

1                   **PHYSICAL-BIOLOGICAL COUPLING AND THE CHALLENGE OF**  
2                   **UNDERSTANDING FISH RECRUITMENT IN LARGE LAKES**

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1 **ABSTRACT**

2 Physical processes are known to directly and indirectly regulate early life growth and  
3 survival, and ultimately recruitment to the fishery, primarily in marine ecosystems. Herein, we  
4 demonstrate that 1) research exploring linkages between physical processes and fish recruitment  
5 in large-lake ecosystems (e.g., Laurentian Great Lakes) is comparatively scant, despite these  
6 ecosystems exhibiting similar physical processes and their important fishes having life-history  
7 characteristics that make them equally as vulnerable to physical controls, and 2) physical  
8 processes also can regulate fish recruitment in freshwater lakes through both direct or indirect  
9 mechanisms that often involve complicated interactions between biological processes (e.g.,  
10 competition, predation) and chemical conditions (e.g., hypoxia, eutrophication). Given these  
11 complexities, we argue that ability to understand, predict, and manage recruitment variation in  
12 large freshwater ecosystems would benefit from coupled physical-biological research and  
13 modeling approaches that are more typical of marine studies. Additionally, we call for a  
14 continued erosion of the barriers between marine and freshwater recruitment research, as doing  
15 so would deepen our understanding of fish population and community dynamics in both  
16 ecosystems.

## INTRODUCTION

Achieving the ability to understand and predict recruitment is considered the “holy grail” of fisheries management as it can assist agencies in numerous ways, including 1) developing robust models for understanding and forecasting fluctuations in fish populations and the broader food web, 2) determining harvest regulations and quota allocations, and 3) managing user-group (e.g., recreational anglers, commercial fishers) expectations such that they do not surpass the capacity of the ecosystem to produce the desired result. While empirical “black box” relationships between simple environmental variables and recruitment are common in both the large marine and smaller freshwater fisheries literature, their equally common failures (Myers 1998) highlight the need for a mechanistic understanding of the key processes that underlie recruitment. An integrated, multidisciplinary approach is needed to achieve this understanding (Rose 2000). If dependable forecasting of recruitment with simple statistical (e.g., correlation) models is impossible, we cannot use them to inform the broader considerations that are important to ecosystem management goals.

Fortunately, fishery management agencies have been making progress in understanding and forecasting recruitment variation in recent decades. Some of this headway can be attributed to the gradual attainment of needed data and mechanistic knowledge via continued monitoring and research, as well as technological improvements that have advanced our ability to describe and model aquatic ecosystems and their fishery dynamics (Hansen et al. 1993; Pauly et al. 2000; Miller 2007). In addition, the willingness to abandon old ecological paradigms for new ones—or old ones cast in a new light—has been instrumental to our progress (Underwood and Fairweather 1989; Grosberg and Levitan 1992). This latter notion is best exemplified in coral reef ecosystems, where three relatively recent (post-1980) paradigm shifts have occurred. These

1 include 1) recognition that ecosystems generally are not closed nor in equilibrium, 2) re-  
2 discovery of the importance of recruitment variation as a driver of fish population demographics,  
3 and 3) realization that stochastic physical processes (e.g., meteorology/climate, hydrodynamic  
4 processes) can play a dominant role in regulating fish populations through both density-  
5 dependent and -independent effects on recruitment of individual species (see reviews by Booth  
6 and Brosnan 1995 and Caley et al. 1996).

7 Awareness that recruitment within a population can play a large role in structuring aquatic  
8 communities also has increased. Its relative importance, however, will vary spatiotemporally (e.g.,  
9 Caselle and Warner 1996; Casini et al. 2008) and has been shown to be scale-dependent in both  
10 space (e.g., local versus regional) and time (e.g., seasonally versus annually) (Michener and Kenny  
11 1991; Caselle and Warner 1996). Booth and Brosnan (1995), Caley et al. (1996) and Duffy-  
12 Anderson et al. (2005) provide examples of how variable recruitment of a species can alter marine  
13 invertebrate and fish community structure (e.g., species composition and diversity) and dynamics  
14 (e.g., energy flow, biotic interactions). Similar examples also exist for north-temperate freshwater  
15 lakes and reservoirs (Carpenter and Kitchell 1993; Vanni et al. 2005; Fitzgerald et al. 2006).

16 With these recent changes in the conceptualization of how coral reef fish populations and  
17 communities are regulated, rapid growth has occurred since the mid-1980s in reef fish  
18 recruitment studies that involve early life stages (Fig. 1). Similarly, the number of biophysical  
19 coupling investigations in reef ecosystems has increased through time such that 50–60% of the  
20 early-life (i.e., egg, larval) reef fish studies conducted since 1994 have explored linkages  
21 between water circulation, early-life transport processes, and recruitment (Fig. 1). These  
22 investigations have undoubtedly improved our basic understanding of how coral reef fish

1 populations and communities are regulated and have provided a wealth of management advice  
2 (e.g., Marine Protected Area design and placement; Leis 2002; Levin 2006).

3 Early-life studies exploring the effects of physical processes on fish recruitment (focused  
4 on water circulation and propagule transport processes) also have become more common in other  
5 marine ecosystems (e.g., estuaries, open ocean, coastal oceans) in recent years, following a  
6 similar trajectory as reef ecosystems (Fig. 1; also see Miller 2007). Adoption of these paradigms  
7 to large-lake ecosystems (such as the Laurentian Great Lakes), which show many of the same  
8 physical processes (e.g., eddies, gyres, along- and cross-system circulation) and biological  
9 properties (e.g., highly fecund organisms with pelagic early life stages that receive no parental  
10 care) of their marine counterparts, is still at an early stage. Published Great Lakes biophysical  
11 studies, as reviewed below, have increased within the last five years (i.e., six published studies  
12 during 2008 versus none or one in all previous years), but still are few in number relative to  
13 marine ecosystems (Fig. 1).

14 In the following sections, we aim to demonstrate the potential value of biophysical  
15 approaches to exploring fish recruitment in large-lake ecosystems, which ultimately will advance  
16 our basic understanding of how fish recruitment is regulated, and in turn, lead to sustainable fishery  
17 management approaches. We review the basis for our hypothesis that early life stages, and physical  
18 processes acting upon them, are frequently critical to recruitment. We then compare large-lake  
19 (exemplified by the Laurentian Great Lakes) and marine (e.g., pelagic marine, estuarine, coral reef)  
20 ecosystems in terms of their physical and biological properties to illustrate their many similarities.  
21 Knowledge of physical forcing of fish recruitment in the Great Lakes is then surveyed. Afterwards,  
22 we seek to show that the Great Lakes are in many ways a favorable arena in which to pursue such  
23 research and test ideas about patterns of biophysical forcing among habitats and ecosystems.

1 Lastly, we provide a range of general research avenues concerning the effects of physical  
2 processes on fish recruitment that would lead to better understanding and forecasting of  
3 recruitment variation in both marine and freshwater ecosystems.

## 5 **BIOPHYSICAL PROCESSES AND RECRUITMENT**

### 6 *Recruitment and the Role of Early Life Stages*

7 We define recruitment as the addition of new members of a population to the first life stage  
8 at which natural mortality tends to stabilize near adult levels (Ludsin 1994; Booth and Brosnan  
9 1995). Johan Hjort, a pioneer in fisheries-based recruitment research, was the first to contend that  
10 processes influencing survival during the larval stage, and not just those operating during adult life  
11 stages (e.g., spawning fish biomass), drove inter-annual recruitment variability and ultimately  
12 population structure of marine fishes (Hjort 1914). While work has moved well beyond Hjort's  
13 initial emphasis on larval starvation (see reviews by Leggett and Deblois 1994; Rothschild 2000;  
14 McCann et al. 2003), the conviction that recruitment is regulated during early life stages (ELS),  
15 which are characterized by extremely high mortality rates (Houde 1994, 1997; Horwood et al.  
16 2000), has only grown stronger through time.

17 Mechanistic investigations into how biotic (e.g., competition, predation) and stochastic  
18 abiotic (e.g., storm events, temperature) elements regulate recruitment have become more common  
19 in aquatic ecosystems (e.g., Doherty and Fowler 1994; Ludsin and DeVries 1997; North and  
20 Houde 2003). Because the absolute number of individuals recruiting to a population is limited by  
21 how many pre-recruits are produced (Houde 1987, 1989), much of this mechanistic work has  
22 focused on understanding growth and survival of organisms during ELS (e.g., egg and larval  
23 stages). A focus on ELS seems especially appropriate for highly fecund species that provide little

1 parental care, as small size renders these life stages susceptible to more abiotic and biotic mortality  
2 controls than during later life stages (e.g. Houde 1987; Horwood et al. 2000; Rothschild 2000).

### 3 *Mechanisms of Physical Processes and Their Importance*

4 Physical processes such as sub- or supra-optimal temperatures (Brett 1956; Shafland and  
5 Pestrak 1982), low oxygen availability (i.e., hypoxia; Breitburg 2002; Pollock et al. 2007), and  
6 storms (e.g., Tabb and Jones 1962; Walsh 1983; Steinhart et al. 2005) can cause direct mortality  
7 during all life stages. However, physically-driven *direct* mortality is considered most important  
8 during ELS (especially the egg stage)—when propagules are small and active movement (e.g.,  
9 avoidance) is difficult or impossible (but see Clay et al. 2004; Bradbury et al. 2006; Leis et al.  
10 2009)—with its importance declining with increasing body size and development (Lassig 1983;  
11 Houde 1987, 1989; see Fig. 2). Instead, *indirect* regulation of recruitment by physical processes  
12 that alter feeding, growth, condition, and survival (Fig. 2) is generally viewed to be more important  
13 than direct mortality during ELS (Houde 1989). Minor fluctuations in early growth and survival  
14 rates can exert even stronger control of future recruitment success than brief, but intense, periods of  
15 direct mortality (Houde 1987).

