Chapter 19
The Ecology of Lifetime Growth in Percid Fishes

Michael D. Rennie and Paul A. Venturelli

Abstract The factors responsible for the lifetime growth patterns of percids in natural populations can provide meaningful insights for culture operations. Here, we present a summary of a number of well-studied factors and review the current state of knowledge. We illustrate an informative approach to describe lifetime growth of percid species by applying a biphasic growth model to European perch and pikeperch populations, and discuss life-history constraints considering biphasic growth. An evaluation of proposed hypotheses for proximate mechanisms of female-biased sexual size dimorphism in percids is presented, indicating that reduced feeding in males is the most parsimonious explanation given the current evidence. Growth rates in percids are strongly temperature-dependent, and show strong evidence of countergradient growth. Percids also show significant density-dependent growth, demonstrating twofold variation in individual growth rates. Predation, food availability and prey particle size can also affect the efficiency of percid growth. Parasitism and disease in percids are not as well studied as other factors reviewed here within an ecological context, but the reported effects on percid growth vary from negative to neutral to positive. Our review of drivers of natural variation in percid growth will assist culture operators with regards to broodstock selection, husbandry and maintenance of cultured percids.

Keywords Percids • Growth • Broodstock selection • Sex dimorphism • Husbandry

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19.1 Introduction

As the culture of percid fishes becomes more common in both North America and Europe, it is important to keep in mind the evolutionary and environmental forces that have shaped the life histories of these fishes in the wild. Fish life histories are intimately related to individual growth rates, which are typically targeted for maximization by the culture industry. The life histories of many cultured strains of fish demonstrate incredible variability in the wild, providing the raw materials for artificial selection of desirable traits under culture conditions. For example, percids exhibit up to 3.5-fold variation in growth rate (using fork length at age 2 as a proxy for growth rate) and up to fourfold variation in asymptotic length (Table 19.1).

In this chapter, we review some of the driving forces behind this tremendous variability in growth and size. The net balance of these drivers and constraints allows for the optimization of growth within a given set of circumstances or any particular environment. Where wild populations optimize their growth given a particular set of conditions, the economics of fish culture rely on the maximization of individual growth rates to ensure the greatest rate of return on operations. Understanding the role of environment and life history in this optimization process in wild populations may assist managers in achieving their goals for cultured stocks.

We begin our review by describing how the biphasic von-Bertalanffy growth model improves our understanding of lifetime growth patterns (Sect. 19.2). Using this model as a backdrop, we then explore the primary intrinsic (Sect. 19.3) and extrinsic (Sect. 19.4) factors driving or constraining percid growth. Intrinsic factors include life history constraints or 'invariants' (Sect. 19.3.1), and sexually dimorphic growth (Sect. 19.3.2). Extrinsic factors include temperature (Sect. 19.4.1), predation (Sect. 19.4.2), density dependence (Sect. 19.4.3), resource availability and type (Sect. 19.4.4), and parasitism and disease (Sect. 19.4.5). This review focuses primarily on those species that are most familiar to the authors (walleye, *Sander vitreus*, and yellow perch, *Perca flavescens*), but also draws on relevant literature from other large, well-studied percids.

19.2 The Biphasic Growth Model

In this chapter, we introduce the biphasic growth model (BGM) as a general framework for describing and interpreting the lifetime growth pattern of percids. Lester et al. (2004) proposed the BGM as an alternative to the von Bertalanffy model (von Bertalanffy 1934, 1938), which is ubiquitous in the fish literature and routinely applied to percid species (e.g., Quist et al. 2003; Sass et al. 2004; Heibo et al. 2005; Jackson et al. 2008; Perez-Bote and Roso 2012). Although the von Bertalanffy model is based on bioenergetic principles (but see Roff 1980 and references therein, Lipinski and Roeleveld 1990) and tends to provide a good fit to lifetime growth (but see Katsanevakis and Maravelias 2008), it is criticized for failing to describe the

Table 19.1 Published range of observed asymptotic length (L_∞) and fork length at age 2 (FL_2) for common percid species. Only those species with a reasonable number of growth curves/populations listed (N) are included. Sex indicates the gender for which lengths apply to; either females or mixed (sexes not separated)

		Walleye (*Sander vitreus*)	Pikeperch (*Sander lucioperca*)[b]	Eurasian Perch (*Perca fluvatilis*)	Yellow perch (*Perca flavescens*)[c]	Ruffe (*Gymnocephalus cernua*)[b]
L_∞[a]		518–992	400–1413	200–700	173–318	125–353
	N	435	22	68	56	16
	Source; sex	Purchase et al. (2006); females	Fishbase.org (Froese and Pauly 2013); mixed	Heibo et al. (2005); females	Purchase et al. (2005a); females	Fishbase.org (Froese and Pauly 2013); mixed
TL_2		134–373	112–394[d]	75–215	77–169	52–159
	N	198	20	68	70	16
	Source; sex	Venturelli et al. (2010); Females	Fishbase.org (Froese and Pauly 2013); mixed	Heibo et al. (2005); females	Purchase et al. (2005a); females	Ogle (1998); mixed

[a] L_∞ (expressed as mm fork length) from the standard von Bertalanffy formula (Eq. 19.2 in text) applied to length-at-age data, to make comparisons across species and studies equivalent

[b] Lengths converted to total lengths using formulae listed for each species at www.fishbase.org (Froese and Pauly 2013). Populations for which length units were not reported or could not be standardized to *TL* were excluded from range estimates

[c] Fork lengths converted to total lengths using factor of 1.044 (Schneider 2004)

[d] TL_2 estimated from published von Bertalanffy parameters. Two outlier estimates of TL2 from a Turkish lake were removed

change in growth that occurs when a juvenile fish that is investing solely in somatic growth becomes mature and thereafter invests in both somatic growth and reproduction (Nikolskii 1969; Ricker 1975; Charnov 1993; Day and Taylor 1997; Charnov et al. 2001; Lester et al. 2004).

Unlike the von Bertalanffy growth model, the BGM explicitly accounts for the change in growth rate that occurs when a fish matures. The BGM comprises two separate length functions; a linear function that describes immature growth in length in the lead-up to maturity and an asymptotic function that describes adult growth in length thereafter (Lester et al. 2004). The qualifying phrase "in the lead-up to maturity" is important because it recognizes that growth rate over the entire immature life phase is unlikely to be constant. For example, immature percids can exhibit non-linear growth as a result of ontogeny and changes in diet or behavior (Moodie et al. 1989; Buijse and Houthuijzen 1992; Diehl and Eklov 1995; Hoxmeier et al. 2004).

In the BGM, immature length at age (L_t) growth is given by the linear function

$$L_t = h\left(t - t1\right), \tag{19.1}$$

where h is immature growth rate (e.g., mm/year), t is age, and t_1 – the hypothetical age at which immature length is zero – is a parameter that allows for a change in immature growth rate in the lead-up to maturity (Lester et al. 2004; Shuter et al. 2005). See Quince et al. (2008a, b) for a BGM that relaxes the assumption that immature growth is linear. Adult growth in the BGM is then described by the conventional form of the von Bertalanffy function

$$L_t = L_\infty\left(1 - \mathrm{e}\left(-K\left(t - t_0\right)\right)\right), \tag{19.2}$$

where L_∞ is asymptotic length, K is the rate of deceleration of growth, and t_0 is the hypothetical age at which adult length is zero. Lester et al. (2004) showed that the von Bertalanffy parameters can be approximated by

$$L_\infty = 3h / g, \tag{19.3}$$

$$K = \ln\left(1 + g/3\right), \text{ and} \tag{19.4}$$

$$t_0 = T + \ln\left(1 - \mathrm{g}\left(T - t_1\right)/3\right) / \ln\left(1 + g/3\right), \tag{19.5}$$

where g is annual investment in reproduction expressed as a proportion of somatic mass (a close proxy for the gonadosomatic index in female percids, Shuter et al. 2005), and T is the age at which investment in reproduction begins.

The BGM is a valuable tool because it describes growth in a way that allows for inferences about important life history traits and their constraints. For example, fitting a BGM allows one to predict length at the onset of maturity (L), investment in reproduction, and mortality rate after the first year of life (Lester et al. 2004). These inferences are simply impossible with other growth models. To date, the BGM has been used to describe the life history of two percids: walleye and yellow perch (Lester et al. 2004; Shuter et al. 2005; Quince et al. 2008a, b; Rennie et al. 2008). We applied the BGM to published data from two European percids (pikeperch, *Sander lucioperca*, and European perch, *Perca fluviatilis*) (Fig. 19.1). The model accurately describes the change in growth rate that occurs with maturity, and provides an estimate of *L*, *g* and age-1+ mortality rate for these populations. We encourage further application of the BGM to European percids, which can provide exciting new insights into growth and related life history traits.

