# A conceptual model of muskellunge spawning habitat

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**Abstract**

The muskellunge is an economically important and often declining sport fish restricted to eastern and central North America. To assist research and management, especially in the Georgian Bay area, a conceptual model of muskellunge spawning habitat was developed from a meta-analysis of available peer-reviewed and technical literature. The model incorporates three primary variables: water temperature (7.5-15$^{o}$C), dissolved oxygen (> 5 mg/L) at the sediment-water interface, and adequate separation of individual eggs after deposition. The model also assumes that muskellunge spawning occurs in wetlands because of their known association with aquatic vegetation. Secondary variables influencing primary conditions include (1) depth, current and substrate colour (assumed to have an effect on temperature); (2) current, sediment oxygen demand, sediment compactness and plant density (assumed to have an effect on dissolved oxygen concentrations); and (3) particle size and plant density (assumed to have an effect on egg separation). Field validation of these results will help to clarify the relative importance of each variable, and thus allow for refinement of the model.

## Introduction

Muskellunge (also referred to as muskie) are an economically important, and in many cases, declining sport fish (e.g. Trautman 1981; Crossman 1986; Inskip 1986; Lebeau 1995) with a home range from the central United States to Northwestern Ontario (Crossman 1978). In addition to their status as a sport fish, muskellunge were once exploited commercially in Ontario in the late-19th and early 20th century, presumably until decreasing stocks made the fishery non-viable (Crossman 1986). The body of scientific literature on this fish is small, with most research occurring in Wisconsin, Minnesota and the St. Lawrence River. Few studies have been conducted for muskie in the Georgian Bay area (Arunas Liskauskas, Ontario MNR, personal communication). Considering Georgian Bay's exceptional potential to produce trophy-status fish (according to Muskies Canada), the growing demand for specialist muskellunge angling throughout its range (Crossman 1986), and evidence of population declines in other areas due to human impact (Dombeck et al. 1986; Lebeau 1995) and water-level (Trautman 1981) modifications, the need for further research into this particular population is great. Because of threats arising from increased cottage and resort development in the area, it is important that at least baseline knowledge of the natural history of this fish be assembled so that appropriate management plans can be developed to monitor its population health and habitat quality.

Of particular concern to the health of any muskellunge population is the quality of its spawning and nursery habitat, upon which this fish may be particularly dependent. Studies with the northern pike, a related esocid, have shown a correlation between year-class strengths and nursery habitat conditions (Casselman and Lewis 1996). Although the muskellunge is relatively long-lived (>20 years, Casselman and Crossman 1986), it has been associated with extremely high egg mortality (>99%), both under natural conditions (Farrell 2001) and experimental incubations carried out *in situ* (Zorn et al. 1998). This suggests that high early-life mortality is the norm for this broadcast-spawning species which can produce 22,000 to 225,000 eggs in a single spawning period (Oehmcke et al. 1958), and that there is a slim margin of survivorship to ensure adequate recruitment. Large-scale changes that reduce spawning success even fractions of a percent could have serious consequences for juvenile survivorship and overall recruitment.

Unlike other esocids, muskie sac fry, which are the product of hatched eggs, are sessile for ten days after hatching (Zorn et al. 1998). Should environmental conditions become de-oxygenated during this period, they would not be able to relocate, and would die. Thus, muskellunge populations are quite dependent on high-quality spawning habitat. Since spawning adult muskie are philopatric (Crossman 1990; Lebeau 1992), consistent annual spawning-site quality is especially important for both individual and population survivorship. More definitive research into this aspect of muskie ecology is essential.

Management of spawning sites is considerably easier than that of nursery or adult habitat, owing first to the discrete nature of the sites which contain non-motile eggs and sac fry, and secondly to the high relative availability of spawning literature from which one can derive an understanding of this environment and then make informed management decisions. With the conservation and management interests of this species in mind, it is therefore prudent to focus research efforts on spawning habitat specifically, since this habitat is both critical to the fish and relatively easily characterized. We thus present a literature-based conceptual model of idealized spawning habitat for the muskellunge, the result of data obtained from approximately 40 papers. This model will hopefully assist managers in identifying, assessing, protecting and restoring spawning sites in the future.