16 Given this framework, we contend that the physical processes likely to be most important  
17 to understanding recruitment variation of both marine and freshwater fishes are those that  
18 indirectly act to delay an individual's development (i.e., reduce growth rates), thereby extending  
19 time spent in vulnerable ELS (Houde 1987, 1989, 1997). Below, we review a few of the many  
20 indirect mechanisms by which physical processes can influence early-life growth, and in turn,  
21 future recruitment.

22 Prey availability. Hjort (1914) first proposed starvation during the transition from  
23 endogenous to exogenous feeding as the key regulatory process of recruitment, with physical

1 processes that affect the overlap of first-feeding larvae with planktonic prey exerting critical  
2 influence. The term “match-mismatch” was later coined to describe how the spatiotemporal  
3 coincidence of larvae with their food supply could determine their survival (Cushing 1975, 1990).  
4 A large body of observational and theoretical work on this recruitment paradigm among marine  
5 fishery scientists continues unabated (e.g., Leggett and DeBlois 1994; James et al. 2003;  
6 Castonguay et al. 2008). A more limited amount of study among freshwater fishery ecologists also  
7 has developed (e.g. Schindler et al. 2005; Straile et al. 2007; Reichert et al. 2010), stimulated in  
8 part by interest in climate change effects.

9 Match-mismatch effects can be exerted through large-scale physical processes (e.g.,  
10 meteorology) that drive mesoscale circulation features that advect larvae and their prey  
11 differentially (Fig. 2; e.g., Sinclair 1988; Lewis et al. 1994; Gonzalez-Quiros et al. 2004), and  
12 modeling of larval fish drift/retention processes in relation to habitat (e.g., planktonic prey)  
13 availability continues to develop (e.g., Hinrichsen et al. 2001). Coastal upwelling is a special case  
14 of advection that produces variable degrees of match between larvae and their prey, depending on  
15 its strength and timing (e.g., Landaeta and Castro 2002; Ward et al. 2006). Marine estuaries also  
16 have circulation features (e.g., fronts, estuarine turbidity maxima) that affect larval distributions  
17 and overlap with prey (e.g. Brandt et al. 1992; North and Houde 2003).

18 Additional physical mechanisms, both fine- and meso-scale, can affect spatiotemporal  
19 overlap between larvae and their prey. For example, the Stable Ocean Hypothesis (Lasker 1978)  
20 proposes that variations of mixing processes (e.g., due to large-scale forcing such as storms or  
21 inputs of low density water) alter the distribution and density of both larvae and prey with stable  
22 conditions encouraging higher coincident concentrations and better recruitment (e.g., Wroblewski  
23 et al. 1989; Werner et al. 1997). Fine-scale processes, such as Langmuir circulation, which

1 concentrate planktonic prey and larvae on small (meters) spatial scales for periods of hours or more  
2 (Megard et al. 1997; Malinen et al. 2001), can influence recruitment of individuals to older life  
3 stages. Likewise, small-scale turbulence has been shown to affect not only larval fish distributions  
4 but also their feeding success (e.g., Leggett and DeBlois 1994; Gallego et al. 1996; Landry et al.  
5 1995). Large-scale forcing of river discharge is another example of a physical process that has been  
6 shown to alter the match between larvae and prey through differential advection and development  
7 rates (e.g., North and Houde 2003; Mion et al. 1998) and formation of nutrient-rich, turbid offshore  
8 plumes (Grimes and Kingsford 1996; Grimes 2001).

9 Temperature. The thermal environment plays a critical, indirect role in the recruitment  
10 process (Fig. 2), owing to its ability to influence developmental rates, growth, and survival through  
11 numerous pathways, both endogenous (e.g., effects on metabolism, digestion, and energy  
12 assimilation) and exogenous (e.g., predator and competitor production; alteration of refugia that  
13 influence energy requirements, vulnerability to predators, and access to prey). Owing to the many  
14 ways in which temperature (via heating and cooling) can influence individuals, studies  
15 documenting statistical relationships between temperature and recruitment success have become  
16 commonplace in both the freshwater and marine fisheries literature (e.g., Pepin 1991; Myers 1997;  
17 Beaugrand et al. 2003). Unfortunately, predictive models of recruitment based solely on  
18 temperature generally fail to give robust, consistent results, except possibly where temperatures  
19 commonly approach lethal limits (Myers 1998). The various indirect ways (some of which may  
20 counter one another) that temperature has been shown to influence the performance of an  
21 individual and its predators/competitors contribute to such inconsistency in simple empirical  
22 models.

1           Dissolved oxygen. Availability of dissolved oxygen may influence fish recruitment and can  
2 be regulated by physical processes such as thermal and density stratification (Turner et al. 1987;  
3 Stanley and Nixon 1992), river discharge that supplies nutrients that limit primary production  
4 (Hagy et al. 2004), and wind forcing that influences horizontal and vertical mixing (e.g., Rao et al.  
5 2008). In Chesapeake Bay, for example, hypoxia (dissolved oxygen < 3 mg· L) likely influences  
6 recruitment of bay anchovy (*Anchoa mitchilli*), this ecosystem's most abundant zooplanktivorous  
7 fish, by reducing access to bottom habitat and altering the spatial overlap of both predator and  
8 prey. Specifically, hypoxia has been suggested to 1) increase predation risk of juvenile and adult  
9 bay anchovy to vertebrate predators (striped bass *Morone saxatilis*; Costantini et al. 2008) and of  
10 larval bay anchovy to invertebrate predators (sea nettle *Chrysaora quinquecirrha*; Breitburg et al.  
11 1997); 2) reduce access of bay anchovy to zooplankton prey, which appear to use hypoxic areas as  
12 a refuge (Taylor et al. 2007; Ludsin et al. 2009); and 3) increase energetic expenditures of bay  
13 anchovy that are displaced from bottom refugia (Taylor et al. 2007). Fish mortalities due to  
14 upwelling of hypoxic water also have been documented (e.g., Wanink et al. 2001), although  
15 upwelling effects on ELS are not well understood at present. Further, although numerous  
16 laboratory and *in situ* studies have documented short-term effects of hypoxia on individual  
17 behavior, foraging, growth, condition, reproduction, and survival (see reviews by Breitburg 2002;  
18 Wu 2002; Pollock et al. 2007), definitive linkages between hypoxia and fish recruitment have  
19 remained elusive with the exception of the negative influence of hypoxia on Baltic cod (*Gadus*  
20 *morhua*) via mortality of eggs that sink into the hypoxic bottom layer (Breitburg 2002; Breitburg et  
21 al. 2009).

22           Other variables. Other physical variables have the potential to influence fish recruitment  
23 via indirect control of early life growth and survival. For example, ultraviolet radiation penetration

1 appears to indirectly limit yellow perch (*Perca flavescens*) recruitment by limiting successful  
2 reproduction to depths where temperatures are too low for optimal egg development and hatching  
3 success (Huff et al. 2004; Williamson et al. 1997). Likewise, tributary-driven inputs of sediments  
4 and freshwater can influence recruitment of fishes by forming open-water plumes that provide  
5 spawning and foraging habitats with reduced predation risk for eggs and larvae (Grimes and  
6 Kingsford 1996; Reichert et al. 2010).

7 Synergies and interactions. While studies documenting the importance of one or more  
8 physical process(es) to the recruitment process abound, a full, integrated understanding of the  
9 recruitment mechanisms of any single species is lacking. Several reasons underlie our inability to  
10 reliably understand and especially forecast the effects of physical processes on recruitment. First,  
11 numerous density-dependent and -independent variables can operate simultaneously during ELS to  
12 drive variation in feeding, growth, condition, and survival (e.g., Sanvicente-Anorve et al. 2006;  
13 DingsØr et al. 2007; Keyl and Wolff 2008). For example, weather-driven variations in heating and  
14 cooling rates can alter population phenology (e.g., Beaugrand et al. 2003; Freund et al. 2006),  
15 causing varying degrees of overlap between larvae and their prey, while water circulation can  
16 operate concurrently to influence survival via advection (Platt et al. 2003). Likewise, temperature  
17 variations associated with the North Atlantic Oscillation and interspecific interactions (including  
18 predation and competition) both appear important to understanding recruitment dynamics of  
19 capelin (*Mallotus villosus*), northeast Arctic cod, northeast Arctic haddock (*Melanogrammus*  
20 *aeglefinus*), and Norwegian spring spawning herring (*Clupea harengus*) in the Barents Sea (Duffy-  
21 Anderson et al. 2005; DingsØr et al. 2007). Second, the importance of recruitment mechanisms  
22 (and their interactions) can vary both spatially and temporally within and among life stages (see  
23 Booth and Brosnan 1995 and Caley et al. 1996 for reviews). For instance, in Lake Erie's western

1 basin, enhanced river discharge can increase mortality of walleye (*Sander vitreus*) yolk-sac larvae  
2 via physical scouring in the river proper (Mion et al. 1998), but subsequently enhance survival of  
3 older, first-feeding larvae in the open lake through creation of plankton-rich nursery areas (Jones et  
4 al. 2003). Where ontogeny involves a major change in habitat or diet, the potential complexity of  
5 interactions further increases, as discussed by Gopalan et al. (1998) for the case of fish that switch  
6 from planktivory to benthivory in the course of their development and by Ludsin and DeVries  
7 (1997) for fish that switch to from invertivory to piscivory. Finally, ELS are inter-dependent such  
8 that growth success (for example) in one life stage can influence growth or survival during later  
9 stages (Houde 1989; Ludsin and DeVries 1997; Rothschild 2000).