The BGM can be fit to both males and females from a given population, but we caution that the interpretation of *g* for male fishes remains ambiguous. In female fish, *g* corresponds well to another index of reproductive investment, the gonadosomatic index (Shuter et al. 2005). However, the interpretation of *g* for male fish has not yet been mechanistically explored. Generally, when the BGM is applied separately males and females from the same population, male *g* is somewhat higher than female *g* (Rennie et al. 2008). This pattern is unexpected because male gonads are relatively small and there is little to suggest that males experience higher activity costs during

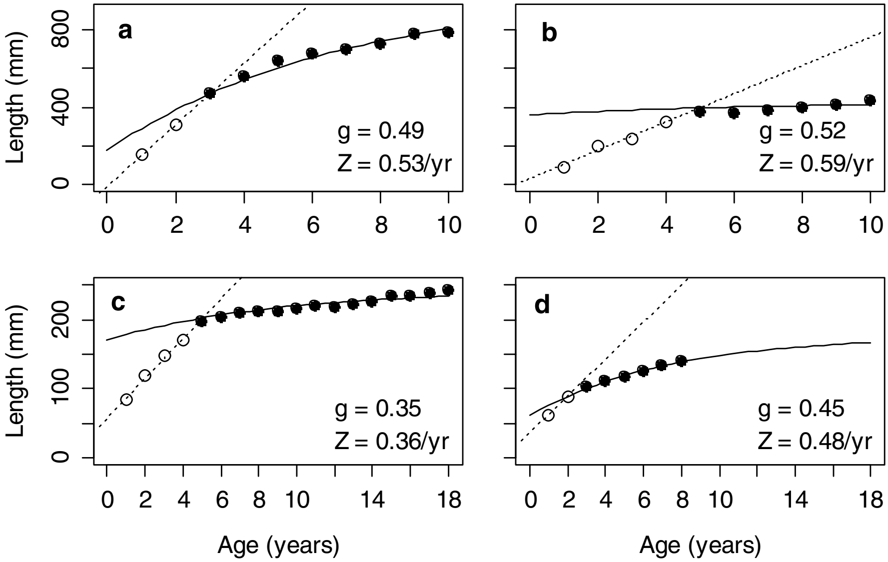


Fig. 19.1 Lifetime growth patterns of female pikeperch in (**a**) the Szczecin Lagoon, Germany/Poland (Neuhaus 1934, cited in Lehtonen et al. 1996; Lappalainen et al. 2003) and (**b**) Taivassalo Bay, Finland (Lehtonen 1987, cited in Lehtonen et al. 1996; Lappalainen et al. 2003), and female European perch in (**c**) Lake Windermere, UK (Craig 1980) and (**d**) Lake Horkkajarvi, Finland (Rask 1983). *Open* and *closed circles* are observed immature and mature length-at-age data, respectively, and *broken* and *solid lines* are predicted immature and mature growth trajectories, respectively, according to the biphasic model. *g* is investment in reproduction (expressed as a proportion of somatic mass) as predicted from the von Bertalanffy parameter *K* (Eq. 3.3 in Lester et al. 2004) and *Z* is the mean total mortality rate of age-1+ females as predicted from *g* (Eq. 4.6 in Lester et al. 2004)

reproduction (Sect. 19.3.2). Rather, higher g for males is likely due to lower growth efficiency in males and potential metabolic differences between genders (see Sect. 19.3.2). Gender-specific metabolic costs and/or inefficiencies are not reflected in the derivation of the BGM from first principles (Lester et al. 2004). Specifically, the mass scaling exponents around energy acquisition and losses (m_1 and m_2 in Lester et al. 2004, their Eq. 2.1) may differ between genders. Similar arguments have been made regarding a need for sex-specific parameterization of bioenergetic growth models (Rennie et al. 2008). More research is required to better understand g estimates from BGM as applied to male fish. Regardless, given the level of information and additional insight that can be yielded with the BGM versus traditional approaches, we strongly advocate using the BGM to describe the lifetime growth of female percids.

19.3 Intrinsic Factors Affecting Growth

19.3.1 Optimization of Growth Rates in Natural Environments and Life History Invariants

The fish culture industry seeks to bring fish to a marketable size in the most economically efficient manner. In contrast, individual growth in natural populations is optimized to a range of environmental and ecological conditions. This optimization is part of a general strategy to maximize fitness (i.e., maximize lifetime reproductive output while minimizing mortality risk) within a given set of environmental and biological constraints. These intrinsic and extrinsic forces lead to the large variation in observed growth rates both within and among wild percid populations (Table 19.1), and also explain why individuals from different populations can exhibit different growth rates in controlled environments (e.g., aquaculture).

There is a wealth of literature describing how certain life history parameters – growth among them – trade off with other life history traits in a predictable fashion. In the classic literature, the major tradeoffs that are described exist between (1) mortality rate (Z) and age at first reproduction (T_m), (2) growth rate (K) and mortality (Z) and (3) length at maturity (L_m) and asymptotic size (L_∞; Beverton and Holt 1959; Charnov 1993; Jensen 1981). The mechanism behind these relationships result from a fundamental tradeoff between survival and fecundity (Jensen 1996).

These relationships listed above form the basis for what are termed the Beverton-Holt life history invariants (Charnov 1993); that is, constants that describe the relationship between life history variables. These invariants are

$$C_1 = ZT_m, \tag{19.6}$$

$$C_2 = Z / K, \text{ and} \tag{19.7}$$

$$C_3 = L_m / L_\infty. \tag{19.8}$$

According to biphasic growth theory, C_1 can be shown analytically (Lester et al. 2014), and C_2 and C_3 reflect trade-offs associated with investment in reproduction and immature growth rate, respectively (Lester et al. 2004). Values for each of these invariants can and have been derived for fishes in general (Charnov 1993; Jensen 1996), for specific species (e.g., Beverton 1963), and for specific genders within a species (e.g., Purchase et al. 2005a, 2006).

Life history trade-offs and invariants provide useful information for broodstock selection. For instance, relationships 19.6–19.8 show that adult growth rate increases with either an increase in adult mortality rate or a reduction in age at maturity. Similarly, early reproduction has a negative impact on both reproductive potential (Jensen 1981) and asymptotic length (Lester et al. 2004). Early maturity, rapid lifetime growth and a small asymptotic length are seen in many populations subject to intense fishing mortality (Reznick et al. 1990; Law 2000), and these traits can be generated from evolutionary models that simulate the application of fishing mortality over a number of generations (Dunlop et al. 2007).

The evidence for life history invariants among percids is mixed. Although both Heibo and Vollestad (2006) and Purchase et al. (2005a) report results that are consistent with invariance, the evidence among walleye populations is limited (Beverton 1987; Purchase et al. 2006).

A potential conundrum for culturists in the traditional understanding of tradeoffs (e.g., those that assume a single lifetime growth trajectory) is the negative relationship between rapid growth and asymptotic length; the ideal fish in an aquaculture setting not only grows quickly but attains a marketable size. As discussed previously (Sect. 19.2) it is often unreasonable to describe lifetime growth as a single trajectory. Allowing for separate immature and mature growth trajectories leads to the prediction that fish can both grow rapidly and achieve large asymptotic length (Rennie et al. 2010). This prediction is based on the relationships presented in Eq. 19.3 above: if reproductive investment is invariant (i.e., does not vary among populations), then asymptotic length can increase with pre-maturation growth rate. This outcome was demonstrated in a recent study in which populations of yellow perch exposed to higher predation on immature fish demonstrated both rapid immature growth rates and larger asymptotic sizes (Rennie et al. 2010). Further, age at maturity and reproductive output in this study were invariant (similar among populations). In the scenario explored by this study, rapid growth rates allowed immature perch to escape a predator window; the consequence was a larger asymptotic length. Evolutionary models predict the same response from a fishery that targets small-bodied, immature individuals (Dunlop et al. 2007). Given that there is substantial evidence that reproductive investment in percids can vary both within (Craig 1980; Heins et al. 2004) and among populations (Heibo et al. 2005; Moles et al. 2008), variation in g in other study species or broader geographic comparisons could either dampen or enhance associations between immature growth and asymptotic length.

19.3.2 Sexual Dimorphism

Sexual dimorphism is observed throughout the natural world, and is a consequence of differential selection on sex (Darwin 1871). When sexual selection results in sexual size dimorphism (SSD) as a consequence of differences in growth rates, optimal life history strategies are also expected to differ between males and females. Proximate explanations for SSD are typically centered on differences in energy acquisition or allocation between sexes (e.g., Roff 1983; Holtby and Healey 1990; Henderson et al. 2003). Typically, the sex with the greater investment in reproduction (through either gonadal products, competition for mates, or nest defense) exhibits the larger body size (Parker 1992). In fishes, a wide range of SSD has been described, from female-biased to male-biased, though female-biased SSD appears to be most common (Breder and Rosen 1966). Among percids, female-biased SSD appears to be common in species of commercial interest, having long been documented in yellow perch (Carlander 1950), European perch (Le Cren 1958), ruffe (*Gymnocephalus cernuus*) (Lorenzoni et al. 2009 and references therein), walleye (Carlander 1945) and sauger (*Sander canadensis*) (Bozek et al. 2011). Pikeperch typically do not display sexually-dimorphic growth (Korbuly et al. 2007) and display parental care (Marshall 1977). As well, male-biased SSD has been documented in some darter species (George et al. 1996; Johnston and Haag 1996; Kelly and Alonzo 2011; Hughey et al. 2012 and references therein), some of which also exhibit paternal care (DeWoody et al. 2000; Kelly et al. 2012; Harrington et al. 2013).