## Physical Variables

In our review of available literature, we identified five common variables that have been used to characterize muskellunge spawning habitat: 1) depth; 2) ambient temperature; 3) current flow; 4) dissolved oxygen content, especially near the substrate-water interface; and 5) the nature of the associated wetland plant communities, which were almost invariably present. In addition, several less commonly expressed variables were noted, including the degree of isolation of individual eggs. Based on the strength and consistency of the documented evidence, three of these factors emerged as being critical conditions for successful spawning habitat, and were incorporated into the conceptual model (Figure 1). These factors are: 1) **temperature**; 2) **dissolved oxygen at the substrate-water interface**; and 3) **spatial separation** (**isolation) of individual eggs**.

### Variable 1: Temperature

Muskellunge eggs require a certain amount of heat in order to develop. The limited distribution of this fish in Ontario probably reflects an intolerance to cold temperatures, since muskie are restricted to the Great Lakes and to a small area in northwestern Ontario. Temperature is particularly important for this fish compared to its more generalist cousin and competitor, the northern pike (Inskip 1986), which can thrive under much colder conditions, and which occurs throughout water bodies in Ontario and beyond into the Northwest Territories (Crossman 1978). The more cold-tolerant pike also begins spawning a few weeks before the muskellunge, when water temperatures are significantly lower (Scott and Crossman 1973). Temperature fluctuations of more than a few degrees have been shown to have deleterious effects on muskellunge egg and embryo development and survival (Oehmcke et al. 1958; Zorn et al. 1998), and the muskies' preference for warmer water has been noted anecdotally by Dombeck et al. (1979), who observed muskie spawning areas to be approximately 1.5$^{o}$C warmer than surrounding areas at his Wisconsin study site. Therefore, consistent, reliable warming of water temperatures to the preferred range appears to be necessary before spawning can take place (Farrell et al. 1996). The literature involving cultured animals suggests that ideal incubation temperatures are approximately 12-14°C (Klingbiel 1986), with approximately 180 degree-days allowed for incubation before hatching (Zorn et al. 1998). However, field measurements at active spawning sites cover a broader range of temperatures (see Table 1). Therefore, in our model, we have used a similarly broader range of temperatures to represent optimum spawning conditions and we consider **temperatures between 7.5°C and 15°C** to be suitable for spawning.

### *Conditions Influencing Temperature*

#### *Water Depth*

The most direct influence on the temperature of a water body is its depth. The reviewed literature therefore understandably identifies shallow, and therefore warm, areas as being favoured by muskellunge for spawning, with depths being generally less than 2m (Lane et al. 1996a, 1996b), and almost always closer to 1m (Oehmcke et al. 1958; Minor and Crossman 1978; Lapan 1985; Farrell et al. 1996). We recognize there are some exceptions (Leech Lake (Minnesota) and Lake St. Clair (Dombeck 1986)) in which spawning depths approach 2.75m; however, in general, our model assumes that **depths < 1.5m** would be suitable for spawning.

#### *Current Flow*

Spawning sites for muskellunge tend to be associated with flowing water. While rivers are frequently used, even lakes used by muskie often have an associated current flow such as that caused by a groundwater influx (Dombeck et al. 1984b; Zorn et al. 1998). In addition to assisting in egg development by flushing out toxic or deoxygenated water, current flow may also help thaw any ice present, allowing for increased sunlight penetration and thus help to raise ambient temperatures (Dombeck et al. 1984b). Based on the fish's habitat preferences, its slender body shape (Lapan 1985) and its non-perpendicular egg deposition angle (Lebeau and Pageau 1989), Crossman (1978) has speculated that muskellunge are adapted for life in riverine environments, and therefore derive fitness benefits from lotic conditions.. We therefore assume that good spawning habitat should have a **measurable current flow.**