10 All of these considerations point to a need for more comprehensive mechanistic  
11 investigations that 1) incorporate individual behavior and life-stage interactions, 2) recognize the  
12 fundamental non-equilibrium nature of most fish populations, and 3) acknowledge that a fish  
13 population should not be studied independently of its ecosystem and the food web within which it  
14 resides (Ludsin and DeVries 1997; Rose 2000; DingsØr et al. 2007). Concepts of biophysical  
15 controls on fish recruitment (see Fig. 2) must consider not only the direct and indirect physical  
16 influences but also the inter-population and inter-life stage interactions that occur on a range of  
17 time and space scales.

18

## 19 **GREAT LAKES COMPARISONS TO MARINE ENVIRONMENTS**

20 Although the foregoing concepts and mechanisms have been elucidated mainly in marine  
21 ecosystems, they are clearly applicable to large freshwater ecosystems that also contain organisms  
22 at the mercy of abiotic factors (e.g., wind, water currents, temperature). We contend that large-lake  
23 ecosystems can serve as a useful analogue to marine environments in terms of how recruitment and

1 community structure of fishes are regulated by physical processes. Most obviously, they offer  
2 practical advantages to the researcher in that they provide environments that are smaller and less  
3 speciose than most marine ecosystems of similar physical complexity. Further, large-lake  
4 ecosystems tend to be rich with historical and ongoing monitoring data, likely owing to their inland  
5 location and small size, both of which facilitate sampling. While some valuable insights have  
6 arisen from observations in tropical Great Lakes, we focus our discussion on the North American  
7 Great Lakes, which support numerous species of recreational and commercial import, have a  
8 wealth of physical and biological information due to past and ongoing research and monitoring  
9 programs, and have management agencies (federal, state, and provincial) that are seeking to  
10 support physical-biological coupling research approaches in their effort to develop integrated,  
11 ecosystem-based fisheries management strategies (Great Lakes Fishery Commission 2001).

### 12 *Physical Attributes*

13 Obvious differences between a typical pelagic ocean setting and the Great Lakes include  
14 the lack of a true open (deep sea) boundary and a greater influence from topography (including  
15 coasts) in the Great Lakes, the smaller relative size of the lakes as compared to major atmospheric  
16 disturbance ecosystems, the lack of significant solunar tides in the Great Lakes, and the unique  
17 density-temperature relationship in freshwater ecosystems. Owing to the latter difference,  
18 freshwater ecosystems have two water-column mixing periods (i.e., spring and fall), as well as the  
19 thermal bar phenomenon, which can limit exchange between coastal and offshore waters (Holland  
20 and Kay 2003; Rao et al. 2004). Topographic boundaries more strongly influence large-scale  
21 circulation patterns and internal wave behavior in the Great Lakes than in the open ocean, as does  
22 the seasonal progression between stratified and unstratified conditions (Boyce et al. 1989; Beletsky  
23 et al. 1999; Beletsky and Schwab 2001). Short and long-term circulation also is more responsive to

1 wind forcing in the Great Lakes than in open ocean ecosystems (Boyce et al. 1989), although wind  
2 forcing can be equally as important in coastal marine and estuarine settings (Gordon and Spaulding  
3 1987; Blumberg and Goodrich 1990). Despite these differences, a brief consideration of the  
4 physical and biological complexities associated with Lake Erie, the smallest in volume of the Great  
5 Lakes (and hence, the least likely to operate like a marine environment), as well as a ecosystem  
6 with which we are intimately familiar, further shows grounds for proposing that biophysical  
7 coupling research could benefit our understanding of Great Lakes fish recruitment and fisheries  
8 ecology generally.

9 Oceans are complex, heterogeneous environments both biologically and physically (e.g.,  
10 Sale 1991; Valiela 1995; Mann and Lazier 1996). However, Lake Erie displays much of the same  
11 complexity, despite its relatively small size. The spatial scales and seasonal density stratification of  
12 Lake Erie lead to many of the same physical phenomena that occur in coastal oceans, with  
13 rotational (Coriolis) forces playing a significant role (e.g., Boyce et al. 1989). A distinct coastal  
14 boundary layer exists in all of the Great Lakes, the dynamics of which have many similarities to  
15 those in marine ecosystems (Rao and Schwab 2007). At least 12 distinct physical phenomena  
16 known from coastal ocean ecosystems can be identified in Lake Erie, with length scales for  
17 horizontal motion ranging from tens of meters (e.g., surface gravitational waves) to tens of  
18 kilometers (e.g., internal waves, coastal currents, upwelling) to hundreds of kilometers (e.g.,  
19 horizontal wind-driven circulation) and corresponding time scales from seconds to months (Boyce  
20 1974). Seiches, eddies, gyres, and lakewide water currents that vary with depth, wind, and  
21 temperature are observable in Lake Erie (Sly 1976; Mortimer 1987; Saylor and Miller 1987).  
22 Water movements are complex because exchange occurs between a small, shallow western basin, a  
23 larger, deeper central basin, and an eastern basin that includes the deepest point in the lake.

1 Seasonal average circulation patterns inferred from hydrodynamic models show complex gyre  
2 structures at the basin scale (Leon et al. 2005; Schwab et al. 2009), as well as major coastal  
3 currents; however, circulation patterns are highly variable on the smaller scales (days to weeks)  
4 relevant to foraging, growth, and survival during ELS (Zhao et al. 2009).

5 Ice cover varies greatly among and within the Great Lakes and on various time and space  
6 scales (Assel et al. 2003). The dynamic and spatially patchy nature of ice cover presents another  
7 similarity with many marine ecosystems and a contrast with the behavior of smaller lakes. Recent  
8 decades have witnessed less ice cover than in past decades in the Great Lakes region (Jensen et al.  
9 2007), and the Great Lakes specifically (Austin and Colman 2008; Howk 2009), raising the  
10 prospect of a systematically different ice regime in the foreseeable future. Lake Erie is an  
11 interesting example because it is the only one of the Great Lakes that has historically developed  
12 virtually complete ice cover in most winters (Assel et al. 2003). Even so, the presence and  
13 thickness of ice varies widely across the lake and over periods of days to weeks while inter-annual  
14 variations are large (Assel et al. 2003). Thus, Lake Erie can serve as a good model for study of how  
15 climate-induced changes in ice regimes may influence fish populations.

16 Similar to marine environments, a great deal of physical habitat complexity exists in Lake  
17 Erie, which varies spatiotemporally. Examples include wetlands and lake estuaries (or  
18 “lacustuaries” per Odum 1990; e.g., Sandusky Bay, OH) that span parts of the shoreline and  
19 undergo significant seasonal and storm-related water level variations. A heterogeneous array of  
20 sand, gravel, and bedrock substrates includes shallow reef complexes (both natural and artificial)  
21 that are highly important as spawning sites in the lake proper. This habitat complexity results in  
22 widely varied distributions of spawning habitats both within and among species (Goodyear 1982;

1 Table 1), as well heterogeneous environments in which organisms can live during larval, juvenile,  
2 and adult life stages.

### 3 *Biological Attributes*

4 Similar to any marine environment (see Sinclair 1988 for examples), primary and  
5 secondary production varies spatiotemporally in Lake Erie. For example, as in marine ecosystems,  
6 a pronounced spring to early summer maximum in availability of crustacean zooplankton and  
7 rotifers that are commonly preferred as prey for larval fish occurs in Lake Erie, as does pronounced  
8 patchiness on sub-basin and between basin spatial scales (e.g., Barbiero et al. 2001; Frost and  
9 Culver 2001; Stockwell et al. 2002). Likewise, benthic macroinvertebrate populations that are  
10 important to juvenile fish growth and survival (e.g., *Hexagenia* spp., Tyson and Knight 2001) vary  
11 considerably within and across basins, as well as through time (Krieger and Ross 1993; Schloesser  
12 et al. 1995; Roberts et al. 2009).

13 Many similarities exist between marine ecosystems and the Great Lakes with regard to fish  
14 populations. For example, Great Lakes fish recruitment and production vary considerably (orders  
15 of magnitude) in time and space within and across basins (Cooper et al. 1981; Knight and  
16 Vondracek 1993; Ludsin et al. 2001). The life histories of some ecologically and economically  
17 important Lake Erie fishes (e.g., walleye, lake trout *Salvelinus namaycush*, whitefish *Coregonus*  
18 *clupeaformis*, rainbow smelt *Osmerus mordax*, yellow perch) can include migration within basins,  
19 between basins, and/or between the lake proper and spawning tributaries (e.g., Wolfert 1963;  
20 MacDougall et al. 2007; Oldenburg et al. 2007), analogous to the short- and long-distance  
21 migratory behavior observed in countless marine species. As in marine ecosystems, the life  
22 histories of these and most other important Lake Erie fishes include a long pelagic, planktivorous  
23 larval stage in which larvae and their zooplankton prey appear susceptible to water currents (Houde

1 1969; Siefert 1972; Zhao et al. 2009), followed by a demersal, benthivorous juvenile stage (Wu  
2 and Culver 1992; Gopalan et al. 1998) (Table 1). Further, all of these Great Lakes recreational and  
3 commercial fishes (and likely many others) have local spawning (sub-) populations associated with  
4 specific offshore reefs or tributaries (e.g., Mion et al. 1998), which mix during older life stages  
5 (e.g., Miller 2003; Strange and Stepien 2007). Such population structure is quite common in  
6 marine fishes (see Sinclair 1988 for examples).