Currently, there are three leading hypotheses to explain female-biased SSD in percid fishes: (1) males have smaller size as a result of decreased consumption and activity as a predator avoidance mechanism (Roff 1983), (2) males have smaller size due to increased allocation of energy to activity costs associated with spawning (Henderson et al. 2003), and (3) females have larger size due to more efficient foraging on large-particle-sized prey (Lepak et al. 2012). Although these have been described as competing hypotheses (Stacey and Lepak et al. 2012), they may not necessarily be mutually exclusive.

Direct tests of these hypotheses in the recent literature tend to support hypothesis 1 (reduced male activity and consumption). Rennie et al. (2008) compared resource allocation and consumption between male and female yellow perch and walleye populations. Specifically, they used a BGM (Sect. 19.2) to compare sex differences in reproductive investment (g from Eqs. 19.3, 19.4, and 19.5), and a combined contaminant-bioenergetic model to compare sex differences in consumption and total metabolic costs. Results showed greater g in males vs. females (1.3, 1.2 times greater on average for walleye and yellow perch, respectively). As noted previously (Sect. 19.2), g is a close approximation of gonadal investment in females (Shuter et al. 2005), but its meaning in male fish is not well characterized. If we assume that g includes reproductive costs beyond investments in gonadal tissue (e.g., spawning activity, competition for mates), then a higher g for males supports hypothesis 2 (Henderson et al. 2003). However, bioenergetic results were more consistent with hypothesis 1 (Roff

1983) in that male perch had lower consumption and total metabolic costs compared with females. Further, these differences were such that females were still afforded a greater growing efficiency (Rennie et al. 2008). While Rennie et al. (2008) highlighted the need for sex-specific bioenergetic parameters, their analytical approach (i.e., the use of mass-relative, lakes-specific energetic residuals) best reflects potential sex differences among perch in the absence of sex-specific model parameters. Another experimental study reported increased feeding activity of female European perch with increasing water clarity, whereas male feeding activity remained the same across water clarity treatments, presumably to avoid predation risk (Horppila et al. 2011). Greater SSD was observed in clear water treatments.

Sexual differences in metabolic costs among percid fishes are supported by at least two recent studies. Sexually mature male walleye collected in fall samples had 25 % greater scope for anaerobic activity (as indicated by lactate dehydrogenase enzyme assays, Kaufman et al. 2006). Another study demonstrated a higher scope for anaerobic activity in male yellow perch in spring (e.g., during spawning), as well as summer and fall (Schoenebeck and Brown 2012). However, previous work examining two independent measures of activity found no significant differences between male and female yellow perch collected from two populations in late summer (Rennie et al. 2005).

Despite these two studies reporting significant differences in putative activity rates between male and female fish, neither appears to support hypothesis 2 (higher male activity costs during spawning; Henderson et al. 2003), as both studies indicated higher male activity outside of the spawning season. If anything, Kaufman et al. (2006) and Schoenebeck and Brown 2012 support increased activity in males *generally* as a possible explanation for reduced growth efficiency and smaller size-at-age compared to female perch and walleye.

An alternative test of hypothesis 2 (and that of higher male activity in percids generally as an explanation for female-biased SSD) is an examination of sex ratios from fish captured using passive sampling. Fishes with different activity rates are predicted to have different encounter rates with passive sampling methods (Rudstam et al. 1984). Thus, if males are more active during spawning (Henderson et al. 2003), or generally (Schoenebeck and Brown 2012), we expect male-biased catches in passive sampling gear deployed during those periods. Two studies report male-biased sex ratios during spawning in yellow perch (Henderson et al. 2000) (Fig. 19.2) and European perch (Olin et al. 2012), but not at other times of the year. Outside of the spawning season, only 27 % of Ontario perch populations exhibited male-bias in sex ratio (Appendix 1 in Rennie et al. 2008, Fig. 19.3). Female-biased sex ratios for yellow perch outside of the spawning season may be the norm in the Great Lakes (Henderson et al. 2000), but may become more male-biased under high fishing effort (Lauer et al. 2008).

Spawning sex ratios in walleye appear to tell a different story. Koupal et al. (1997) compared passive (gillnetting) with active (electroshocking) fishing methods on the sex ratio of walleye collected during spawning in two Colorado reservoirs. They found that females were two to three times more common in gillnets (passive sampling) than in electroshock catches (active sampling) over the same spawning

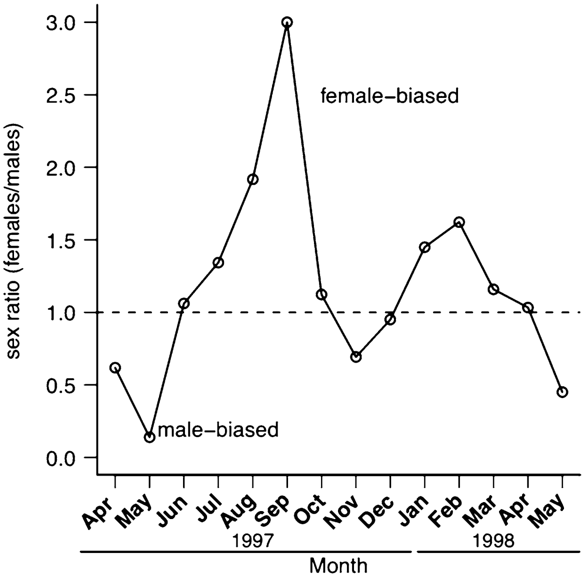


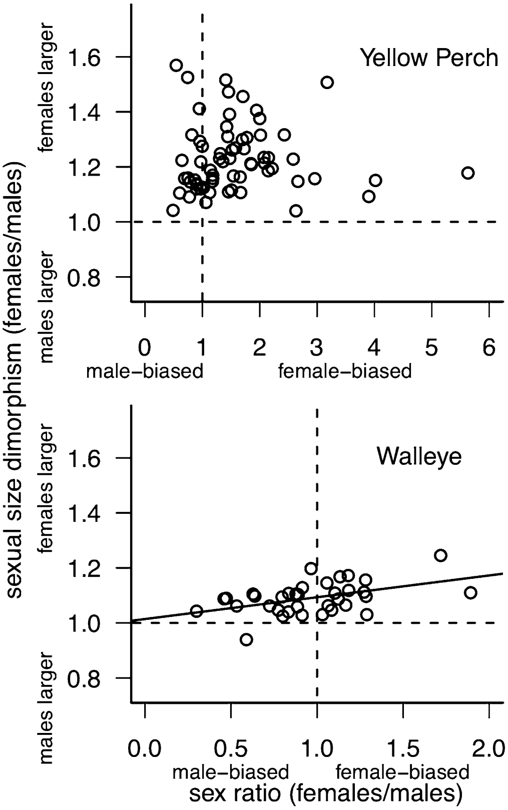
Fig. 19.2 Sex ratio (male:female) in Lake Erie index nets, April 1997–May 1998. Ratios are based on totals of age 3 and 4 perch, presented in Table 19.1 of Henderson et al. (2000)

shoals, and that males were far more common in electroshock catches. These differences in catch rates indicate that males on spawning shoals may actually be *less* active than females. During non-spawning times, 60 % of Ontario walleye populations were male-biased (Appendix 1 in Rennie et al. 2008, Fig. 19.3).

If sex ratios of percids captured in passive fishing gear reflects differential activity, and if these activity-based differences in sex ratios are linked to dimorphic growth, then SSD should be more exaggerated in populations with male-biased sex ratios. To evaluate this hypothesis, we re-evaluated previously published data by Rennie et al. (2008, Appendix 1), where fish were captured during autumn in passive fishing gear (gillnets). We detected no significant relationship between sex ratio (ratio of female:male in sample) and SSD (ratio of female:male size) in yellow perch (Fig. 19.3a). Contrary to predictions, walleye SSD *decreased* significantly as the sex ratios of populations were more male-biased (Fig. 19.3b); SSD in male-biased walleye populations (female:male ratio <1) was slightly lower than in female-biased populations (female:male ratio >1), but not significantly so (t-test, $t_{30.6}=1.85$, $P=0.07$; mean SSD for male-biased sex ratio= 1.07, mean SSD for female-biased sex ratio= 1.11). Neither of these results supports the hypothesis that greater male activity (as reflected in gillnet encounter rates) is the driver of female-biased sexual dimorphism in percids.