### *Substrate Colour*

**Ideally, spawning substrates should be dark in colour** in order to absorb the sun's radiant energy, and thus create a warmer submerged microclimate that benefits both egg and fry development. This has been observed anecdotally in at least three studies (Dombeck 1986; Lebeau 1992, 1995). In addition, some studies (e.g. Oehmcke et al. 1958) indicate that spawning takes place on muck, which is presumably also dark in colour. However, there is usually a trade-off between a substrate's ability to absorb sunlight and its oxygen demand because darker substrates are often associated with decomposing organic matter. Since muskellunge eggs and fry are susceptible to low dissolved oxygen (DO) levels, **spawning sites should feature a dark substrate, but only if it has a low intrinsic oxygen demand**.

## Variable 2: Dissolved Oxygen at the Substrate-Water Interface

Some of the most conclusive, quantitative experimental evidence concerning the importance of dissolved oxygen to successful spawning comes from work by Dombeck *et al*. (1984b). The authors investigated **i)** the effects of different substrate types (n=7, 5 replications) on the dissolved oxygen (DO) values at the sediment-water interface of stagnant microcosms, and the impact of these DO levels on muskellunge egg survival; and compared **ii)** differences in field-measured values of sediment/water interface DO in self-sustaining lacustrine populations (n=4) with lacustrine populations supported by stocking (n=4). They demonstrated through their laboratory experiments that **i)** microcosm DO values that were very low (0-0.1 mg/L) led to egg death presumably due to asphyxiation, while levels above a certain value (>3.8 mg/L) tended to favour early mortality due to the rapid onset and proliferation of fungal colonies (which fared well under these oxygen regimes). DO levels intermediate to these two values (0.4-1.7 mg/L) achieved the highest survival rates, presumably due to the trade-off between fungal infestation and asphyxiation (Dombeck et al. 1984b). In addition, Dombeck et al.'s (1984b) field studies demonstrated that **ii)** self-sustaining muskellunge populations used spawning sites that were consistently more oxygenated at the substrate-water interface than those of stocked populations. In the field, the most successful habitats had higher DO values in the (high) range of 6-8.4 mg/L, whereas the spawning sites of stocked (non-self-sustaining) populations had DO values closer to 4 mg/L. The disparity between the successful laboratory DO values (0.4-1.7 mg/L) and the successful field DO values (6-8.4mg/L) may exist because stagnant laboratory conditions cannot suppress fungal infections as well as *in situ* conditions (where current flow and other countermeasures are more likely), and thus a lower DO value may be of greater relative importance *in vitro*. In general, the study implies that there is a minimum DO value essential for successful spawning.

To investigate this point further, Clapsadl (1993) exposed muskellunge sac fry (n=10 treatments of 5 fry each) to different oxygen regimes in the field and demonstrated that low DO values (<0.43 mg/L) can lead to increased mortality. In addition, Gilbertson (1986) noted that radio-tagged juvenile muskellunge preferentially avoided areas of low oxygen concentration in shallow winterkill lakes, and that significant mortality (23% of trapped individuals) occurred at concentrations below 0.4 mg/L. Muskellunge eggs and sac fry are especially vulnerable to oxygen depletion at the sediment-water interface because they lack the cephalic gland found in pike and other esocids that allows them to attach to vegetation higher up in the water column upon hatching (Dombeck et al. 1984b).

Although the available field evidence suggests that successful spawning depends on DO levels above 6 mg/L (Dombeck et al. 1984b; Lebeau 1992), some laboratory results suggest that eggs can persist at lower levels (Dombeck et al. 1984b); hence, in our conceptual model, we assume that **substrate-water interface DO must exceed 5 mg/L.** Table 2 summarizes the minimum DO concentrations at the substrate-water interface associated with successful spawning. This dataset is not extensive because the technique used to collect the information (i.e. micro-Winkler collection method (Dombeck et al. 1984a)) is not commonly used for routine monitoring, and so published sources are limited.