7 In summary, the community of Lake Erie fishes and their planktonic and benthivorous prey  
8 vary both spatially and temporally against a backdrop of high physical variability at a range of  
9 space and time scales. This situation is typical of the other Great Lakes, as well as marine  
10 ecosystems.

#### 11 *Mechanisms of Recruitment: Previous Comparisons*

12 Collectively, the limited body of comparative marine and freshwater recruitment research  
13 has portrayed freshwater fish populations as being more strongly localized, less influenced by  
14 indirect abiotic influences during the larval stage, and more heavily regulated by biotic factors  
15 during the juvenile stage than their marine counterparts. For example, Houde (1994) concluded  
16 that life-history differences between marine and freshwater fishes are indicative of more  
17 localization, and less wide-scale mixing, of stocks in freshwater than marine ecosystems. Houde  
18 (1994) also found that pelagic larval stages were generally shorter, and egg sizes larger, in  
19 freshwater versus marine fishes. In turn, his analysis suggests that 1) catastrophic processes (e.g.,  
20 direct mortality from short but intense storm events and lethal temperature extremes) would be  
21 more important in freshwater than marine ecosystems and 2) abiotic effects on larval foraging  
22 success and other indirect effects that play out over longer periods of time might be less important  
23 in freshwater ecosystems as the organisms grow more quickly through the vulnerable stages.

1 Additionally, Myers (1997) analyzed spatial variability in recruitment among stocks for 19 fishes,  
2 suggesting a larger role for abiotic environmental control in marine ecosystems and a greater role  
3 for predation and competition in freshwater environments.

4 While much support for the observations, and in some cases conjectures, of Houde (1994)  
5 and Myers (1997) has been generated, we do not feel that their expectations fully reflect population  
6 structure and recruitment mechanisms in the Great Lakes. For example, Miller (2003) documented  
7 wide-scale mixing of stocks in one Great Lakes fish population (yellow perch in Lake Michigan),  
8 and genetic evidence reveals the same for walleye in Lake Erie (Strange and Stepien 2007). One  
9 reason that the generalizations of Houde (1994) and Myers (1997) may not apply to the Great  
10 Lakes is that these studies did not include freshwater species important in the Great Lakes.  
11 Furthermore, even if the duration of the vulnerable larval stage is shorter in freshwater than marine  
12 fishes, the frequency and severity of indirect abiotic forcing is likely to be greater in freshwater  
13 ecosystems than is recognized by these comparative studies. The smaller size and more intimate  
14 contact with the catchment in lakes, as compared to most marine ecosystems, would be expected to  
15 allow for more rapid environmental change (e.g., warming and cooling) and steeper gradients in  
16 relevant properties (e.g., plankton concentrations) such that even brief larval stages may be  
17 exposed to strong but nonetheless indirect abiotic forcing. Current knowledge, as reviewed below,  
18 already points to some cases of indirect abiotic forcing similar to those found in marine  
19 ecosystems.

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# 1                    **BIOPHYSICAL RECRUITMENT RESEARCH IN THE GREAT LAKES**

## 2                                    *Physical Forcing of Lower Trophic Levels*

3                    A large effort has been expended in marine research to elucidate the patterns and  
4 processes in phyto- and zooplankton communities associated with physical features such as  
5 seasonal and event-scale mixing, upwelling zones, fronts, and currents. Plankton dynamics on  
6 and near Georges Bank (Lewis et al. 1994; Franks and Chen 2001), on the Nova Scotia shelf  
7 (Platt et al. 2003), and in the North Sea (Beaugrand et al. 2003), for example, appear to be  
8 largely controlled by seasonal and inter-annual variations in water-column stability and  
9 mesoscale surface advection, at least at certain times of year. The resulting variations of plankton  
10 dynamics have in turn been linked to variations in fish recruitment (see Sinclair 1988 for  
11 examples). In large lakes, the seasonal cycle of thermal stratification is recognized as an  
12 important control on plankton dynamics (e.g., Fahnenstiel et al. 1987) but the role of other  
13 physical processes is less well characterized.

14                    Upwelling, for example, is a recurrent feature in large lakes. However, field  
15 demonstrations of its role in plankton abundance and productivity in the Great Lakes are largely  
16 lacking, although mesoscale circulation and downwelling have been implicated in transport of  
17 nuisance phytoplankton in Lake Ontario (Rao et al. 2003). Some of our best information on  
18 physical forcing of the lower food web is from the Episodic Events – Great Lakes Experiment  
19 (EEGLE) Program, which documented linkages between winter storm events, sediment  
20 resuspension, lake circulation, the microbial food web, and phytoplankton and zooplankton  
21 dynamics and distributions during 1998 and 1999 (e.g., Chen et al. 2002, 2004; Kerfoot et al.  
22 2004). However, the significance of such physical processes for the long-term structure and  
23 function of plankton communities is still uncertain (Millie et al. 2003). Further, and with a few

1 exceptions (e.g., Freeberg et al. 1990; Mion et al. 1998; Reichert et al. 2010), field investigations  
2 seeking to link physical processes (e.g., storm events, river discharge, ice cover, upwelling,  
3 circulation features) to plankton dynamics and ultimately fish recruitment have not even been  
4 attempted. Even so, the importance of these linkages has been speculated about and is implied by  
5 much of what we presently know about the role of physical processes in the recruitment  
6 processes of several important Great Lakes fishes, including walleye, yellow perch, alewife  
7 (*Alosa pseudoharengus*), and lake whitefish.

### 8 *Physical Forcing of Upper Trophic Levels*

9 Lake Erie walleye. Walleye is the most important recreational fish in Lake Erie and also  
10 an important commercial species in Canadian waters. Reproduction of walleye in Lake Erie  
11 emanates primarily from western basin rivers (e.g., Mion et al. 1998; MacDougall et al. 2007;  
12 Manny et al. 2007), embayments (Roseman et al. 2002), and offshore reefs (e.g. Roseman et al.  
13 1996, 2001). The diversity of spawning sites is reflected in complicated population structures in  
14 Lake Erie (e.g., Merker and Woodruff 1996; Gatt et al. 2003; Strange and Stepien 2007) and  
15 elsewhere in the Great Lakes (Fielder 2002). Major variation in walleye recruitment among years  
16 in Lake Erie has been associated with variable prey availability (e.g., soft-rayed fishes such as  
17 gizzard shad *Dorosoma cepedianum*), adult growth and condition, and spawning success (e.g.,  
18 Knight and Vondracek 1993; Henderson and Nepszy 1994; Madenjian et al. 1996), and such  
19 biological interactions must contribute to at least some of the variability of stock-recruitment  
20 relationships for Lake Erie.

21 The determinants of recruitment in Great Lakes percids (e.g., walleye, yellow perch)  
22 were reviewed by Neuman et al. (1996), who concluded that stock-recruitment relationships  
23 were generally weak and that events in the first year of life, including abiotic factors, were

1 decisive to year-class strength. Considerable evidence exists to support this contention that  
2 physical processes are critical to walleye recruitment in Lake Erie. For example, Mion et al.  
3 (1998) found that larval survival in two major western basin tributaries (Maumee and Sandusky  
4 rivers) was inversely related to discharge, and suggested that high discharge causes mortality  
5 during the larval stage via physical scouring and/or flushing of pre-feeding larvae into  
6 unproductive, open-lake waters. For lake spawners, Busch et al. (1975) reported a strong positive  
7 relationship between the warming rate during spring and both walleye egg production and year-  
8 class strength, suggesting that higher temperatures reduced the period of vulnerability of eggs to  
9 low dissolved oxygen associated with siltation on open-lake reefs. Busch et al. (1975) also found  
10 that recruitment was negatively correlated with storm events during the incubation period that  
11 could lead to temperature reversals (i.e., rapid drops in temperature) and high winds that could  
12 cause eggs to become buried in sediments. Koonce et al. (1977) reported a negative relationship  
13 between recruitment and the frequency of wind events during egg and larval development.  
14 Likewise, Roseman et al. (1996) proposed that water temperatures are important in regulating  
15 egg development times for lake spawners, modifying susceptibility to predation (Roseman et al.  
16 2006) and storm-driven displacement from spawning reefs, a process documented by Roseman et  
17 al. (2001).

18         Research on the mechanisms underlying such correlations has continued. Larvae in their  
19 early feeding stages in the western basin of Lake Erie, where the majority of walleye  
20 reproduction is currently believed to occur, are present during April through June (Table 1) and  
21 are believed to originate largely from reef-spawning populations. Roseman et al. (2005) noted  
22 that the walleye larvae, together with other ichthyoplankton that include potential prey, were  
23 distributed preferentially in the southern margins of the basin and suggested an important nursery

1 role for these southern coastal waters. Crustacean zooplankton is an important food for first-  
2 feeding walleye larvae and is often present earlier and in larger concentrations in these southerly,  
3 more coastal waters (Frost and Culver 2001; Roseman et al. 2005). The zooplankton  
4 distributions may reflect earlier warming of the shallow southern waters, fertilization by the  
5 adjacent, nutrient-rich Maumee River, import of plankton from the Maumee, reduced planktivory  
6 by older, juvenile fishes in turbid Maumee waters (Wellington et al. 2010), or some combination  
7 of the above. Zhao et al. (2009) modeled the hydrodynamic transport of walleye early larval  
8 stages and compared the predicted spatial distribution of first-feeding stages in two years of high  
9 versus two years of low documented recruitment. Interestingly, the predicted transport was  
10 towards the putative southerly nursery areas in good recruitment years but away (northwards) in  
11 poor recruitment years. This result suggests that wind-driven advection of larvae and associated  
12 indirect physical forcing mechanisms (especially starvation and predation; see Fig. 2) are  
13 important determinants of recruitment in Lake Erie walleye, just as in many marine fishes.