Hypothesis 3 (females are larger because they forage more efficiently on large prey) was recently proposed to explain sex-specific differences in mercury concentrations of walleye in two Colorado reservoirs (Lepak et al. 2012). Lepak et al. (2012) reported that females grew more efficiently due to their consumption of

Fig. 19.3 Sexual dimorphism (expressed as the ratio of male:female mean size) as a function of sex ratio (number of male:female encountered during survey). *Top panel*, yellow perch, *bottom panel*, walleye. Regression in *bottom panel* is significant ($F_{1,33} = 8.96$, $P = 0.005$) (Data from Rennie et al. 2008, Appendix 1)



larger-sized prey. However, it is difficult to know whether sex-specific diets are driving SSD or if the opposite is in fact true: are females larger because they consume larger prey, or do females consume larger prey because they themselves are larger? Feeding in fishes is limited by gape, which varies with body size. Thus, larger fish would be expected to have access to larger-sized particles, if present, regardless of their sex. While Lepak et al. (2012) included body size as a covariate in their analysis of diet differences between male and female walleye, there is very little overlap between the covariate (weight) and the independent variable (sex; Lepak et al. 2012, their Fig. 19.4). A major assumption of ANCOVA and other tests that include covariates is that the value of the covariate must not differ with respect to the independent variable (Quinn and Keough 2002). A more rigorous test of this hypothesis (SSD resulting from differences in diet between sexes, leading to increased growth efficiency in females) would be to compare males and females over more similar size ranges, or use a different size covariate that permits greater overlap between sexes.

A fourth hypothesis for SSD that does not seem to have been considered in the percid literature is that of sex-specific habitat segregation. Sex-specific habitat segregation is common among other taxa that show SSD (Ruckstuhl 2007), and could

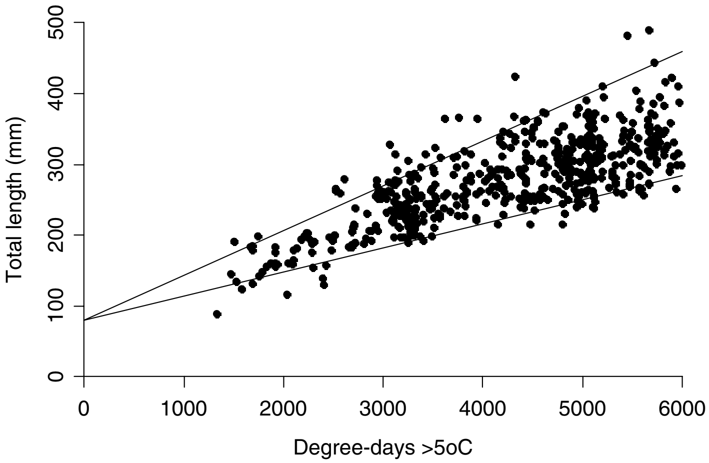


Fig. 19.4 Immature length of female walleye versus cumulative degree-days >5 °C in 85 populations. Each point ($n = 551$) is an age class that was observed during a sampling year. We assumed that an age class was immature if cumulative degree-days were <6000 °C·days (Venturelli et al. 2010). *Upper* and *lower lines* are 5 % and 95 % quantile regression lines assuming a common intercept of 80 mm (Lester et al. 2014). These lines imply growth rates of 0.03 and 0.06 mm/°C·day, respectively (Walleye data are from Venturelli et al. (2010) and Colby et al. (1979) and degree-day data are from Venturelli et al. (2010) and NOAA (2013) at a base temperature of 5 °C (Chezik 2013))

be even more significant among percids and other fishes if males and females distribute themselves at different depths. Sex-specific habitat selection during the growing period could lead to sexual dimorphism in diets (sensu Lepak et al. 2012). Further, because growth is temperature-dependent, sexual segregation in stratified lakes could lead to SSD via sex-specific thermal regimes. If males and females did have different thermal preferences, then SSD should be more exaggerated in stratified lakes than in polymictic lakes. To test this hypothesis, we reexamined the data in Rennie et al. (2008, their Appendix 1) and classified lakes as either stratified or polymictic. Thermocline depth was estimated using lake area (Hanna 1990), and a lake was defined as polymictic if the estimated thermocline depth exceeded the mean lake depth. A t-test comparing perch SSD between lake types showed that SSD was slightly less prominent in polymictic lakes (female:male size ratio = 1.19) than in stratified lakes (1.23), but the difference was not significant ($t_{7.7} = 0.9$, $P = 0.2$, one-tailed test). This lack of significance may be because most lakes in this dataset were stratified, and were not selected to specifically address this question. Other studies have demonstrated that water clarity contributes to the degree of SSD in European perch via interference with feeding activity (Horppila et al. 2011), which may also play a role in reduced SSD in turbid, polymictic lakes.

Regardless of the proximate mechanism, the ultimate cause of SSD in percids very likely results from the action of sex hormones, and their influence on the behaviour and metabolism of percid fishes. Sexually dimorphic growth in percids does not appear until maturity (Rennie et al. 2008). Laboratory experiments clearly demonstrate positive effects of estrogen and negative effects of androgen hormones on growth of both yellow perch (Malison et al. 1985, 1988) and European perch (Mandiki et al. 2004, 2005). What remains unresolved in both wild and culture settings is the degree to which these responses to hormones are behavioural (influencing foraging efficacy and field rates of activity) or strictly metabolic (increased/decreased rates of basal metabolism). Evidence to date seems to suggest that a combination of both behavioural and metabolic differences are responsible.

19.4 Extrinsic Factors Affecting Growth

19.4.1 The Thermal Environment

Temperature is arguably the most important determinant of growth rates in fishes (Paloheimo and Dickie 1966; Fry 1971; Kitchell et al. 1977). Temperature affects fish growth directly through metabolic rates and processes (Chap. 15), and indirectly through the rate of food production. Direct effects of temperature on percid growth are well documented, especially early in life. For readers interested in minimum, maximum, and optimum temperatures for percid growth, we recommend existing reviews by Thorpe (1977) and Colby et al. (1979).

In this section, we use degree-days to describe the growth patterns of percid fishes. The degree-day is an agricultural index of the ambient thermal energy that is available to growth over some period of interest. Degree-day calculations include upper and lower temperature thresholds that constrain the thermal sum to temperatures that are relevant to growth. However, it appears that a precise estimate of the lower threshold is only necessary when evaluating growth across a wide thermal range (e.g., broad spatial scales, large differences in culture conditions) (Chezik 2013). We also suspect that the upper threshold is only necessary when fish experience prolonged thermal stress.

Degree-days are useful for describing general growth patterns because they (i) are more physiologically relevant than calendar time (e.g., age in years) and therefore explain more variation in growth (Neuheimer and Taggart 2007; Venturelli et al. 2010), (ii) simplify the job of estimating how other factors have contributed to growth (e.g., consumption, reproductive status, genetics) (Mooij et al. 1994, Venturelli et al. 2010), and (iii) facilitate the comparison and aggregations of growth data over broad spatial and temporal scales (Colby and Nepszy 1981).

To date, 16 studies involving four percid species have used degree-days to gain insight into growth patterns and processes (Table 19.2). The most comprehensive of these studies (Bozek et al. 2011) summarized data from 431 walleye populations spanning 1000–4630 degree-days >5 °C (~13 degrees of latitude). This analysis indicated that walleye growth over this range was remarkably consistent and characterized by (i) strong temperature-dependence in the first year of life, (ii) linear

Table 19.2 Summary of percid studies that have used degree-days to gain insight into growth patterns and processes

Species	Study	Study lake(s)	Findings
Perca flavescens	Mills et al. (1989)	Oneida Lake (New York, USA)	Age-0 growth limited by temperature in cold years, prey in warm years
	Power and Van Den Heuvel (1999)	4 lakes in Alberta and Manitoba, Canada	Temperature dominates seasonal patterns of age-0 growth
	Chong (2000)	12 lakes in Ontario, Canada	Age-0 growth per unit temperature increases with latitude
	Purchase et al. (2005b)	72 lakes in Ontario, Canada	Maximum size negatively related to length and strength of growing season
	Tardif et al. (2005)	Lake Saint-Pierre (Quebec, Canada)	Age-0 growth limited by temperature in some years, other factors in others
Perca fluviatilis	Le Cren (1958)	Lake Windermere (Westmorland, UK)	The strength of the growth-temperature relationship varies with age
	Goldspink and Goodwin (1979)	4 lakes in the UK	Lifetime growth less sensitive to temperature when food limiting
	Le Cren (1992)	Lake Windermere (Westmorland, UK)	Adult growth controlled by temperature, not density
	Houthuijzen et al. (1993)	Volkerak Lake (Noord-Brabant, The Netherlands)	Immature ages fed zooplankton and macrofauna grow quickly and large at low densities
	Mooij et al. (1994)	Tjeukemeer Lake (Friesland, The Netherlands)	Age-0 growth not food limited
	Mooij (1996)	Tjeukemeer Lake (Friesland, The Netherlands)	Temperature affects recruitment through effects of age-0 growth on survival
	Romare (2000)	Lake Dagstorpssjon (Scania, Sweden)	Age-0 growth limited by diet in mid-summer, density in late summer
	Tolonen et al. (2003)	Lake Ainijarvi (Lappi, Finland)	Age-0 growth density-dependent, even at the northern edge of the range
	Heynen et al. (2011)	Lake Speldrop (North Rhine-Westphalia, Germany)	Age-0 growth delayed but final size greater when fed fish instead of zooplankton

