Reproduction of walleye in Lake Erie: allocation of energy


Abstract: An energetics mechanism is proposed to explain the trade-off between current and future reproduction. Surplus energy can be used for reproductive tissue (current reproduction) or somatic tissue (needed for future reproduction); therefore, we needed to determine first, when does growth of somatic and reproductive tissues occur, and second, how and when is energy allocated to reproduction. Walleye were sampled monthly from the commercial fishery in Lake Erie. Morphological attributes were recorded from these walleye, as well as the lipid composition of a smaller subsample. Energy for reproduction is acquired in the winter, spring, and summer before spawning and stored as visceral lipids. Ovarian lipids are largely derived from visceral fat deposits; thus, females appear to be capital breeders. Females elaborate gonadal tissue only if there is sufficient visceral fat. The circannual endocrine switch to reproduction may occur in midsummer (August) and in October. Females may discontinue ovarian development during the early winter if there is insufficient surplus energy (visceral fat). Year-class variations may be partly explained by the energy condition of the females and the proportion of the stock able to spawn successfully each year.

Résumé : Nous proposons un mécanisme énergétique pour expliquer le compromis entre la reproduction actuelle et future. Le surplus d’énergie peut servir à constituer du tissu reproducteur (reproduction actuelle) ou du tissu somatique (nécessaire pour la reproduction future); nous devions donc déterminer premièrement quand se produit la croissance des tissus somatiques et reproducteurs et, deuxièmement, comment et quand l’énergie est affectée à la reproduction. Nous avons prélevé chaque mois des échantillons dans les captures commerciales de dorés du lac Érié. Nous avons consigné les caractéristiques morphologiques de ces poissons, ainsi que la composition lipidique d’un sous-échantillon plus petit. L’énergie destinée à la reproduction est acquise pendant l’hiver, le printemps et l’été, avant la frayée, et est stockée sous forme de lipides viscéraux. Les lipides ovariens proviennent en bonne partie des dépôts de graisse viscérale; les femelles semblent donc jouer un rôle crucial dans la reproduction. Elles élaborent du tissu gonadique seulement si la quantité de graisse viscérale est suffisante. Le tournant endocrinien circannuel vers la reproduction peut se produire au milieu de l’été (août) et en octobre. Les femelles peuvent interrompre leur développement ovarien pendant le début de l’hiver si l’énergie excédentaire est insuffisante (graisse viscérale). Les variations des classes d’âge peuvent s’expliquer en partie par la condition énergétique des femelles et par la proportion du stock qui est capable de se reproduire avec succès chaque année. [Traduit par la Rédaction]

Introduction

Walleye (Stizostedion vitreum) abundance in Lake Erie decreased markedly in the late 1950s, primarily because of a largely inexplicable and progressive deterioration in recruitment starting in the mid-1940s (Parsons 1967, 1970). The effects of water and habitat contamination, exacerbated by exploitation, were associated with the decline, but the mechanism was not clear (Parsons 1970). Blue walleye (Stizostedion vitreum glaucum) did not recover in the eastern portion of Lake Erie, but the yellow walleye (Stizostedion vitreum vitreum) did recover in western and central Lake Erie in the 1980s (Hatch et al. 1990), largely as a result of a few strong year-classes in 1977, 1982, 1986, and 1991 (Henderson and Wong 1991). Annual recruitment varied considerably and yields have been dependent upon the appearance of good year-classes every 3–5 years. Recruitment was shown to be affected by wind, water temperatures, and spawning stock (Busch et al. 1975; Shuter and Koonce 1977), but generally was highly unpredictable. Henderson and Nepsy (1994) suggested that year-class strength may also be associated with the energy condition of the mature females. At present the fishery is managed for optimal yield consistent with an assumed natural mortality rate, without any explicit consideration given to the reproductive potential of the stock. In this study our aim was to develop a model of a mechanism that could explain variations in reproductive effort in terms of the costs of reproduction, constrained by the energy needed to mature and continue to spawn annually. Thus, we were trying to provide another explanation for annual variations in recruitment.