14 Walleye recruitment in Lake Erie currently presents one of the stronger examples of the  
15 potential linkage between recruitment and physical transport processes for Great Lakes fishes  
16 and highlights a feature of large lakes that is unlikely to be as important or noticeable in smaller  
17 lakes. Even so, more work is required to increase the realism of the modeling of transport and  
18 related phenomena. For example, Zhao et al.'s (2009) model did not incorporate larval behavior  
19 (e.g., vertical and horizontal migration), which has been shown to be important in coral reef  
20 ecosystems, nor has the model's ability to predict growth and distributions of larvae been tested.  
21 The mechanistic basis for this apparent transport-recruitment relationship also is in need of  
22 further development as the evidence linking larval walleye distributions with zooplankton prey is  
23 currently incomplete (Roseman et al. 2005). Additionally, the relative importance of direct

1 physical influence on feeding success versus other biotic controls (e.g., predation risk from other  
2 piscivores such as alewife; Fielder et al. 2007) remains unresolved.

3 Yellow perch. Yellow perch is another important recreational and commercial species in  
4 the Great Lakes and shares with walleye the characteristics of spring spawning and, especially in  
5 the case of yellow perch, a prolonged planktonic larval phase that depends significantly on  
6 zooplankton as prey (Ludsin 2000; Bremigan et al. 2003; Table 1). As with walleye, correlative  
7 evidence exists to indicate that lake temperatures and physical disruption of eggs can drive inter-  
8 annual recruitment variation (Clady 1976; Henderson and Nepszy 1988). In Lake Erie, Reichert  
9 et al. (2010) used otolith microchemical approaches to demonstrate higher contributions of  
10 larvae to the new year-class in August (which is when recruitment to the fishery at age-2 is set in  
11 Lake Erie; Ludsin 2000; Yellow Perch Task Group 2010) from nutrient-rich, highly turbid  
12 waters associated with the Maumee River plume in western Lake Erie relative to other (i.e.,  
13 nutrient-poor, less turbid) areas of the western basin. Reichert et al. (2010) implicated indirect  
14 physical control of predation mortality (primarily) and zooplankton availability (secondarily)  
15 during the larval stage in the recruitment process. Their findings helped explain a strong positive  
16 relationship observed between Maumee River discharge just before and during the larval  
17 production period in spring (i.e., March-May) and yellow perch recruitment to both the new  
18 year-class and the fishery (Ludsin 2000). Long-term monitoring also has found a negative  
19 relationship between winter temperature and recruitment the following spring (Ludsin 2000;  
20 Crane 2007), perhaps through effects on ovarian development during winter (Hokanson 1977).

21 The importance of physical processes to yellow perch recruitment also has been  
22 demonstrated in Lake Michigan. Beletsky et al. (2004) showed persistent, but variable,  
23 circulation features that can either retain larvae in suspected nursery areas or transport them

1 away from spawning and nursery areas. Dettmers et al. (2005) documented offshore transport of  
2 yellow perch larvae and discussed implications for potential matching with prey concentrations.  
3 Beletsky et al. (2007) extended their larval yellow perch transport modeling to elucidate  
4 expected effects of both biological (consumption rates, settlement size) and physical (circulation,  
5 temperature) effects on potential recruitment from the larval stage. To date, however, a  
6 relationship between advective processes that affect dispersal of larvae and their zooplankton  
7 prey and recruitment has not been established for any yellow perch population, including those  
8 in Lake Michigan.

9 Alewife. The percid examples described above currently constitute some of the strongest  
10 examples of physical processes affecting fish recruitment in large lakes. Evidence is mounting,  
11 however, for the importance of physical control of recruitment for other species. The non-native  
12 alewife has become an important, even dominant, member of the planktivorous prey fish  
13 assemblage in many of the Laurentian Great Lakes. Although Great Lakes alewife populations  
14 are not anadromous, they are potamodromous, migrating between open waters of the lake and  
15 coastal areas, embayments, drowned river mouths, or tributaries to spawn during spring. In Lake  
16 Michigan, the stock-recruitment relationship over the course of large population changes (from  
17 highs in the late 1960s to recent lows) displays high variability (Madenjian et al. 2005). While  
18 empirical models for alewife recruitment in Lake Michigan (Madenjian et al. 2005) have shown  
19 positive and negative correlations with stock size and indices of predation pressure, respectively,  
20 spring and summer temperatures also have been important predictors of recruitment. In fact,  
21 warm water temperatures during spring and summer 1998 are believed to have allowed alewife  
22 to recruit to adult stages despite high salmonine (predator) abundance (Madenjian et al. 2005).  
23 Further, Höök et al. (2007, 2008) showed—through comparison of Lake Michigan proper with

1 Muskegon Lake (a drowned river mouth)—that early, rapid spring warming can promote early  
2 hatching, fast growth, large larval size at the beginning of winter, and strong over-winter  
3 survival.

4         Similar to Lake Michigan, alewife recruitment in Lake Ontario was positively correlated  
5 with spawning stock size and negatively correlated with an index of predation (O’Gorman et al.  
6 2004). Additionally, in Lake Ontario, but not Lake Michigan, winter temperatures and an index  
7 of lake productivity were positively associated with recruitment (O’Gorman et al. 2004). The  
8 importance of these additional physical variables likely results from higher alewife densities and  
9 lower zooplankton resources in Lake Ontario than Lake Michigan, which may enhance the role  
10 of intraspecific competition for zooplankton prey during ELS and cause Lake Ontario individuals  
11 to enter the winter in poorer condition at the end of the first growing season than Lake Michigan  
12 individuals. Additionally, winter conditions in Lake Ontario appear closer to the limits of alewife  
13 tolerance than in Lake Michigan (Madenjian et al. 2005).

14         Thus far, these considerations are not fundamentally different from those that might  
15 apply for fishes in smaller lakes, where temperature is often a correlate of recruitment. In the  
16 Great Lakes, however, additional evidence exists to suggest that upwelling and circulation exert  
17 a strong influence on larval alewife distributions and consequent conditions for growth and  
18 survival.

19         Young alewives appear to spend their first few months of life in their natal habitat,  
20 which, for the majority, is the open coastal zone (Dufour et al. 2005). In Lake Michigan,  
21 variation in larval alewife distributions was associated with upwelling in the coastal zone,  
22 suggesting that both transport and mortality associated with temperature shock could influence  
23 recruitment of this species (Edsall 1970; Heufelder et al. 1982). Spatially-explicit modeling

1 conducted by Höök et al. (2003) indicated high spatial variability of habitat quality for young  
2 alewife but failure of alewife distribution to correlate with it; they proposed various mechanisms  
3 (including lake circulation) to explain this inconsistency. Further, Höök et al. (2006)  
4 demonstrated variable drifter tracks during the alewife larval production period in Lake  
5 Michigan, as well as current speeds much greater than larval swimming speeds, supporting the  
6 idea that currents can distribute fish larvae widely. However, Höök et al. (2006) also found  
7 evidence that larvae were not simply moving with their resident water mass, at least when  
8 advection was offshore. Although this finding could arise from sampling biases, it also could  
9 reflect the real phenomenon of limited coherence of advection and larval motility, pointing to a  
10 need for more knowledge of linkages between physics and fish behavior. Similar to the case for  
11 percids, no full and direct link has been established yet between larval transport processes and  
12 recruitment for alewife in the Great Lakes.

13 Lake whitefish. Physical processes also play a major role in the recruitment of lake  
14 whitefish, an important commercial species throughout the Great Lakes basin. This species  
15 spawns during late autumn or winter on coastal and offshore shoals, and larvae do not emerge  
16 until early spring (Goodyear 1982; Table 1). Given that ELS are present during winter, it should  
17 not be surprising that winter meteorology and ice cover strongly determine whitefish population  
18 dynamics (Freeberg et al. 1990; Brown and Taylor 1993; Oldenburg et al. 2007; McKenna and  
19 Johnson 2009), with winter storms causing major egg mortality and failed year-classes in years  
20 with little ice cover. Further, lake whitefish larvae, which feed primarily on crustacean  
21 zooplankton (Davis and Todd 1998), have been reported to associate with shallow, nearshore  
22 waters during spring, moving to offshore waters during early summer in northern Lake Huron  
23 (Faber 1970; Reckahn 1970). Thus, we expect that this life-history strategy would be prone to

1 many of the same physical influences that appear to play a role in the recruitment process of  
2 percids and alewife. Additionally, benthic feeding habits and a requirement for cold temperatures  
3 that typically are only found in the hypolimnion during summer may make lake whitefish  
4 recruitment susceptible to regulation by bottom hypoxia in ecosystems such as Lake Erie (Ludsin  
5 et al. 2001). Given the various ways in which physical processes can potentially influence lake  
6 whitefish recruitment, investigation into the importance of such processes would benefit the  
7 ability of agencies to understand abundance variations in this species.