### ***Conditions Influencing Dissolved Oxygen at the Substrate-Water Interface***

#### *Current Flow*

In addition to promoting thawing and warmer temperatures, current flow may also play a role in maintaining good oxygenation at the substrate-water interface. By flushing out anoxic water and naturally-occurring toxins such as hydrogen sulphide (Adelman and Smith Jr. 1970), a slight current can help prevent deoxygenation at the substrate-water interface normally resulting from respiration and chemical reduction processes (Whittemore 1986; Clapsadl 1993). For its role in promoting higher high DO levels, our model thus re-emphasizes the need for some **measurable current flow for successful spawning**.

#### *Sediment Oxygen Demand*

Sediment oxygen demand (SOD) refers to the bacterial and chemical processes that use up oxygen at the sediment/water interface (Hatcher 1986). Oxygen at this stratum is also used by eggs and fry as they develop. Ideal spawning habitat features minimal SOD, maximizing the oxygen available to young muskellunge. Experiments have confirmed that substrates with lower intrinsic SODs, such as gravel, sand and wood (in order of increasing SOD) (Dombeck et al. 1984b) can result in higher egg survival than can high-SOD substrates such as decaying leaves. This is been echoed in field situations where successful spawning is often associated with low-SOD substrates (e.g. Lebeau 1983; Dombeck et al. 1984b; Lebeau 1992; Lane et al. 1996a; Zorn et al. 1998). The conceptual model presented here assumes that **substrates with a low sediment oxygen demand (e.g. gravel)** will be most suitable for successful spawning.

The SOD at a particular habitat depends on a number of site-specific factors, and no single reliable predictor has emerged for all sites. Current methods of direct measurement involve expensive and time-consuming *in situ* or laboratory-based measurements. Although Dombeck et al. (1984b) and Clapsadl (1993) have assumed organic carbon content to be a good predictor of SOD, evidence from Hatcher (1986) disputes this, showing that the relationship between a sediment's organic characteristics and oxygen demand to be inconsistent. Although some studies have shown that carbon input (Borsuk et al. 2001) or organic content (House 2003) can account for substantial amounts of the variation in the SOD of a site, other studies have shown that other variables such as the chemical (e.g. Polak and Haffner 1978; Walker and Snodgrass 1986) and biotic composition of the sediment (Walker and Snodgrass 1986), as well as its overall degradability (Walker and Snodgrass 1986) may have confounding effects. Studies of successful muskellunge spawning habitats show that organic contents can range from 15% (Lebeau 1983; Dombeck et al. 1984b) to 25% (Lebeau 1992; Zorn et al. 1998) to 100% (Lebeau 1992).

In addition to this seeming lack of consistency between organic content and SOD and spawning success, there is often considerable within-site variability of sediment organic content (Walker and Snodgrass 1986), and thus a coarse-grained sampling effort that relies on organic carbon values to estimate SOD and spawning potential on large scales may lead to inappropriate generalizations. Identifying a more consistent predictor of SOD for a given area, as well as knowing the boundaries associated with any given prediction, would be useful for future spawning habitat evaluations.

At present, particle size may be the best predictor of sandy or gravely substrates (vs. silt or loam), which generally have a lower SOD, and which in turn can correlate positively with spawning-site success (Werner 1990). For relatively heterogeneous substrates however, this technique may not be particularly powerful or informative.

### *Sediment Compactness*

Oxygen depletion at the sediment-water interface is directly related to the surface area of sediment exposed to the water (House 2003), and therefore to its degree of compactness. Therefore, sediments that are more compact, with less surface area and correspondingly lower SOD, may be more desirable in spawning habitats. The degree of compactness is particularly important for substrates consisting of materials with a high intrinsic oxygen demand, such as those made of mostly organic materials. Compacting high-SOD substrates helps to minimize their overall impact on the surrounding DO.

Dombeck (1986) speculates that compacted sediment may often be created as the result of late-summer drops in water level and exposure of the substrate to air. This process probably also helps to re-oxygenate sediments before the next seasonal inundation (Dombeck et al. 1986), contributing to high DO levels at the sediment-water interface the following spring. Thus, in addition to having a lower intrinsic oxygen demand, compacted sediments may also be indicative of regular external oxygenation.