(continued)

Table 19.2 (continued)

Species	Study	Study lake(s)	Findings
Sander lucioperca	Mooij et al. (1994)	Tjeukemeer Lake (Friesland, The Netherlands)	Age-0 growth food limited in some years
	Mooij (1996)	Tjeukemeer Lake (Friesland, The Netherlands)	Temperature affects recruitment through effects of age-0 growth on survival
Sander vitreus	Venturelli et al. (2010)	8 lakes in Ontario and Quebec	Immature growth response to abundance changes consistent across 8 populations; adult growth sexually dimorphic
	Bozek et al. (2011)	431 lakes in Canada and USA	Age-0 growth mostly explained by temperature; growth patterns similar across species range; maximum size unaffected by length and strength of growing season

juvenile growth (~0.06 mm/dd), (iii) non-linear and sexually-dimorphic adult growth, and (iv) an asymptotic length that is unaffected by latitude. However, these data also showed twofold variation in immature growth rate that was independent of temperature (Fig. 19.4). This residual variation is likely due to among-population differences in population density (e.g., Houthuijzen et al. 1993; Tolonen et al. 2003; Venturelli et al. 2010) and food (e.g., Mills et al. 1989; Goldspink and Goodwin 1979; Mooij et al. 1994), which are factors that we review in more detail below (Sects. 19.4.3 and 19.4.4).

Analyses using degree-days also suggest that percids exhibit countergradient growth variation (e.g., Chong 2000; Purchase et al. 2005b). Countergradient growth variation is the tendency of a species to compensate for shorter growing seasons (i.e., at higher latitudes or elevations) by growing more quickly (Conover and Present 1990). We analyzed published data from yellow perch, European perch, and walleye and found positive relationships between age-0 growth rate and latitude for all three species (Fig. 19.5). The relationship for walleye was relatively weak, at least in part because of a gill net bias that selects for the fastest growing members of the youngest age classes (Walker et al. 2013). An analysis of all ages classes for which data were available show that countergradient growth in walleye persists well into adulthood (Table 19.3), but with the acknowledgement that adult growth patterns may be confounded by among-population differences in investment in reproduction. Countergradient growth variation has been observed in at least 15 non-percid fishes (Power and McKinley 1997; Conover et al. 2009; Chavarie et al. 2010; Rypel 2012a, b). Because countergradient growth is adaptive (Conover et al. 2009), latitudinal analyses to determine the genetic capacity for growth in percids (e.g., Zhao et al. 2008) have implications for both resource management and broodstock selection. However, given the potential for thermal adap-

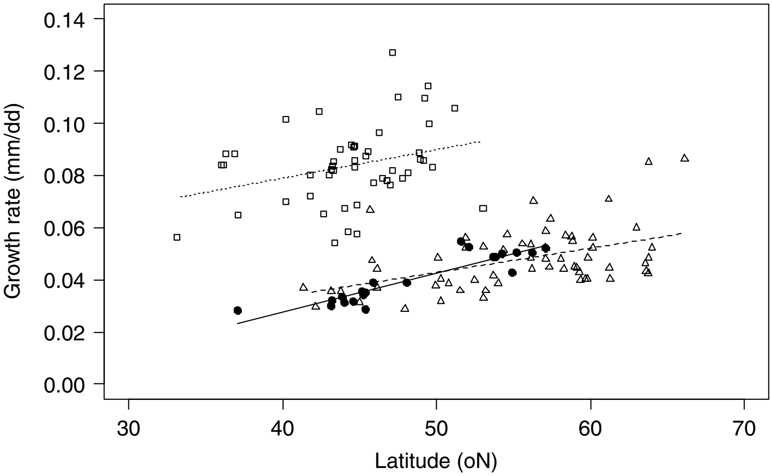


Fig. 19.5 Re-analyses of published data showing evidence for countergradient growth variation in the first year of life of yellow perch (*closed circles*, *solid line*) (Power and Van den Heuvel 1999), European perch (*open triangles*, *dashed line*) (Heibo et al. 2005), and walleye (*open squares*, *dotted line*) (Colby et al. 1979; Venturelli et al. 2010) (We obtained degree-day data from Venturelli et al. (2010), or calculated degree-days from online temperature data (McKenney et al. 2006; Haylock et al. 2008) using a base temperature of 5 °C for walleye and 10 °C for perch (Chezik 2013)). All linear regressions were significant (a: $F_{1,19}=87.71$, $P=1.50\cdot10^{-8}$, $r^2=0.82$; b: $F_{1,59}=19.95$, $P=3.66\cdot10^{-5}$, $r^2=0.25$; c: $F_{1,48}=5.03$, $P=2.96\cdot10^{-2}$, $r^2=0.09$)

Table 19.3 Strength of the linear relationship (r^2) between walleye growth rate (mm/°C·day) and latitude (°N) over the range of walleye ages for which data were available. Preliminary analyses found relatively weak evidence for a log-linear model at any age. Age-1 data are plotted in Fig. 19.5 (Walleye data are from Venturelli et al. (2010) and Colby et al. (1979), and degree-day data are from Venturelli et al. (2010) and NOAA (2013) at a base temperature of 5 °C (Chezik 2013))

Age (years)	*N* populations	Latitude range	Intercept	Slope	r^2	*P*
1	50	33.1–53.0	$3.50\cdot10^{-2}$	$1.10\cdot10^{-3}$	0.09	$2.96\cdot10^{-2}$
2	166	33.1–53.0	$6.21\cdot10^{-3}$	$6.48\cdot10^{-4}$	0.12	$1.53\cdot10^{-6}$
3	258	33.1–53.0	$2.33\cdot10^{-3}$	$3.84\cdot10^{-4}$	0.11	$4.27\cdot10^{-9}$
4	253	33.1–53.0	$6.09\cdot10^{-5}$	$2.85\cdot10^{-4}$	0.15	$8.17\cdot10^{-12}$
5	215	33.1–53.0	$2.34\cdot10^{-4}$	$2.06\cdot10^{-4}$	0.13	$9.63\cdot10^{-9}$
6	170	33.1–53.0	$-1.74\cdot10^{-3}$	$1.96\cdot10^{-4}$	0.24	$6.86\cdot10^{-13}$
7	123	33.1–53.0	$-1.81\cdot10^{-3}$	$1.66\cdot10^{-4}$	0.30	$1.54\cdot10^{-12}$
8	91	33.1–53.0	$-1.02\cdot10^{-3}$	$1.24\cdot10^{-4}$	0.31	$1.72\cdot10^{-10}$
9	63	36.0–53.0	$-1.16\cdot10^{-3}$	$1.09\cdot10^{-4}$	0.37	$2.52\cdot10^{-8}$
10	31	36.0–53.0	$-1.65\cdot10^{-3}$	$1.08\cdot10^{-4}$	0.51	$5.07\cdot10^{-7}$
11	20	41.8–52.3	$-1.35\cdot10^{-3}$	$8.97\cdot10^{-5}$	0.40	$5.55\cdot10^{-4}$
12	13	43.4–52.3	$-2.75\cdot10^{-3}$	$1.11\cdot10^{-4}$	0.34	$2.26\cdot10^{-2}$

tation at local or regional scales (Angilletta 2009), results of latitudinal analyses that assume a fixed growth-temperature curve should always be corroborated by common-garden experiments.

19.4.2 Predation

Mortality rate plays a major role in shaping the life histories and growth rates of fishes, including percids (Sect. 19.3.1). In nature, predation is a significant source of mortality in fishes, and can play a substantial role in shaping the life histories of prey (Abrams and Rowe 1996). For small percids and the early life stages of large percids, predation and inter-cohort cannibalism can contribute significantly to total mortality (Frankiewicz et al. 1999; Nielsen 1980; Persson et al. 2000; Post and Evans 1989; Szalai and Dick 1991).