8 Other fishes. Although we have only discussed four Great Lakes species, we fully believe  
9 that physical processes play a role in the recruitment process of all species through either direct  
10 or indirect pathways (Fig. 2). Of course, the ways in which physical processes can influence  
11 recruitment will vary both within and among species. In most cases, the likely importance of  
12 physical processes can be deduced from knowledge of habitat-use patterns and life-history  
13 attributes (e.g., spawning habitat and timing preferences, amount of parental care provided,  
14 ontogenetic habitat and diet use). For example, freshwater drum (*Aplodinotus grunniens*)  
15 distribution and recruitment should be more regulated by wind-driven circulation than most other  
16 Great Lakes species, given that it has both pelagic eggs and larvae, whereas other species with a  
17 pelagic larval stage have a benthic egg stage (Table 1). By contrast, we hypothesize that spring  
18 storm events that can lead to egg burial, dislodgement, and temperature reversals would drive  
19 recruitment variation more than wind-driven circulation for nearshore, benthic spawners that lack  
20 pelagic eggs and larvae (e.g., smallmouth bass *Micropterus dolomieu*, yellow bullhead *Ameiurus*  
21 *natalis*, rock bass *Ambloplites rupestris*, trout-perch *Percopsis omiscomaycus*, and rainbow trout  
22 *Oncorhynchus mykiss*), with both factors being relatively unimportant for offshore (deepwater),  
23 benthic spawners, including bloater (*Coregonus hoyi*) and some lake trout (*Salvelinus*

1 *namaycush*) strains (Table 1). Likewise, salmonines such as lake trout, chinook and coho salmon  
2 (*Oncorhynchus tshawytscha* and *O. kisutch*, respectively), brook trout (*Salvelinus fontinalis*), and  
3 lake whitefish, which have eggs that overwinter in bottom substrates, should be more negatively  
4 affected by future winter climate warming (Kling et al. 2003) than would species such as  
5 emerald and spottail shiners (*Notropis atherinoides* and *N. hudsonius*, respectively), freshwater  
6 drum, or the round goby (*Neogobius melanostomus*), which reproduce during late spring and  
7 summer and overwinter as juveniles and adults only (Table 1).

8 Knowledge of system-specific environmental conditions or species tolerances, however,  
9 also may be required to fully hypothesize the relative importance of any given physical process.  
10 For instance, we would expect temperature to play some role in the recruitment process of all  
11 fishes, given its ability to indirectly influence foraging, growth, and survival. But, we also would  
12 expect climate warming to be more important to populations that already are at geographical  
13 limits imposed by temperature and related habitat characteristics (e.g., cold-water stenotherms  
14 such as lake trout and lake whitefish in southerly Lake Erie) relative to those that are not (e.g.,  
15 these species in the upper Great Lakes). Likewise, the effect of stressful winter temperatures on  
16 the recruitment process of a species (e.g., alewife, yellow perch) would be expected to be  
17 exacerbated in ecosystems of low prey production (e.g., Lake Ontario; O’Gorman et al. 2004) or  
18 severe hypoxia (e.g., Lake Erie; Vanderploeg et al. 2009; Roberts et al. 2009) during summer,  
19 which can reduce condition of individuals entering the stressful winter period.

20

## 21 **VALUE OF GREAT LAKES RECRUITMENT STUDIES TO MARINE RESEARCHERS**

22 Similar to marine ecosystems, the aforementioned work on Great Lakes fishes has  
23 provided supportive examples for the importance of physical factors (e.g., physical disturbance,

1 temperature, currents) to the recruitment process in large-lake populations through direct,  
2 catastrophic mortality (supporting Houde 1994) and indirect effects on larval transport, habitat  
3 (including prey) availability, and ontogeny (countering expectations of Houde 1994 and Myers  
4 1997). Given these similarities, Great Lakes and marine fishery scientists alike would benefit  
5 from comparing physical-biological coupling processes between ecosystems, especially now that  
6 more than a decade has passed since the semi-comprehensive reviews of Houde (1994) and  
7 Myers (1997). Certainly, such comparisons would allow us to better understand generalities in  
8 the recruitment process of fishes, which could advance fishery science and management in both  
9 sets of ecosystems by providing a framework to begin to tackle the recruitment problem and  
10 potentially reducing the need to study every ecosystem to infinite detail (i.e., mechanisms  
11 derived in one ecosystem could be applied to another ecosystem with similar processes, saving  
12 time and money).

13         The Great Lakes also offer some practical advantages over marine ecosystems with  
14 regard to understanding the recruitment process, owing to their smaller size, closer location to  
15 the mainland laboratories, reduced biodiversity, less complicated chemical characteristics (e.g.,  
16 no salinity stratification), and in many cases, less complicated jurisdictional boundaries. As a  
17 case in point, Reichert et al. (2010) seemingly is the first study in any ecosystem to definitively  
18 quantify linkages between river plume formation in open waters and recruitment to the fishery,  
19 testing hypotheses in Lake Erie that were espoused by marine scientists more than a decade ago  
20 (Grimes and Kingsford 1996). Reichert et al.'s (2010) ability to test these hypotheses was  
21 certainly facilitated by Lake Erie's small size, easy accessibility, and inter-agency cooperation.  
22 Finally, the Great Lakes also offer the opportunity to explore the implications of unique physical  
23 phenomena (e.g., thermal bar), and likely can serve as the proverbial "canary in the coalmine"

1 when it comes to forecasting the effects of continued climate change, given that the Great Lakes  
2 region is expected to experience one of the largest temperature and precipitation changes in the  
3 U.S.A. by the end of this century (IPCC 2007).

#### 4 **RESEARCH GAPS AND OPPORTUNITES**

5 The characterization of linkages between physical processes and fish recruitment is  
6 demanding of resources and requires a range of expertise in physical limnology, modeling, and  
7 the biological aspects of fisheries ecology. At the same time, complex biological interactions are  
8 still expected to operate in both large-lake and marine ecosystems, which cannot be ignored, if  
9 we are to make progress in attaining a predictive understanding of the role of physical processes  
10 in the recruitment process. Hence, if fishery management agencies expect to make headway in  
11 their ability to understand and forecast recruitment variation, comprehensive, multidisciplinary  
12 investigations must be conducted (e.g., development of individual-based coupled physical-  
13 biological models; Miller 1997) and the results of these investigations integrated.

14 In addition, while the recent increase in physical-biological recruitment investigations  
15 (see Fig. 1; Miller 1997) has improved our understanding of how physical processes can  
16 influence fish recruitment in marine ecosystems, and is expected to do the same in large-lake  
17 ecosystems such as the Laurentian Great Lakes, many important, unanswered research questions  
18 remain in both sets of ecosystems (Appendix B). Information gaps exist with respect to both  
19 physical (e.g., What are the physical processes and features that show significant predictability  
20 on time scales of a year or less and to which fish may have adapted their life history?) and  
21 biological (e.g., At what size or age do individuals have the ability to move at will, and how do  
22 climate- or biologically-driven delays in development influence future success?) aspects of  
23 ecosystems. Unresolved questions also exist about their coupling (e.g., How is recruitment

1 regulated by direct mortality from physical stressors versus indirect effects mediated through  
2 biological interactions, and how does the relative importance of each vary with climatic regime  
3 or across a gradient in ecosystem productivity?). Beyond answering such questions for specific  
4 ecosystems, we feel that comparative efforts aimed at identifying commonalities between  
5 ecosystem types regarding the effects of physical processes on the recruitment process would  
6 benefit our understanding, forecasting ability, and ultimately management of fisheries in both  
7 sets of ecosystems. Only through such cross-ecosystem comparisons will we truly learn whether  
8 our primary thesis (i.e., our understanding of and ability to predict fish recruitment in both large-  
9 lake and marine ecosystems will increase through a cross-fertilization and synthesis of research  
10 findings and ideas) is supported or if a different model of physical-biological coupling is needed  
11 to understand fish recruitment in these disparate ecosystems.

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1 **Table 1.** Spawning and early life stage attributes of the five most harvested (by total numerical catch) 1) commercial fishes (by lake)  
2 during 2000-2005 (data source: Baldwin et al. 2009) and 2) recreational fishes (by lake) during 2005 (data sources: Wesander  
3 and Clapp 2006; Fisheries and Oceans Canada 2008). Also included are forage (prey) species found in all five Great Lakes.  
4 Recreational and commercial species that also are considered major forage species are denoted (in Common Name column).  
5 SPR = spring, SUM = summer, AUT = autumn, and WIN = winter; Near = Nearshore, Off = offshore, and Tribs = Tributaries;  
6 E = Erie, H = Huron, M = Michigan, O = Ontario, and S = Superior. <sup>c</sup> = commercial species, <sup>r</sup> = recreational species, and <sup>f</sup> =  
7 forage species. Note: some species are only commercially or recreationally important in some lakes, whereas others are both  
8 commercially and recreationally important in multiple lakes.