Furthermore, looser sediments are suspected to contribute to increased burying and suffocation of eggs during adult spawning behaviours, which usually resuspend fine particles as the caudal region of the fish is swept from side to side (Dombeck et al. 1984b). Organic sediments are generally lighter and more likely to be resuspended than silicaceous ones, and so this concern applies more so to organic particles than to sand and gravel.

For the reasons discussed above therefore, in this conceptual model, s**uitable spawning habitat should have heavy and compacted sediment.**

### *Plant Density*

Clapsadl (1993) theorized that excessively dense plant growth over a spawning site may contribute to reduced water exchange, and consequently to increased muskellunge egg and sac fry mortality. His research found a negative association between the dominance of *Chara* sp., a densely-growing macroalgae, and the success of spawning habitats in the St. Lawrence River (Clapsadl 1993; Werner et al. 1996). Since *Chara* grows at far greater densities than other submergent macrophytes at his test sites, it seemed likely that this physical property was responsible for the observed increase in egg mortalty. By comparison however, other researchers (Black and Craig 1982; Dombeck et al. 1984b) found that the presence of abundant *Chara* in Minnesota and Georgian Bay did not interfere with spawning success. Clapsadl (1993) explained the apparent inconsistency by suggesting that sites in the St. Lawrence River may have sediments with a higher average SOD than those in Minnesota or Georgian Bay, and that the combination of *Chara*-induced current reduction *as well as the high SOD* created an overall oxygen depletion that gave rise to unfavourable conditions there. Combined with a high sediment oxygen demand and a low current flow therefore, high plant density could severely limit reproductive success, and so is not desirable at muskie spawning sites.

Still, most good nursery sites appear to have moderate, rather than low plant density (e.g. Black and Craig 1982), presumably because the adults and newly-emerged fry benefit from protection provided by the plant cover, without having to sacrifice foraging opportunities. Since nursery habitats are generally contiguous with spawning sites (Black and Craig 1982) and likely involve some overlap, in our conceptual model, we have assumed that **suitable spawning habitat should have moderate plant density,** since this maximizes both DO levels and protection from predators/foraging success after hatching.

Our definition of what is optimal plant density is more plastic than others in this model. We recommend that the degree of current flow and sediment oxygen demand for any particular site be considered along with plant density, and that optimal plant densities be adjusted accordingly, with lower SOD and higher current flows allowing for somewhat denser plant growth.

### Variable 3: Spatial Separation of Eggs

Fungal (*Saprolegnia sp.)* infections have been frequently observed in aggregated, high-density cultures of muskellunge eggs (e.g. Dombeck 1986; Zorn et al. 1998); it is for this reason that culturists often add dilute amounts of formalin during the incubation process (Klingbiel 1986; Farrell and Werner 1999). Incidental observations by Dombeck et al. (1984b) suggest that substrates that encourage the spatial separation of eggs may also inhibit the proliferation of fungal infections. Added advantages of spatial separation probably include a reduced intraspecific competition for oxygen, and an increased chance of survival because of the increased diversity of microhabitats that are likely to be encountered by the broadcast eggs (Zorn et al. 1998). Muskellunge females have a urogenital structure that propels eggs from the body at an angle, which, in combination with fin movement, assists in their dispersal (Lebeau and Pageau 1989). The northern pike, with its increased post-hatching adaptations to low dissolved oxygen, is less dependent on spawning microhabitat quality and lacks this propelled-egg dispersal ability (Dombeck et al. 1984b). Compared with pike, muskellunge therefore appear to be at least somewhat behaviourally and morphologically designed to maximize the spatial separation of their eggs, and therefore spatial separation must provide some reproductive advantage, presumably one or more of those discussed above. In this model, we assume that **high spatial separation of eggs should contribute to spawning success.**

### *Conditions Influencing Spatial Separation of Eggs*

#### *Particle Size*

By definition, larger particle sizes should lead to larger gaps between particles. Assuming that muskellunge eggs are dispersed in a propelled, broadcast fashion (as discussed above), there is a greater chance that eggs will remain separated from each other after settling if substrate gap sizes are sufficiently large to prevent further egg movement. Therefore, in addition to the correlation between low sediment oxygen demand and particle size (Werner 1990), **particles that approach or exceed the size of muskellunge eggs** (which consequently create interstitial spaces that separate the eggs from each other) **are a desirable attribute of successful spawning substrates**.