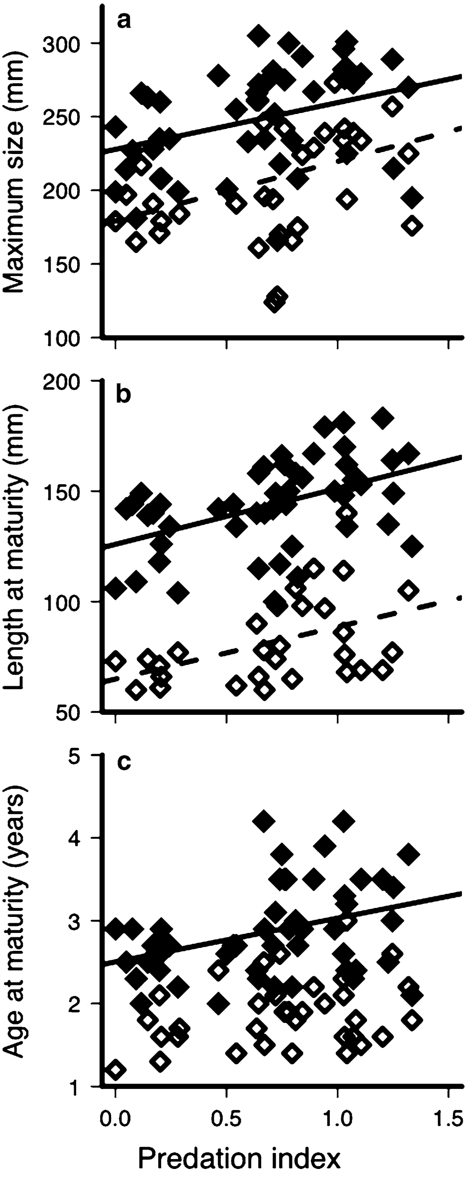
Predation applied to immature life stages of prey may have a very different effect on prey growth and body size than when applied to adult life stages. When mortality is imposed on large adults, life-history theory predicts faster growth, earlier age/shorter length at maturity and smaller asymptotic length. However, in a stage-dependent model like the BGM, early growth is a function of reproductive investment and asymptotic length (Eq. 19.3). Thus, if early growth is rapid to escape size-dependent predation, asymptotic length is predicted to increase but age at maturity remains a function of adult mortality (Shuter et al. 2005). Both of these outcomes are supported by predictions of an evolutionary life history model that imposed mortality at both early (small) and late (large) stages of life (Dunlop et al. 2007). This evolutionary model predicted faster somatic growth rates, increased size at maturation and increased asymptotic length with an increase in mortality imposed on immature age-0 fishes.

Observations in the field appear to match these theoretical and modeled predictions closely (Rennie et al. 2010). In yellow perch, higher predator densities resulted in larger asymptotic length, later maturation and maturation at larger sizes (Fig. 19.6). Individual growth rates also appeared to increase with higher predator densities (Rennie et al. 2010).

Predator mortality can affect prey growth rates, but so too can be the threat of predator mortality. Commonly, prey adjust their behaviour to the perceived threat of predation. One strategy is to reduce activity so as to avoid detection (e.g., Peacor 2002). Reduced activity can translate into reduced foraging (Peacor 2002), though the indirect responses on prey resources and growth rates as a result of this strategy may vary (Abrams and Rowe 1996). A second strategy among prey populations facing gape-limited predators is to grow rapidly through the range of vulnerable sizes (Biro et al. 2005; Urban 2007). Increased foraging (and therefore exposure to predators) may be required to maintain rapid growth, but with the benefit of escaping a predator window (Urban 2007).

Risky behaviour so as to grow rapidly through a predator window has been referred to in the literature as “boldness” or “bold personality;” that is, an apparent disregard

Fig. 19.6 Relationships between an index of *Perca flavescens* predation {estimated as the log10-transformed $\left[\log10(x+1)\right]$ mean catch per unit effort of *Esox lucius*, *Sander vitreus* and *Micropterus dolomieu* combined} with *P. flavescens* (**a**) asymptotic size (LF), (**b**) LF at maturity and (**c**) age at maturity for females (filled symbols, *solid lines*) and males (open symbols, *dashed lines*). Only significant relationships are shown (Reproduced with permission from Rennie et al. 2010)



for predation risk to obtain food for growth. This behaviour has been documented in salmonid aquaculture strains (e.g., Biro and Post 2008) and among European perch populations (Sect. 15.5, Magnhagen et al. 2012 and references therein). Although boldness may seem to be a counterproductive means of avoiding predation, it can be an effective strategy for obtaining food if individual predation risk can be limited by schooling. Hellstrom et al. (2011) found that the degree of boldness observed in the presence of perceived predation risk is more common in larger groups of European perch. Further, there is evidence that risk-taking behaviour is plastic among European perch, reflecting the immediate perceived risk of predation (Magnhagen and Bocherding 2008; Magnhagen et al. 2012). By contrast, decreased swimming activity in the presence of predators seems to be the common response to predation risk among percids; European perch exposed to a perceived risk of predation reduced their swimming activity (Vainikka et al. 2005), and modelled estimates of yellow perch activity declined with increasing predator densities in lakes (Rennie et al. 2010).

It is important to note that activity also represents a metabolically costly endeavour (Weatherley 1966); given equal rates of consumption, increased activity means less energy available for growth (Johansson and Andersson 2009). Rennie et al. (2010) found that yellow perch growth rates and conversion efficiencies (rates of growth per unit food consumed) increased as the risk of predation increased, and that this was primarily due to reduced activity at higher predator densities. This relationship was present despite a reduction in consumption rates at higher predator densities. Similarly, an individual-based model found that roach (*Rutilus rutilus*) incurred higher activity costs and consumed less energy in the presence of predatory pikeperch (Holker and Mehner 2005).

Decreased activity may also result in increased growth rate by indirectly stimulating resource abundance. In a mesocosm experiment, Peacor (2002) found that the tadpoles (prey) reduced their activity in response to dragonfly larvae (predators). However, this reduction in activity released primary producers from tadpole grazing, to the point that less active tadpoles consumed more food than tadpoles that were more active. Ultimately, growth rates of low-activity tadpoles were greater in tanks with a perceived threat of predation than those with no predators present.

The growth response of prey to predators can be further modulated by the presence of a refuge. Diehl and Eklov (1995) reported that increased refuge use by European perch in the presence of predators resulted in slower growth. Similarly, Shoup et al. (2012) documented reduced growth rates of bluegill sunfish (*Lepomis macrochirus*) in refugia with no predators present. These findings imply a tradeoff between resource availability and protection from predators. However, other authors report no significant effect of refuge use on growth rates of juvenile European perch (Persson and Eklov 1995). If resources become too limiting, prey may abandon refugia and adopt more bold feeding strategies in the presence of predators (Magnhagen and Borcherding 2008). Declining resources have been found to have a positive effect on the activity rates of European perch (Olsson et al. 2007).

19.4.3 Density Dependence

Density-dependent growth is a change in individual growth rates that occurs in response to a change in population (or cohort) abundance, relative to carrying capacity. Density-dependent growth is easy to imagine in a culture setting in which fish density is allowed to vary in a fixed volume of water that receives a constant ration. Because aquaculture seeks to maximize biomass production at a given ration, the role that density plays in determining growth rates is well studied.

Density-dependent growth in nature is expected but this phenomenon can be difficult to observe and quantify in nature (Rose et al. 2001). We expect growth to change with population abundance because plasticity in growth can play an important role in determining how quickly a population recovers from a catastrophic event or to what extent a population compensates for increased mortality due to exploitation (Lester et al. 2014). However, attributing an observed change in growth to a change in population abundance relative to carrying capacity is difficult because (i) population abundance and carrying capacity are both variable and difficult to estimate; (ii) growth measurements can be biased by selectivity, both during a sampling event and via exploitation; and (iii) growth itself is influenced by numerous direct and indirect food-web linkages of varying strength. Our ability to detect density-dependent growth also depends on the extent to which data are available from both extremes of abundance. As a result of these challenges, examples with direct evidence of density-dependent growth in nature are rare (Rose et al. 2001).

The indirect evidence for density-dependent growth in walleye populations suggests that immature growth in length can approximately double in response to a large change in abundance. Much of this evidence is from heavily exploited lakes and is summarized in Bozek et al. (2011). The largest growth responses have been observed in Escanaba Lake (Kempinger and Carline 1977), Lake Erie (Spangler et al. 1977; Venturelli et al. 2010), and Red Lakes (Ostazeski and Spangler 2001). However, a 1.3-fold increase in growth in length appears to be more common, as evidenced by numerous single-lake studies (e.g., Anthony and Jorgensen 1977; Shuter and Koonce 1977; Reid and Momot 1985; Muth and Wolfert 1986; Schueller et al. 2005) and one meta-analysis (Venturelli et al. 2010). Density-dependent growth variation of this magnitude is also evident in young-of-the-year pikeperch (Table 19.4, Buijse and Houthuijzen 1992).

The indirect evidence for density-dependent growth in wild perch populations is also compelling (Table 19.4). Like walleye, both *Perca* spp. appear capable of a twofold increase in growth in length following large declines in population abundance (e.g., Linlokken and Seeland 1996; Ostazeski and Spangler 2001; Headley and Lauer 2008; Irwin et al. 2009). Large growth responses are evident in all perch life stages from YOY to juvenile to adult (Table 19.4). In perch, these growth responses may result indirectly from density-dependent habitat selection whereby crowding forces some perch to prey on sub-optimal, pelagic prey (e.g., Post et al. 1997; Svanback and Persson 2009; Bacheler et al. 2011). This mechanism has also been observed in pikeperch (Frankiewicz et al. 1999) and may be a general phenomenon among percids. Although the exact relationship between growth and population abundance in the wild is unknown, the form of this relationship is likely log-linear. LeCren (1958) found that the length increments of adult perch in Lake Windermere increased more than sevenfold as the mean number of adults per trap decreased from 610 to 10, but half of this growth response occurred at <100 adults per trap.

