013. Variables are log-transformed.

Fig. 4. Pair-wise correlations of SSB, age-0 and age-1 juvenile densities, and recruitment of yellow perch in the western basin of Lake Erie between 1999 and 2013 showing relationships between (A) SSB in year t and age-0 juvenile density in August in year t , (B) age-0 juvenile density in August in year t and age-1 juvenile density in August in year $t+1$, and (C) age-1 juvenile density in August in year $t+1$ and age-2 recruitment in year $t+2$. All data were log transformed before analyses.

Fig. 5. Model fit of the Ricker-R models representing effects of SSB, early-term and middle-term factors on yellow perch recruitment in the western basin of Lake Erie between 2001 and 2013. The black dots are the estimates of recruitment, the solid line is the recruitment prediction by model representing effects of SSB, the dashed line is the recruitment prediction by model representing early-term effects, and the dotted line is the recruitment prediction by model representing middle-term effects.

Fig. 6. Model fit of Ricker model to the observed stock-recruitment dynamic. The black dots are the estimates of SSB and recruitment, and the solid line is the prediction by Ricker model.

Fig. 1. Life history of yellow perch in the western basin of Lake Erie, and illustration of operationally-defined "early-term", "middle-term", and "late-term" periods encompassing different yellow perch early life-history stages.

Fig. 2. Study location in the western basin of Lake Erie.

296x210mm (300 x 300 DPI)

Fig. 3. Temporal variation of spawning stock biomass (SSB), age-0 juvenile density, age-1 juvenile density and age-2 recruitment of yellow perch in the western basin of Lake Erie between 1999 and 2013. Variables are log-transformed.

211x176mm (72 x 72 DPI)

Fig. 4. Pair-wise correlations of SSB, age-0 and age-1 juvenile densities, and recruitment of yellow perch in the western basin of Lake Erie between 1999 and 2013 showing relationships between (A) SSB in year t and age-0 juvenile density in August in year t , (B) age-0 juvenile density in August in year t and age-1 juvenile density in August in year $t+1$, and (C) age-1 juvenile density in August in year $t+1$ and age-2 recruitment in year $t+2$. All data were log transformed before analyses.

211x176mm (72 x 72 DPI)

Fig. 5. Model fit of the Ricker-R models representing effects of SSB, early-term and middle-term factors on yellow perch recruitment in the western basin of Lake Erie between 2001 and 2013. The black dots are the estimates of recruitment, the solid line is the recruitment prediction by model representing effects of SSB, the dashed line is the recruitment prediction by model representing early-term effects, and the dotted line is the recruitment prediction by model representing middle-term effects.

176x141mm (72 x 72 DPI)

Fig. 6. Model fit of Ricker model to the observed stock-recruitment dynamic. The black dots are the estimates of SSB and recruitment, and the solid line is the prediction by Ricker model.

176x141mm (72 x 72 DPI)