#### *Plant Density*

While moderate submergent plant density may favour esocid foraging opportunities (Casselman 1978) and fry protection, it may also contribute to the spatial separation of eggs by providing supportive surfaces on which the eggs can land (Dombeck et al. 1984b). Submergent macrophytes with a high degree of structural complexity (and associated surface area) such as *Chara sp.* (Dombeck et al. 1984b) are especially good candidates for facilitating this separation. Assuming that sediment oxygen demand is low, the benefits conferred by *Chara* under specific, low SOD conditions may outweigh its potential for deleterious current and DO reduction (see “Plant Density” in “Conditions Influencing Dissolved Oxygen at the Substrate-Water Interface”). Therefore, **a moderate submergent plant density, or alternatively, submergent plants with high structural complexity (and associated density) in combination with a low sediment oxygen demand, are desirable attributes of successful spawning habitats**.

This model has yet to undergo field validation, which is an essential next step in refining and improving the ideas expressed here, in addition to establishing its predictive power and its usefulness as a management tool. We support and encourage future research using this model as a starting point.

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**Table 1. Summary of literature that reported on the range of temperatures associated with muskellunge spawning**

| Source | Location | Data Type | Range of Temperature ($^oC$) |
|---|---|---|---|
| Klingbiel 1986 | Culture | Generalized optimum | 12.8 – 14.4 |
| Scott and Crossman 1998 | Generalized | Generalized | 9.4 – 15 |
| Minor and Crossman 1978 | Kawartha Lakes, Ontario | Empirical | 10.5 - 15.5 |
| Crossman 1990 | Kawartha Lakes, Ontario | Generalized | begins at 7 |
| Strand 1986 | Minnesota | Empirical | 11.6 – 14 |
| Lebeau 1983 | Northwestern Ontario | after Dombeck 1979 | 10 – 14 |
| Lebeau 1983 | Northwestern Ontario | Empirical | 12 – 20 |
| Garland 1972 | Ohio | Generalized optimum | 12.5-14.5 |
| Farrell 2001 | St. Lawrence | Empirical | 13.2 - 18.1 |
| Farrell and Werner 1996 | St. Lawrence | meta-analysis | 7.5 – 15 |
| Gammon 1986 | Wisconsin | Empirical | 14 – 16 (site 1) |
| Gammon 1986 | Wisconsin | Empirical | 7.5 – 10 (site 2) |
| Klingbiel 1986 | Wisconsin | Generalized | 7.2 – 13.3 |
| Oehmcke et al. 1958 | Wisconsin | Generalized | 9.5 – 15.5 |
| Zorn 1998 | Wisconsin | Empirical | 6 – 14 |

**Table 2. Summary of literature that reported on dissolved oxygen (DO) levels at the substrate-water interface associated with muskellunge spawning .**

| | Location | Data Type | DO concentration (mg/L) |
|---|---|---|---|
| Lebeau 1983 | Northwestern Ontario | Empirical | 10.4 (mid-column) |
| Lebeau 1992 | Northwestern Ontario | Empirical | 6.3 (riverine) |
| Lebeau 1992 | Northwestern Ontario | Empirical | 4.65 (lacustrine) |
| Dombeck 1984 | Wisconsin | Empirical | >6 (self-sustaining lakes) |
| Dombeck 1984 | Wisconsin | Empirical | >0.2 (likely minimum for egg stage only) |
| Zorn 1998 | Wisconsin | Empirical | >0.5 (self-sustaining lakes) |