Table 19.4 Evidence for density-dependent growth in wild populations of yellow perch, European perch, and pikeperch (our calculations). See Bozek et al. (2011) for a summary of density-dependent growth in walleye

Species	Study	Study lake(s)	Evidence for abundance change	Evidence for growth change
P. flavescens	Beckman (1950)	2 lakes in Michigan, USA	Severe winterkill (abundance not quantified)	1.61- and 1.35-fold increases in mean growth (weighted average across age classes)
	Bardach (1951)	Lake Mendota (Wisconsin, USA)	0.33-fold decrease in gill net CPUE	1.4-fold increase in mean adult length
	El-Zarka (1959)	Saginaw Bay (Lake Huron, USA)	An estimated 19-fold increase in trap net CPUE (1929–1955)	0.75-fold decrease in age-3 length
	Ivan et al. (2011)	Saginaw Bay (Lake Huron, USA)	0.1-fold decrease in trawl CPUE (1970–2008)	1.2-fold increase in age-2 length
	Kempinger et al. (1982)	Nebish Lake (Wisconsin, USA)	6.5-fold increase in estimated biomass	0.65-fold decrease in age-3 length
	Henderson (1985)	South Bay (Lake Huron, Canada)	0.04-fold decrease in age-4+ trap CPUE	1.4-fold increase in age-3 to age-5 length
	O'Gorman and Burnett (2001)	Lake Ontario (New York, USA)	30-fold difference in YOY trawl CPUE	1.4-fold difference in YOY length
	Ostazeski and Spangler (2001)	Red Lakes (Minnesota, USA)	0.36-fold decrease in gill net CPUE	0.53-fold decrease in age 1–6 growth
	Pierce et al. (2006)	Lake Thirteen (Minnesota, USA)	Ninefold increase in electrofishing CPUE	0.65-fold decrease in age-3 length
	Headley and Lauer (2008)	Lake Michigan (Indiana, USA)	0.01-fold decrease in trawl CPUE	1.8-fold increase in immature growth rate
	Irwin et al. (2009)	Oneida Lake (New York, USA)	0.1-fold decrease in density	Twofold increase in larval growth rate

(continued)

Table 19.4 (continued)

Species	Study	Study lake(s)	Evidence for abundance change	Evidence for growth change
P. fluviatilis	LeCren (1958)	Lake Windermere (Westmorland, UK)	At least a 0.25-fold decrease in perch trap CPUE (<1941 vs. 1952)	1.4-fold increase in age-4 length
	Craig (1982)	Lake Windermere (Westmorland, UK)	0.1-fold decrease in trap CPUE of females (1955 vs. 1968)	1.2-fold increase in age-5 female length
	Linlokken and Seeland (1996)	Munksjoen (Hedmark, Norway)	0.3-fold decrease in biomass density	Twofold increase in adult instantaneous growth
	Persson et al. (2000)	Abborrtjarn (Vasterbotten, Sweden)	0.03-fold decrease in age-2+ abundance	1.6-fold increase in adult length
S. lucioperca	Buijse and Houthuijzen (1992)	Lake Ijssel (central Netherlands)	115-fold variation in YOY trawl CPUE	1.2-fold variation in YOY length

It is important to note that almost every study supporting density-dependent growth in wild percid populations also acknowledges one or more confounding variables. These include changes in temperature, nutrient status, pollution, size-selective exploitation, catchability, invasive species, and the fish community (e.g., predators and competitors). Indeed, the presence of most if not all of these confounds in the Great Lakes provide a complicated backdrop against which to interpret patterns of percid growth (e.g., El-Zarka 1959; O’Gorman and Burnett 2001; Headley and Lauer 2008). Similarly, patterns of yellow perch abundance and growth are often tied up in competitive and predatory interactions with walleye (Rose et al. 1999; Ostazeski and Spangler 2001; Pierce et al. 2006; Irwin et al. 2009; Ivan et al. 2011). Competition and predation among cohorts can also complicate growth responses. For example, although adult perch length in a Swedish lake increased 1.6-fold in response to a two-orders-of-magnitude decline in age-2+ abundance (Persson et al. 2000), this growth response may have been due to a two-orders-of-magnitude increase in YOY perch (an important food item for cannibalistic adults).

19.4.4 Food Availability and Size

Ultimately, the food energy that is consumed by a fish is a function of the quality and quantity of the food that is available to that fish. In the previous Sect. (19.4.3), we described how percid growth is affected by per-capita food availability. In this section, we describe how percid growth is affected by changes in food quality and quantity that are independent of the density of conspecifics.

Because percids are visual predators, spatially complex or turbid environments can impair foraging efficiency. For example, the growth of pikeperch was inhibited in a turbid, Finnish lake (Vinni et al. 2009). Other studies that did not measure growth point to impaired foraging efficiency as a mechanism of growth inhibition: Bartels et al. (2012) reported that European perch consumed smaller prey items as water clarity decreased. Similarly, Wellington et al. (2010) reported decreased consumption of larval and juvenile perch in the presence of phytoplanktonic turbidity. Fullerton and Lamberti (2006) reported that yellow perch in the absence of predators foraged more efficiently in open water than in macrophytes. However, other studies have shown that foraging in complex environments is adaptive when predators are present (Svanback and Eklov 2004).

Growth efficiency depends, not only on rates of energy acquisition and expenditure (e.g., consumption and activity), but also on the size spectrum of prey available for consumption (Sherwood et al. 2002). In environments in which food is limiting (arguably representative of most instances in nature), prey sizes can have significant effects on growth efficiency and growth rates. This process has been well-documented in North American percids. Walleye populations feeding on lake cisco (*Coregonus artedi*; a large-bodied prey fish) grew faster and larger than those feeding on yellow perch (a comparatively small-bodied prey fish) (Kaufman et al. 2006). After controlling for body-size, it was also shown that walleye populations feeding on cisco suffered lower activity costs, suggesting that the increased rates of growth were a direct result of more efficient foraging (i.e., less energy expended and more energy gained by searching for, capturing, and consuming larger prey).

Similarly, yellow perch activity rates increase with body size until an ontogenetic diet shift to larger prey types (e.g., zooplankton to benthos, benthos to fish) (Heath and Roff 1996; Sherwood et al. 2002; Iles and Rasmussen 2005). The authors suggest that the inability to transition to larger particle sizes represents an energetic bottleneck, and places a limit on growth and maximum size in some populations. Other studies have proposed the same mechanism (lack of large prey) in contributing to stunting in both pikeperch (van Densen et al. 1996; Vinni et al. 2009) and European perch (van Densen et al. 1996).

19.4.5 Parasitism/Disease in Natural Settings

Parasitism and disease can have significant impacts on individual growth rates of both wild and cultured populations of percids (Craig 1987; Grignard et al. 1996). In culture conditions, severe bacterial infection can prove disastrous, whereas the extent to which parasites cause concern depends on parasite load (Grignard et al. 1996). Here we briefly review the existing literature regarding the effects of parasites and diseases on percid growth. An exhaustive list of percid parasites can be found in reviews by Craig (1987) and Grignard et al. (1996).

Diseases (i.e., viral or bacterial infection) can have a significant impact on survival, but few studies have assessed impacts on individual growth rates. In one well-studied population, 98 % of the estimated European perch population in Lake Windermere were eliminated by a pathogen-related infection (Craig 1987). However, total perch biomass declined only slightly because compensatory individual growth among the surviving juveniles was so high. Simulation modeling suggests that this increase in individual growth rates was due to reduced intraspecific competition (Ohlberger et al. 2011).

Reports of the effects of parasitic infections on fishes vary, and in some cases include positive effects on growth (Arnott et al. 2000; Voutilainen et al. 2012). Table 19.5 summarizes the literature on the effects of parasites on percid growth. Of the nine parasites listed, all are involved in at least one case of a negative effect. Neutral effects were observed in four cases and positive effects were observed in three cases. Ryman et al. (2008) reported a slight but significantly higher condition factor in perch infected with *Apophallus brevis* that was unrelated to the mass of the parasites themselves. Cloutier et al. (2012) reported increased condition with parasitism by *Ichthyocotylurus spp.*, but the relationship appears to be driven by a single datapoint with high leverage (see their Fig. 3) and it is not clear whether parasite mass was accounted for. Johnson and Dick (2001) report increased reproductive allocation (GSI) under high loads of the parasite *Glugea spp*. Increased allocation of energy to reproduction vs. somatic growth in infected individuals is likely a response to maximize fitness when survival is in jeopardy.