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Life history theory tries to explain why and how an optimal level of reproductive effort is achieved (van Noordwijk and de Jong 1986). The optimal value is constrained mostly by the costs of reproducing; as a consequence there is a trade-off between current reproduction versus survival and future reproduction (Sterns 1992). Life history theory is principally concerned with trade-offs determining optimal fitness on physiological, microevolutionary, or macroevolutionary scales (Sterns 1992). The implication from Henderson and Nepszy (1994) was that some walleye failed to reproduce in the current year because there was a trade-off between current and future reproduction. Residual reproductive value is reduced if elevated mortality is the consequence of spawning. Here we recognize two major constraints on the realization of reproductive value. The first constraint consists of the physiological and anatomical traits that have evolved in response to historical selective pressures; evolutionary trade-offs have resulted in a genetically determined life history tactic that can be considered a constraint in itself. The second constraint is the amount of surplus energy available to realize reproductive value within the context of these previously selected physiological and anatomical traits. The energy demands of spawning and the ability to recover energy deficits could affect both mortality and the ability to spawn in consecutive years. Thus, recruitment may be partly dependent upon the proportion of the spawning stock that can effectively mature each year as a consequence of the energy acquired before spawning, including the recovery of energy from previous spawning (Henderson and Nepszy 1994). In effect we are trying to understand the physiological and energetic mechanism for the microevolutionary trade-off between current and future reproduction, and the plasticity of this tactic to annual variations in availability of energy. Thus, how are variations in recruitment a function of both past evolutionary pressures and present environmental conditions? Our approach was to develop a conceptual model of the circannual acquisition and allocation of energy for growth and reproduction as has been done for a few other species (Craig 1977; Diana and MacKay 1979; Hayes and Taylor 1994). We have focussed on the role of lipid dynamics as the mechanism regulating reproductive development (Frisch 1988) and the anatomical attributes that reflect circannual patterns of lipid composition and allocation, such as somatic lipids, liver, visceral fat stores, and reproductive tissue.

The first hypothesis is that (i) reproduction by females is constrained by the acquisition of energy prior to the elaboration of gonadal tissue and (ii) energy is diverted to reproduction from stored energy (capital breeders), rather than being derived from feeding (income breeders) during ovarian development (cf. Sibly and Calow 1986). In particular, we hypothesized that the energy used to elaborate ovarian tissue was derived from visceral fat stores. When is this surplus energy acquired and when is it transferred to reproductive tissues? We have investigated these hypotheses and questions by describing the allocation of lipids throughout the year as the walleye grew and sexually matured. Thus, we have been able to document when energy was acquired and how energy was allocated to reproduction.

**Methods**

### General comments

An important assumption of this study was that we were able to obtain an unbiased sample of the population for any particular age-class; biased sampling was reduced in part by our length-stratified subsampling of the catch. All of our subsamples were obtained by commercial gill nets with a stretched mesh of about 102 mm, with equal numbers of males and females selected from 8 size-classes in 5-cm intervals from 30 to 65 cm fork length. Thus, the size composition of our subsample did not change throughout the year. Furthermore, we showed that the proportion of lipids in walleye is independent of body size, so that changes in circannual variations in lipid composition do not appear to be influenced by the selectivity of gill nets. We also assume that lipid and energy dynamics are, for the most part, comparable during the normal course of events (Love 1960, 1970; Damberg 1964; Reshetnikov et al. 1970; Newsome and Leduc 1975; Campbell and Love 1978) except during starvation when protein catabolism can become increasingly important as a source of energy (Love 1960; Cunningham and Shuter 1986).

### Sampling design and attributes

Morphological and anatomical attributes and, most importantly, lipid composition of walleye were assessed monthly from June 1992 to May 1993. From these data we derived most of the important life history traits of growth pattern, size and age at maturity, and age- and size-specific reproductive invest-ments; this permitted us to comment on the trade-offs between current reproduction and both survival and future reproduction. Walleye (100 of each sex) were sampled from Lake Erie (42°15′N, 81°15′W) commercial gill-net catches at the beginning of each month; 3 or 4 of each sex were then subsampled from each 50-mm fork-length class from 300 to 700 mm for detailed measurements of organ weight, visceral fat, and lipid composition (Table 1). In October, the walleye sample was derived from catches in experimental gill nets (Henderson and Wong 1991). The distribution of samples corresponded to the annual geographical distribution of walleye; for the most part, walleye migrate from the western basin after spawning to the central basin for the summer, and then move back to the

| Table 1. Date, location, sample size, and sampling gear for subsample of walleye from commercial walleye catch in Lake Erie (June 1992 – May 1993). |
|---|---|---|---|
| Month | Number | Basin | Gear |
| January | 45 | Western | Commercial |
| February | 50 | Western | Commercial |
| March | 39 | Western | Commercial |
| April | 49 | Western | Commercial |
| May | 47 | Western | Commercial |
| June | 45 | Western | Commercial |
| July | 61 | West-central | Commercial |
| August | 44 | Central | Commercial |
| September | 43 | West-central | Commercial |
| October | 36 | Western | Experimental |
| November | 122 | Western | Commercial |
| December | 54 | Western | Commercial |
western basin during the early autumn (B.A. Henderson and J.L. Wong, unpublished data).