Common Name	Scientific Name	Spawning Season	Spawning Habitat	Spawning Mode/ Parental Care	Egg Habitat	Larval Habitat	Egg/Larval Season	Lakes
Alewife <sup>f</sup>	<i>Alosa pseudoharengus</i>	SPR	Near	Broadcast/none	Benthic	Pelagic	SPR/SPR	E, H, M <sup>c</sup> , O, S
Black crappie <sup>1</sup>	<i>Pomoxis nigromaculatus</i>	SPR	Near	Nest guarder/eggs	Benthic	Pelagic	SPR/SPR	E, H, M, O <sup>c</sup> , S
Bloater <sup>f</sup>	<i>Coregonus hoyi</i>	WIN	Off	Broadcast/none	Benthic	Pelagic	WIN/SPR	H, M <sup>c</sup> , S

Bluegill <sup>2, f</sup>	<i>Lepomis macrochirus</i>	SPR	Near	Nest guarder/eggs	Benthic	Pelagic	SPR/SPR	E <sup>f</sup> , H <sup>f</sup> , M, O <sup>c, f</sup> , S
Brook trout	<i>Salvelinus fontinalis</i>	AUT	Tribs; Near	Nest guarder/eggs & larvae	Benthic	Benthic	WIN/SPR	H, M, S <sup>f</sup>
Chinook salmon	<i>Oncorhynchus tshawytscha</i>	AUT	Tribs	Nest builder/none	Benthic	Benthic	WIN/SPR	E, H, M <sup>f</sup> , O, S
Coho salmon	<i>Oncorhynchus kisutch</i>	AUT	Tribs	Nest builder/none	Benthic	Benthic	WIN/SPR	E, H, M <sup>f</sup> , O, S
Emerald shiner <sup>f</sup>	<i>Notropis atherinoides</i>	SUM	Near	Broadcast/none	Benthic	Pelagic	SUM/SUM	E, H, M, O, S
Freshwater drum <sup>f</sup>	<i>Aplodinotus grunniens</i>	SPR & SUM	Near	Broadcast/none	Pelagic	Pelagic	SPR/SUM	E, H <sup>c</sup> , M, O <sup>c</sup> , S
Gizzard shad <sup>f</sup>	<i>Dorosoma cepedianum</i>	SPR & SUM	Tribs; Near	Broadcast/none	Benthic	Pelagic	SPR/SUM	E, H, M, O, S
Lake herring	<i>Coregonus artedi</i>	AUT & WIN	Near; Tribs	Broadcast/none	Benthic	Pelagic	WIN/SPR	E, H, M, O, S <sup>c</sup>

Lake trout	<i>Salvelinus namaycush</i>	AUT & WIN	Near to Off	Egg hider/none	Benthic	Benthic	WIN/SPR	E, H <sup>c</sup> , M <sup>c,r</sup> , O, S <sup>c</sup>
Lake whitefish	<i>Coregonus clupeaformis</i>	AUT & WIN	Near	Broadcast/none	Benthic	Pelagic	WIN/SPR	E, H <sup>c</sup> , M <sup>c</sup> , O <sup>c</sup> , S <sup>c</sup>
Logperch <sup>f</sup>	<i>Percina caprodes</i>	SPR	Near; Tribes	Egg hider/none	Benthic	Pelagic	SPR/SPR	E, H, M, O, S
Rainbow smelt <sup>f</sup>	<i>Osmerus mordax</i>	SPR	Near; Tribes	Broadcast/none	Benthic	Pelagic	SPR/SPR	E <sup>c</sup> , H, M <sup>c</sup> , O, S <sup>c,r</sup>
Rainbow trout	<i>Oncorhynchus mykiss</i>	SPR	Tribes	Egg hider/none	Benthic	Benthic	SPR/SPR	E, H, M <sup>r</sup> , O <sup>r</sup> , S
Rock bass	<i>Ambloplites rupestris</i>	SPR	Near	Nest guarder/eggs & larvae	Benthic	Benthic	SPR/SPR	E <sup>r</sup> , H <sup>r</sup> , M, O <sup>r</sup> , S
Round goby <sup>f</sup>	<i>Neogobius melanostomus</i>	SPR & SUM	Near	Nest guarder/eggs	Benthic	Pelagic	SPR/SUM	E, H, M, O, S
Smallmouth bass	<i>Micropterus dolomieu</i>	SPR	Near	Nest guarder/ eggs & larvae	Benthic	Benthic	SPR/SPR	E <sup>f</sup> , H <sup>f</sup> , M, O, S <sup>f</sup>

Spottail shiner <sup>f</sup>	<i>Notropis hudsonius</i>	SUM	Near	Broadcast/none	Benthic	Pelagic	SUM/SUM	E, H, M, O, S
Trout- perch <sup>f</sup>	<i>Percopsis omiscomaycus</i>	SPR	Near; Tribes	Broadcast/none	Benthic	Benthic	SPR/SPR	E, H, M, O, S
Walleye	<i>Sander vitreus</i>	SPR	Near; Tribes	Broadcast/none	Benthic	Pelagic	SPR/SPR	E <sup>c,r</sup> , H, M, O, S <sup>f</sup>
White bass <sup>f</sup>	<i>Morone chrysops</i>	SPR	Near	Broadcast/none	Benthic	Pelagic	SPR/SPR	E <sup>c</sup> , H, M, O, S
White perch <sup>f</sup>	<i>Morone americana</i>	SPR	Near	Broadcast/none	Benthic	Pelagic	SPR/SPR	E <sup>c</sup> , H, M, O, S
Yellow bullhead <sup>3</sup>	<i>Ameiurus natalis</i>	SPR	Near	Nest guarder/eggs & larvae	Benthic	Benthic	SPR/SPR	E, H, M, O <sup>c</sup> , S
Yellow perch <sup>f</sup>	<i>Perca flavescens</i>	SPR	Near	Broadcast/none	Benthic	Pelagic	SPR/SPR	E <sup>c,r</sup> , H <sup>c,r</sup> , M <sup>r</sup> , O <sup>c,r</sup> , S <sup>c</sup>

1 <sup>1</sup> Recreational landings are reported as “crappies”.

2 <sup>2</sup> Commercial and recreational landings are reported as “sunfish”.

3 <sup>3</sup> Commercial landings are reported as “bullheads”.

## FIGURE LEGENDS

**Fig. 1.** Frequency of peer-reviewed publications during 5-year periods from 1965–2008 for **a)** reef fish recruitment studies involving early life stages (ELS; bar portions with white shading and stippling; N = 84 citations), **b)** reef fish recruitment studies exploring linkages between physical processes and ELS (bar portions with stippling; N = 45 citations), **c)** non-reef marine recruitment studies focusing on linkages between physical processes and ELS (gray bar portions; N = 105 citations), and **d)** Laurentian Great Lakes recruitment investigations exploring linkages between physical processes and ELS (black bar portions; N = 7 citations). See Appendix A for literature search criteria.

**Fig. 2.** Conceptual diagram of physical processes and the mechanisms by which they can potentially influence fish recruitment. The thickness of arrows connecting mechanisms of physical control to the various life stages is proportional to their hypothesized importance to survival during that life stage (see text, *Mechanisms of Physical Processes and Their Importance*, for rationale). The impact of indirect mechanisms is highly dependent on population and community structure, which in turn are influenced by prior recruitment events.

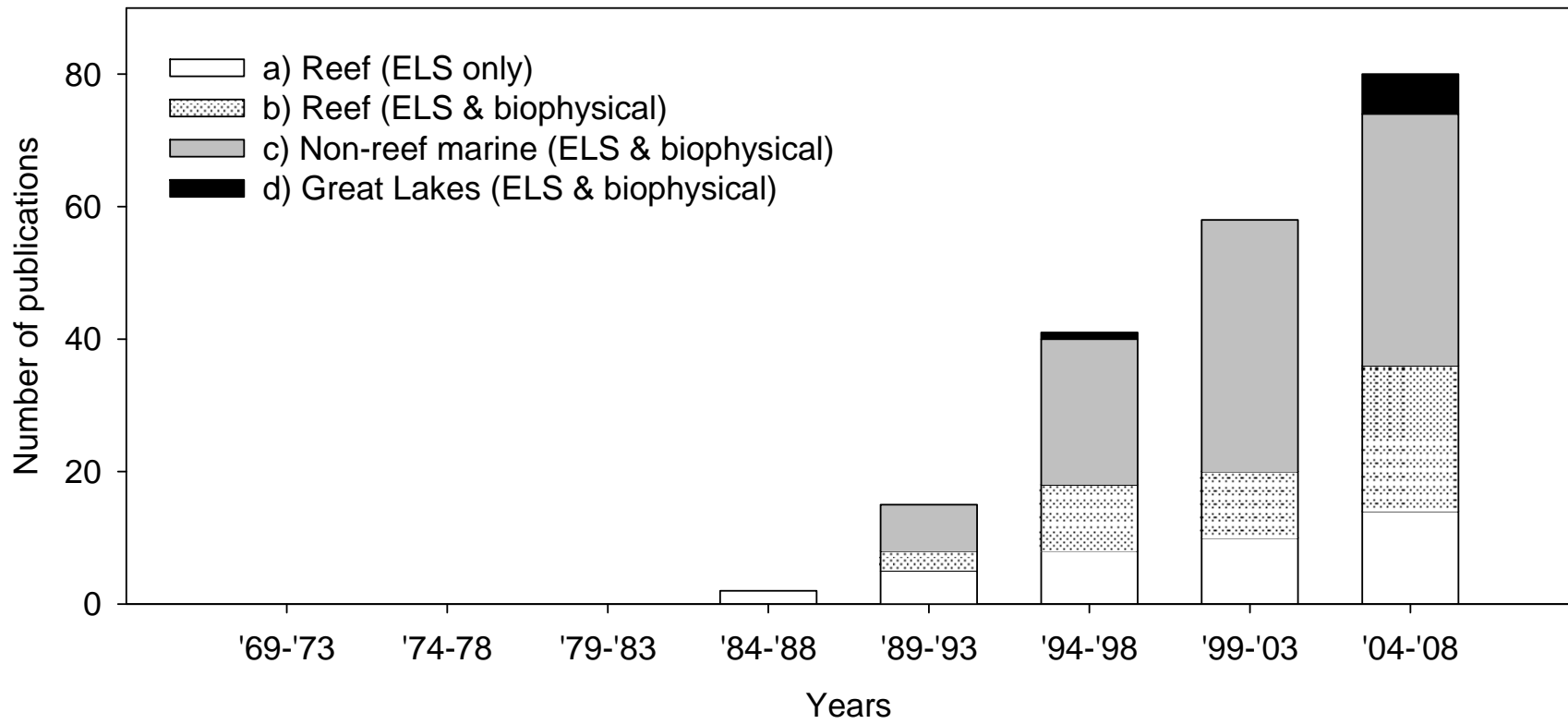


Fig. 1.