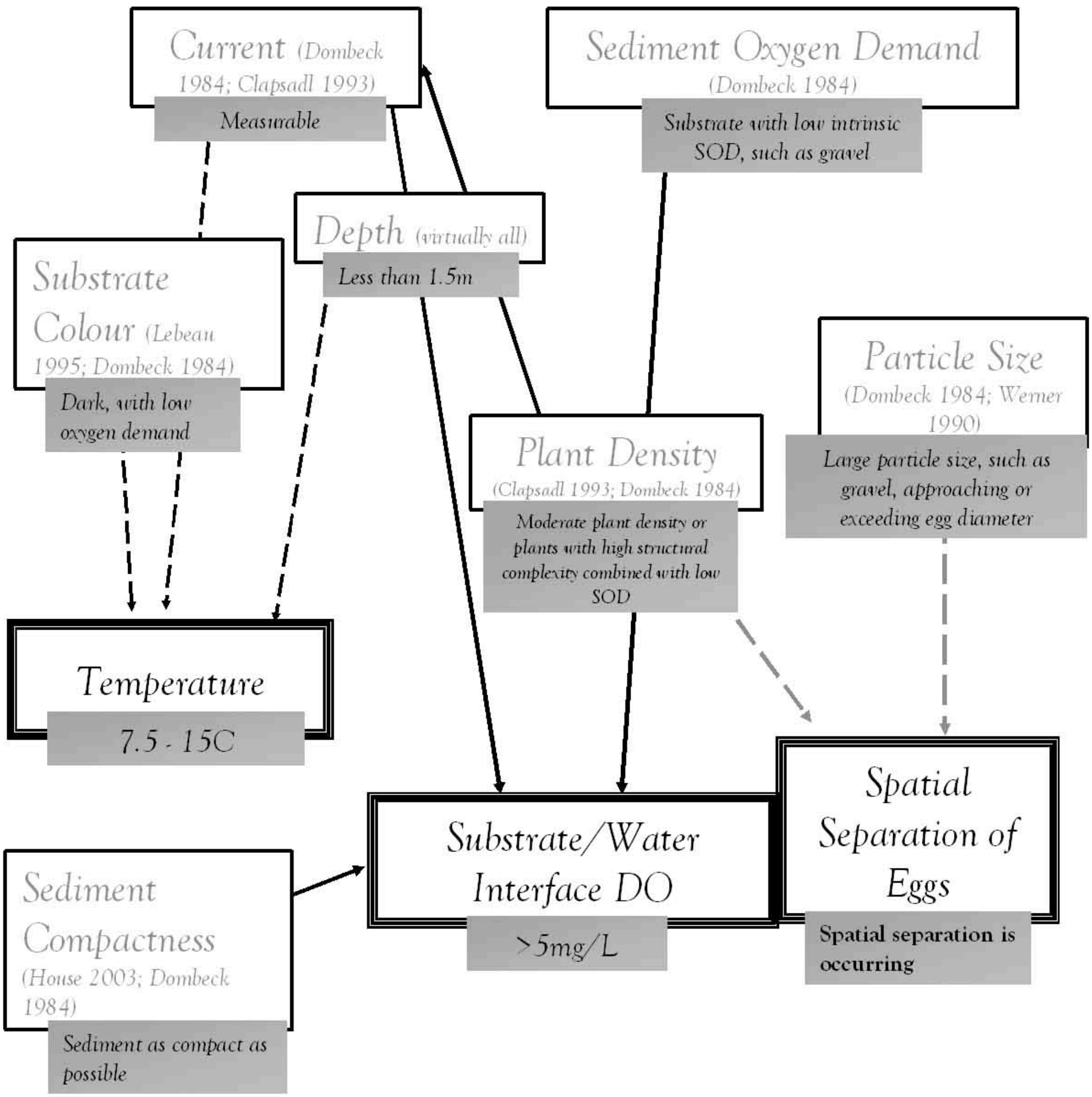


**Figure 1**. **Conceptual model of how factors influence the quality of muskellunge spawning habitat.**

Arrows refer to contributions of these factors to key variables (temperature, substrate-water interface, dissolved oxygen concentration and spatial separation of eggs).