From all of the sampled walleye, attributes were measured to estimate life history traits: fork length (mm), round weight (g), age from scale impressions on acetate slides, sex, maturity, gonadal development, gonad weight (g), and liver weight (g). From the subsample (Table 1), fecundity and lipid composition were assessed. Fecundity was estimated by counting the number of eggs in 1-g subsamples removed from the ovary.

**Lipid extraction**

The method of lipid extraction (methanol–chloroform) was modified from the methods of Bligh and Dyer (1959). The entire carcass, without stomach contents, was homogenized, except when the gonads were analyzed separately. From a wet subsample (100 g) of the homogenate, the dry weight proportion was estimated by drying the sample at 105°C for 24 h. Approximately 2 g of dried homogenate (total carcass, somatic tissue, or gonadal tissue) was transferred to a 125-mL Erlenmeyer flask, to which was added 14 mL of distilled water, 40 mL of methanol, and 20 mL of chloroform. This mixture was homogenized for 3 min in a tissue homogenizer before it was vacuum filtered through a Buchner funnel with Whatman No. 1 filter paper; a small amount of Whatman filter-aid was added to facilitate the removal of the largest particles. The washes from the tissue homogenizer (20 mL of chloroform) and the original Erlenmeyer flask (homogenate, water, chloroform, and methanol) were also filtered. The clear filtrate was then transferred to a 100-mL graduated cylinder containing 25 mL of distilled water; this mixture was allowed to stand for 5 h before the volume of the lower chloroform–lipid layer was recorded both before (volume 1) and after (volume 2) the water–methanol layer was removed by suction. The lipid fraction was then transferred to previously weighed 50-mL beakers and air dried in a fume-hood for 12 h before being dried for 2 h at about 100°C in a drying oven. Then the lipids and beaker were weighed. The proportion of fat in the dried sample was estimated as follows:

$$\text{PDL} = \frac{\text{DFW} \cdot V_1}{\text{DSW} \cdot V_2}$$

where PDL is the proportion dry lipids, DFW is the dry fat weight, DSW is the dry sample weight, V1 is volume 1, and V2 is volume 2.

**Results**

**Seasonal changes in gonad, liver, and round weight**

The weight of males and females at age diverged near the end of the 4th year of life (46 months); females (Fig. 1A) approached an asymptotic size by about the 10th year, and males by the 8th year (Fig. 1B).

Gonadal development of mature walleye, expressed as the weight of the gonad divided by the round weight, began between August and September for both sexes (Fig. 2). Ovarian size increased until March (gonadosomatic index (GSI) = 0.16, ) and the subsequent decline in size was associated with spawning. Variability of GSI tended to increase during development; the bimodal size distribution in April (Fig. 3) was caused by early spawning. In April, fecundity was linearly related to both ovary weight (eggs = –848.138 + 411.7 ovary weight (g), df = 21, $r^2 = 0.63$) and round weight (eggs = –6 4546.2 + 96.9 round weight (g), df = 19, $r^2 = 0.70$). Testicles reached a peak size by October (GSI = 0.040) and then decreased in size to April (GSI = 0.033), before declining abruptly in size at spawning.

The hepatosomatic index (HSI), calculated as the wet weight of the liver divided by round body weight, began to increase between July and August for both sexes (Fig. 4). Female HSI peaked (0.032) in February and then decreased.
quickly between March and May; male HSI increased more slowly to a peak (0.024) by April then decreased to a value (0.011) comparable to that of females (0.012) by May; the

lowest HSI was observed in July. The liver was probably increasingly active in the elaboration of lipoproteins and other constituents deposited in the gonads. Among the females, the largest monthly increment in liver size (September–October) was coincident with the initial increase in the size of the ovary (Fig. 4).

The assessment of maturity of females was subjective; relative ovary mass and egg size were small for immature females. It is possible, but unlikely, that these immature females could have matured much later. The monthly variation in GSI and HSI for these immature females was similar to that of mature females up to October, but then the patterns diverged (Fig. 5). The GSI of immature females did not increase to the same level as that of mature females by October. In contrast, the GSI of mature females continued to increase, whereas the GSI of immature females dropped to levels seen during the summer. The HSI of immature fish also dropped, rising again to higher levels, but not rising to the levels normally recorded for mature females.