Reduced growth rates in parasitized percids may be a result of decreased growth efficiency. Perch with heavy parasite loads were observed to have higher concentrations of MeHg (Ryman et al. 2008), which the authors suspected might be due to spatial differences in MeHg loading where fish were collected. An alternative explanation is that these fish had to consume more food (and thus retained more MeHg) in order to achieve the same body size as conspecifics with lower parasite loads. Other studies have reported a metabolic cost of carrying parasites (e.g., Seppanen et al. 2008). Additionally, Johnson et al. (2004) reported that parasites were important determinants in the nitrogen stable isotope signatures of hosts, which are also sensitive to metabolic processes and efficiencies (Ponsard and Averbusch 1999).

Additional aspects of parasitism and infection in percids remain poorly studied. Yellow perch may act as hosts to the glochidia of freshwater mussels (Jansen 1991), but effects of glochidia parasitism on percid growth rates have not been determined. Also, some evidence exists for percids provisioning eggs with anti-infection properties (e.g., yellow perch; Paxton and Willoughby 2000).

Table 19.5 Published accounts on effects of parasitism on fish growth and growth-related variables. “X” indicates no measured effect on variable of interest. Site/mode of infection listed below taxonomic name of each parasite

Parasite	Host	Source	Details	Effect	Variable measured
Apophallus brevis Metacercariae infect fish musculature	*P. flavescens*	Johnson and Dick (2001)	Infection rates > 50 per g infected tissue	–	Reduced growth
		Ryman et al. (2008)	Compared high (19 cysts/g) vs. low (1 cyst/g) rates of infection	–	Increased MeHg
		Marcogliese et al. (2005)	Effect at >10 metacercariae	–	Increased oxidative stress markers
		Marcogliese et al. (2010)	Effect only at high-pollution sites	–	Increased oxidative stress markers
		Ryman et al. (2008)	Compared high (19 cysts/g) vs. low (1 cyst/g) rates of infection	+	Higher condition
		Cloutier et al. (2012)		X	Growth
Diplostomum spp. Trematode- infects eyes, visual impairment	*P. flavescens*	Marcogliese et al. (2010)	Effect only at high-pollution sites	–	Increased oxidative stress markers
		Cloutier et al. (2012)		X	Growth
	S. vitreus	Marcogliese et al. (2001)		X	Growth
Glugea spp. Intestinal infection	*P. flavescens*	Johnson and Dick (2001)	>100 parasites per individual	–	Reduced growth
		Johnson and Dick (2001)	>100 parasites per individual	–	Reduced visceral fat
		Johnson and Dick (2001)	>100 parasites per individual	+	Increased GSI
Ichthyotylurus spp. Liver pathogen	*P. flavescens*	Marcogliese et al. (2010)		–	Increased oxidative stress markers
		Cloutier et al. (2012)	Effect only at high-pollution sites	+	Increased condition

(continued)

Table 19.5 (continued)

Parasite	Host	Source	Details	Effect	Variable measured
Ligula intestinalis Intestinal infection	*P. flavescens*	Pitt and Grundmann (1957)		–	Reduced growth by 38–55 %
Phyllodistomum superbum Urinary bladder and kidney	*P. flavescens*	Cloutier et al. (2012)		–	Reduced growth
Raphidascaris acus Liver pathogen	*P. flavescens*	Szalai and Dick (1991)	Infection rates > 50 per liver	–	Reduced condition
		Szalai and Dick (1991)	Infection rates > 50 per liver	–	Reduced growth
		Szalai and Dick (1991)	Infection rates >50 per liver	–	Increased mortality
		Marcogliese et al. (2005)	Effect only at high-pollution sites	–	Increased oxidative stress markers
		Johnson and Dick (2001)	Infections >50/g infected tissue	–	Reduced visceral fat
		Cloutier et al. (2012)		X	Growth
Triaenophorus nodulosus Liver parasite	*P. fluvatilis*	Brinker and Hamers (2007)	Infection rate 1–3 per liver	–	Reduced growth
Tylodephys scheuringi Eye pathogen, visual impairment	*P. flavescens*	Cloutier et al. (2012)		–	Reduced growth, but only in the presence of *P. superbum*

19.5 Summary

The lifetime growth of commercially-important percid fishes in the wild is the result of a complex suite of intrinsic and extrinsic factors that interact and vary in importance. Despite this complexity, our review and re-analyses have revealed a number of patterns and consistencies. In summary, percid growth in nature is:

(i) Biphasic (Sect. 19.2). The biphasic growth model allows us to accurately describe growth while gaining insight into other life history traits (e.g., investment in reproduction, mortality) and their constraints.
(ii) Optimized to maximize fitness within a given set of environmental and biological constraints (Sect. 19.3.1). Optimization results in common life history trade-offs (e.g., growth and maturity) that will allow for both rapid immature growth and large adult size.

(iii) Sexually dimorphic, with the exception of pikeperch (Sect. 19.3.2). Adult females typically grow faster and larger than adult males, which appears to result from differences in activity and consumption (as determined hormonally).
(iv) Strongly temperature-dependent (Sect. 19.4.1). Degree-days show that, on average, patterns of growth are consistent across a species' range, but that grow rates increase with latitude.
(v) Shaped by predation (Sect. 19.4.2). Percids respond to both predation mortality and perceived risk; they appear to reduce activity when faced with predation, but "bold" personalities may emerge depending on current perceived risk.
(vi) Strongly density-dependent (Sect. 19.4.3). Although growth-density relationships are confounded in nature, wild percids appear capable of up to twofold variation in individual growth in length.
(vii) A function of food availability and size (Sect. 19.4.4). Independent of population density, food quality and quantity can represent an energetic bottleneck that limits growth efficiency and leads to stunting.
(viii) Shaped by parasitism and disease (Sect. 19.4.5). Parasitism and disease are widespread but poorly studied. Although effects on growth are largely negative, some effects are neutral or even positive.

These findings are based on evidence from four, well-studied species (European perch, yellow perch, pikeperch, and walleye) from two sister sub-families (Luciopercinae and Percinae) (Sloss et al. 2004). We expect similar patterns in other members of these sub-families that are not well studied; for example sauger (a sister-species to walleye), *Gymnocephalus* spp. (which are similar to perch), and *Zindel* spp. (all of which are endangered or vulnerable). However, we recommend further study before extending these growth patterns to darters, which tend to be invertivorous stream-dwellers with very different life histories.

The insight that we have gained into percid growth rates in the wild is also relevant to percid growth in culture. Our finding that percids are capable of up to twofold variation in growth and length under natural conditions (Sect. 19.4.3) suggests that the productivity of a facility will benefit greatly from informed design and operation. The benefits of controlling such factors as temperature, density, and food are fairly obvious. Our results also point to percids from northern populations for broodstock selection because they tend to grow faster at a given temperature and ration, than percids from southern populations (Sect. 19.4.1). Similarly, female percids may be more profitable than male percids for culturing because the former mature relatively later and larger (Sect. 19.3.1). If fish are allowed to mature, then adult females also grow relatively faster than males and reach larger sizes (Sect. 19.3.2) despite investing more in reproduction.

Our review of percid growth focused on most but not all drivers of growth in wild percid populations. Percid growth rates are optimized to a range of environmental and ecological conditions (Sect. 19.3.1), but are also shaped by selective fishing (Jorgensen et al. 2007). Theoretical models show that the selective removal of adults will lead to reductions in both age and size-at-maturity (e.g., Dunlop et al. 2007; Lester et al. 2014), although population models suggest that this response is not guaranteed (e.g., Matsumura et al. 2011). Nonetheless, the potential for fishing pressure to shape growth rates should not be ignored when selecting broodstock. Percid growth in the wild is also negatively affected by pollution and contaminants. In general, contaminants and pollutants affect growth via sub-lethal effects operating at genetic, molecular, and cellular scales. Yellow perch exposed to organic contaminants and heavy metals may have an overall impaired stress response (Hontela et al. 1992). Survival of perch <2 years old was also significantly impaired in metal-contaminated lakes (Sherwood et al. 2000). However, indirect (food-web mediated) effects of contaminants in lakes can be as significant if not more so than direct metabolic effects with respect to growth (Campbell et al. 2003; Rasmussen et al. 2008).

Finally, we note avenues of future research that are relevant to percid growth in both wild and culture settings. The degree to which positive effects of estrogen and negative effects of androgen hormones on growth (Sect. 19.2) are behavioural (influencing foraging efficacy and field rates of activity), metabolic (increased/decreased rates of basal metabolism) or some combination thereof warrants further investigation. Seemingly positive responses of fish growth and condition to parasitism, a counter-intuitive phenomenon, warrants further scrutiny and investigation (Sect. 19.4.5). Last, the mechanism behind the existence of sympatric growth forms of percids in some lakes remains unresolved. For example, dwarf and normal growth forms of walleye in Lake Winnipeg (Johnston et al. 2012) show significantly different patterns of resource allocation that do not appear to be associated with resource polymorphism (Moles et al. 2010, 2011). While increased fishing mortality on normal growth forms may facilitate the coexistence with the normal form to some degree, the driver of these sympatric forms remains unknown.

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