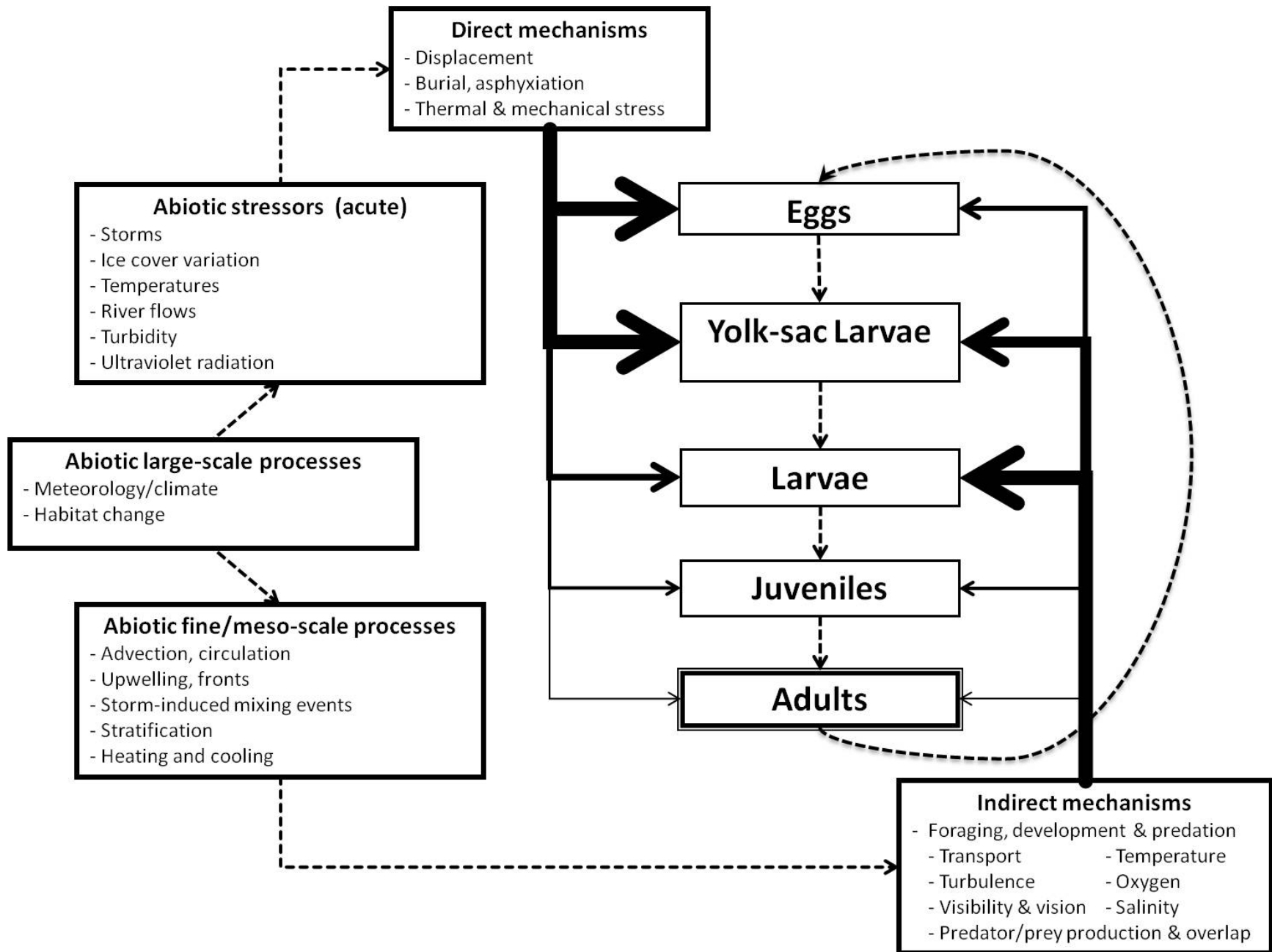


Fig. 2

## APPENDICES

### **Appendix A.** Literature searches used to generate Fig. 1 with bullets a), b), c), and d)

corresponding to respective panels in Fig. 1. The relevance of all references found in searches was verified. Searches were conducted in ISI's Web of Knowledge, using the following criteria: **a)** topic subject (TS) present in title, abstract, or listed keywords = reef, recruitment, fish\*, and [egg\* or larv\*], excluding citations with the word [conch\* or lobster\* or crab or shrimp or zoo\* or hydr\* or shell\*]; **b)** search results from a) but also with TS = dispers\* or advect\* or biophysic\* or biological-physical or current\* or circulation or transport; **c)** TS = reef, recruitment, fish\*, [egg\* or larv\*], [ocean\* or coast\* or coastal marine or shelf or estuar\* or bay or mangrov\* or seagrass\*], and [dispers\* or advect\* or biophysic\* or biological-physical or current\* or circulation or transport], excluding citations from **a)**; and **d)** TS = ["Great Lakes" or "Lake Erie" or "Lake Superior" or "Lake Huron" or "Lake Michigan"], recruitment, fish\*, [egg\* or larv\*], and [dispers\* or advect\* or biophysic\* or biological-physical or current\* or circulation or transport], excluding citations from **a)**, **b)** or **c)**. Additional settings for all searches were: Language = English and Document Type = Article.

1           **Appendix B.** List of research topics and questions relevant to both Great Lakes  
2           and marine ecosystems, which could advance our understanding of the  
3           importance of physical processes to fish recruitment.

4  
5   •   **Improve knowledge of physical and physically-driven features, to which species may**  
6   **have adapted their life histories to maintain sub-population (or even population)**  
7   **fidelity:**

- 8           ○ *What are the physical processes (e.g., upwelling, ice cover) and features (e.g.,*  
9           *currents, gyres, plumes) that show significant predictability on time scales of a*  
10          *year or less and to which fish have adapted their life history?*
- 11          ○ *What are the extent and scale of variability in these (and other) features of*  
12          *relevance, and how do they affect recruitment success?*
- 13          ○ *To what extent does variability in these features on annual or shorter time scales*  
14          *affect early life-history stages and recruitment? What are the dominant scales of*  
15          *effect, and can such effects be generalized to explain similarities and differences*  
16          *between populations within and among ecosystems?*

17   •   **Identify the role of behavior in movement patterns of fishes relative to physically-**  
18   **driven patterns in the environment:**

- 19          ○ *At what size or during which ELS do individuals have the ability to move at will,*  
20          *and how do climate- or biologically-driven delays in development influence future*  
21          *recruitment success?*

- 1           ○ *What capacity do individuals have to respond to physically-driven patchiness of*  
2            *resources (e.g., zooplankton patches associated with Langmuir cells; temperature*  
3            *variation associated with tributary plumes) during ELS?*
- 4           ○ *How do individuals use currents to move and find suitable habitats during ELS,*  
5            *and how much does their ability vary with attributes of the individual (e.g., size,*  
6            *age, condition)?*
- 7    •    **Assess life-history characteristics of fishes to test for evidence of adaptation to**  
8    **exploit/tolerate physical processes, and identify fish stocks likely to be more heavily**  
9    **influenced by physical effects during ELS:**
- 10           ○ *How have fishes (or subpopulations) adapted their life histories to exploit*  
11            *predictable physical features?*
- 12           ○ *Can we generalize about susceptibility of populations or sub-populations to*  
13            *different kinds of physical influence, based on characteristics life-history*  
14            *attributes of the population (or sub-population)?*
- 15           ○ *What is the extent to which ELS can accommodate variability in physical*  
16            *processes (e.g., through migration, altered development rates, phenotypic*  
17            *plasticity, or other responses)?*
- 18    •    **Determine the role of physical processes in explaining population richness (Sinclair**  
19    **1988) or stock structure within a species:**
- 20           ○ *Do relationships exist between numbers of local spawning stocks (sub-*  
21            *populations) and numbers/diversity of hydrodynamic, oceanographic, and*  
22            *tributary features in an ecosystem?*
- 23           ○ *What is the strength of fidelity between local spawning stocks and such features?*

1           ○ *Do subpopulations compensate for one another during periods when a typically*  
2           *predictable physical process fails to emerge in a given year?*

3   • **Quantify the importance of direct and indirect effects of physical processes on fish**  
4   **recruitment:**

5           ○ *How is recruitment regulated by direct mortality from physical stressors (e.g.,*  
6           *temperature variations outside optimal range, mortality due to storm events)*  
7           *versus indirect effects mediated through biological interactions (e.g., match-*  
8           *mismatch between first feeding larvae and zooplankton)?*

9           ○ *How does the relative importance of direct versus indirect mortality on the*  
10          *recruitment process vary with climatic regime or across a gradient in ecosystem*  
11          *productivity?*

12          ○ *How can synergies or interactions with anthropogenic factors (e.g., climate*  
13          *change, invasive species) or other organisms (through food-web interactions)*  
14          *modulate the effects of physical processes on fish recruitment?*

15

16