**Seasonal allocation of lipids in somatic, visceral, and gonadal tissue**

Female total lipids (wet lipids (g)/round weight (g)) remained at about 0.09 throughout the year, except for a transitory peak in August (Fig. 6). Similarly, somatic lipids were relatively constant except for a decline from January (0.048) to April (0.033). Lipids stored as visceral fat peaked briefly in August, then decreased as the total lipids in the ovary increased. Subsequently, the visceral fat deposits increased in the late winter and early spring (January–May). The ovarian lipid level increased between September and October, reaching an asymptote by February (Fig. 6). Thus, it appeared that the largest portion of the lipids in the ovaries was probably derived from the visceral fat. This interpretation is largely based on the observation that ovarian lipid levels increased as visceral fat levels declined. However, the last increase in ovarian lipid level (January–February) was not at the expense of visceral fat levels. Energy derived from feeding in the early winter may have explained the increase in both visceral fat and ovarian lipid levels from January to February.

The monthly variation in the lipid density of immature
females (Fig. 7) was strikingly different from that of mature females. In the early autumn (October), the lipid density in the visceral tissue did not differ much from that of mature females, but the lipid density in the somatic tissues was much lower (immature, 0.024; mature, 0.038). Somatic lipid density increased slightly over the winter, but the visceral lipid density in immature females increased markedly to higher levels than that in mature females by March (immature, 0.075; mature, 0.035).

Male total lipids (wet lipids (g)/round weight (g)) were marginally lower and more variable than female lipid levels (Fig. 8). Males also showed a transitory peak in August (0.102). Total lipids declined (0.073) by September and then recovered between December and January (0.89), followed by a progressive decline in lipid levels until March (0.070). Most of the last decline in total lipids was explained by a loss of somatic lipids, except for a drop in visceral fats from April to May (Fig. 8). Thus, the males started spawning with more available energy (wet visceral fat + wet somatic lipids = 0.080; lipids (g)/round weight (g)) than females (0.070) and finished spawning with less total energy (males, 0.070; females, 0.085). Females may have resorbed some energy from ovarian tissue after spawning.

More than 60% of total lipids for both males and females was stored as visceral fat (Fig. 9; total lipids (g) = 1.631 visceral fat (g) + 27.03, df = 451, $r^2 = 0.64$). More of the variation in total lipids (TL) was explained by visceral fat levels (VF) for males (TL = 1.467 VF + 22.83, df = 185, $r^2 = 0.82$) than females (TL = 1.583 VF + 39.81, df = 264, $r^2 = 0.55$), because there was more variation in visceral fat level amongst females during the year. For walleye greater than 1100 g in weight, the proportion of lipids was not correlated with the size of the walleye (Fig. 10).

**Discussion**

The Panglossian paradigm is that life history traits are optimally adapted to the environment, consistent with the best possible lifetime reproductive value (Gould and Lewontin 1979). This paradigm fails to recognize that selection does not account for all morphological and physiological characteristics that may arise from genetic drift and allometry. Despite these drawbacks, life history theory still provides a
framework for a coordinated interpretation of many of the attributes of populations (mortality, recruitment) and individuals (growth, maturation, fecundity). In this study we have used the conceptual framework of life history theory (Sterns 1992; Roff 1992) to develop hypotheses about the physiological and environmental constraints affecting reproductive values of walleye. Ultimately, we believe that an understanding of the evolutionary and environmental constraints on reproductive value will help with the management of walleye populations in diverse environments. Here we are concerned only with walleye in Lake Erie (a productive and diverse fish community), but we anticipate that the results will provide some insight into the reaction norms of walleye found in less productive and diverse fish communities in the cooler, northern parts of Ontario.

First, are walleye capital or income spawners? More specifically, is reproduction by female walleye constrained by their ability to acquire sufficient energy for the elaboration of the ovary, before gonadal development begins in the early autumn? Second, if walleye are capital breeders, is there a time when the endocrine system either switches to normal gonadal development or alternatively switches to gonadal resorption if there is insufficient energy for vitellogenesis? Capital and income spawners may represent the ends of a continuum; species may compensate for inadequate capital (lipid deposits) with income derived from feeding.

Energy density of visceral fat varied most among mature females during the year. Visceral fat may constitute the bulk of surplus energy that is allocated for reproductive effort (Leon 1976; Schaffer 1974). Female walleye appear to be more capital than income spawners. Visceral fat levels fell from August to January and thereafter increased. The fall in visceral fat levels was associated with most of the increase in ovarian size and ovarian energy density. In contrast, the male visceral fat level was generally lower and relatively constant for most of the year. Ovarian development was initiated after a surplus energy store was replenished. Since visceral fat levels fell as ovarian lipid level increased, visceral fat deposits were probably the main source of lipids deposited in the ovary. Thus, surplus energy was acquired from January to August, and then allocated to ovarian development from August to January.

Is there a circannual endocrine switch from reproductive dormancy to active gonadal development, which is triggered by the energetic status of the female? The test of this hypothesis was weakened by our methodology because we were not monitoring the energy condition and gonadal development of individual females. Hence, we could not determine if females with low energy reserves stopped elaborating gonadal tissue at some stage of development after the summer accrual of stored energy; rather, we were sampling the energetics and reproductive status of the population. However, only females with sufficient surplus energy continued with gonadal maturation as suggested by Henderson and Nepszy (1994). In this study, immature females had lower visceral fat stores in the early summer when gonadal development began. However, there was a smaller, transient increase in the size of the ovaries of these immature females until October, after which the ovarian weight declined to a dormant size. The liver increased to similar sizes in both immature and mature females until October (Figs. 4, 5), then the liver size of the immature females declined. Assuming that the liver is the conduit for the transfer of lipids from the visceral deposits to the ovary (White et al. 1968), this variation in liver size was probably related to the allocation of lipids to the ovary. Although liver size was correlated with gonadal size, it was not necessarily correlated with lipid mobilization rates. During March and April when HSI was maximal, there was no evidence of lipid mobilization. Perhaps the continued increase in liver size was related to other high-energy costs of reproduction. Thus, our data point to two separate times when an endocrine switch could operate: first, after the surplus energy store (visceral fat) is replenished by August, and second, in October when even immature females exhibited a transient development of ovarian tissue.

Visceral lipid deposits seemed to be the most important source of lipids destined for the ovaries. We propose that there is some physiological mechanism (Frisch 1988) for assessing the availability of lipid energy, and if the visceral lipid deposit was below some level, then gonadal development ceased. In fact, the level of visceral fat found in females during the early autumn may be a useful indicator of condition and spawning potential. Possibly, this mechanism could operate at a later stage of ovarian development if the visceral lipid deposits were depleted by the early winter. We were monitoring the development of the population and not individuals, but some of the lower values of GSI observed during the early winter could be explained by the individual reduction of ovarian size as energy was absorbed for other metabolic needs. The pause in the elaboration of ovarian lipids seen from December to January may be a reflection of a period when the reduction in visceral lipids resulted in a temporary cessation of ovarian growth; ovarian lipid levels increased again only as the visceral lipid deposit increased. The increase in visceral fat stores may vary depending on the availability of prey during the winter; both water temperatures and prey density and distribution would affect prey availability. Thus, although the walleye was primarily a capital spawner, income from feeding could provide energy for gonadal development at later stages.

Of what value is the description of the life history strategy of female walleye to a fisheries manager? The conservation of minimum viable stocks of walleye when faced with exploitation or habitat alteration requires information about the risks of extinction of small populations and the characteristics of the spawning populations. For the most part, effective spawning populations may be smaller and more variable than expected, if female maturation is delayed or intermittent, depending on the energetics status of the females. Thus, the apparent residual reproductive value may be overestimated because we underestimate the cost of spawning. This may partly explain the poor relationship between spawning stock size and recruitment (Shuter and Koonce 1977). As suggested by Henderson and Nepszy (1994), recruitment variations may be associated with the energetic condition of the stock. If a harvest was taken from a spawning population that was a fraction of the estimated one, then the acceptable fishing mortality could be too high. Furthermore, the reproductive value of the mature females would be much reduced if fishing mortality were to be maintained at a level based on an incorrect assumption that the population spawns annually after first maturation. The evolved life history strategy depends on the assumption that longevity (as a function of mortality) is increased as spawning frequency declines; senescence may constrain the effectiveness of this strategy by setting an upper limit to the potential number of
spawning episodes. The risks of extinction are then greater for stocks with small spawning populations with lower probabilities of multiple spawning episodes.

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