Haro, A. 2003. Downstream migration of silver-phase anguillid eels. Pages 215-222 in:
Aida, K., K. Tsukamoto, and K. Yamauchi, eds. Eel Biology. Springer, Tokyo.

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Downstream Migration of Silver-Phase Anguillid Eels

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1. Introduction

Downstream migration of adult anguillid eels in freshwater habitats marks the end of a long, generally slow growth phase, abandonment of a home range, and initiation of a seaward spawning migration. Although different species of *Anguilla* exhibit variation in characteristics of this migratory phase, some generalized traits in migration are common to most species. For temperate and subtropical species of *Anguilla*, migratory periods are usually associated with times of year when water temperatures are decreasing and flows are increasing. Species of *Anguilla* in the northern hemisphere usually emigrate between the months of August and December, while those of the southern hemisphere leave freshwater habitats between January and March. In the northern hemisphere, *A. rostrata* tends to emigrate earlier at higher latitudes (Fig. 1). However, Tesch (1977) concluded that the migration date of *A. anguilla* could not be predicted on the basis of geography alone. Onset of the silver migratory phase is generally morphologically characterized in most species of *Anguilla* as a darkening of dorsal surfaces and fin margins, silvering of lateral integument, enlargement of eye diameter, and an increase in gonad development (Lecomte-Finiger 1990). Other endocrinological changes also occur during metamorphosis (Durif et al. 2000).

Studies of the American eel indicate that males mature and migrate at a smaller size and younger age than females, which led to a hypothesis by Helfman et al. (1987) that male American eels use a time-minimizing strategy and migrate at the earliest possible age, whereas females maximize size and migrate at an optimal body size. This strategy (or a variant thereof; see Oliveira 1999) may also hold for other species of *Anguilla* that exhibit similar sexual dimorphism in age and size at migration. Sexes may also differ in that male eels tend to appear in weir catches

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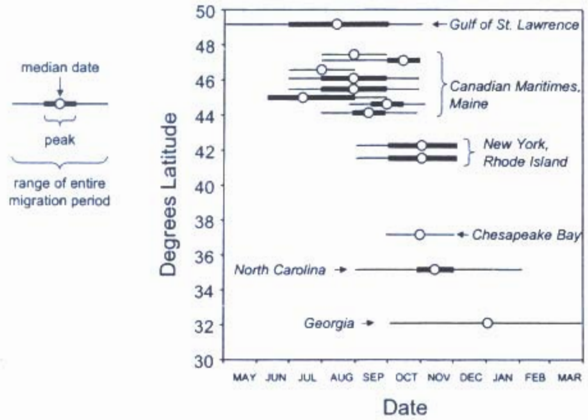

Fig. 1. Estimated dates of emigration of silver-phase *Anguilla rostrata* from North America. Data were compiled from published literature and a survey of management agencies for reported run timing dates from commercial weir catches. (See Haro 1989)

earlier in the migratory season than females (Jessop 1987), but this may be due to differential distribution of sexes within a watershed (e.g., higher proportion of females tending to occur in upper reaches) rather than differences in migration timing between the sexes.

2. Timing of Migration

Downstream migration of eels has been historically investigated and characterized by quantification of commercial eel catches in traps, weirs, and fyke nets. Because most eel catches occur at night, primarily within the first few hours after sunset, downstream migration is assumed to be largely nocturnal. Earlier studies suggest that downstream movements are regulated by the lunar cycle, as evidenced by increased weir catches primarily during the last quarter and dark phases of the moon (Frost 1950; Lowe 1952; Deelder 1954).

In general, timing of downstream migration in *Anguilla* is controlled at both developmental and behavioral levels (Fig. 2). Timing at the developmental level is linked to life history, which determines when a particular individual will emigrate within its lifetime. Primary factors involved in premigration metamorphosis are thought to be either intrinsic, that is, thresholds established by sex, or accumulated over an individual's lifetime: body size, age, and possibly growth rate (Oliveira 1999). Metamorphosis from the yellow phase to the silver phase begins weeks to months before migration (Fontaine 1994) but has been documented to be reversible (Dollerup and Graver 1985).

Migratory timing at the behavioral level is related to environmental factors that determine when an individual will emigrate within a migratory season and can also modulate migration en route. Temperature and photoperiod may act as physiological primers for the onset of migration in eels (Hansen et al. 1995), as they do for juvenile anadromous salmonids. Although eel runs tend to peak within a par-

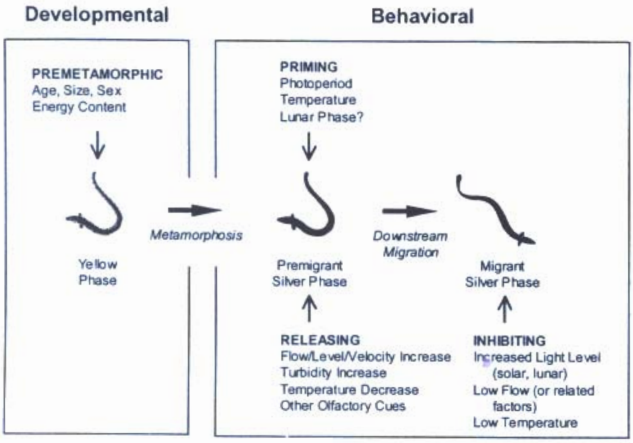

Fig. 2. Hypothetical mechanism for metamorphosis and onset of downstream migratory behavior of *Anguilla*, as influenced by developmental and behavioral (environmental) factors. Note that releasing factors can be indirectly related to significant precipitation events

ticular temperature range (Todd 1981; Vøllestad et al. 1986), or are associated with short-term decreases in temperature, there does not appear to be an absolute temperature that acts a trigger for downstream migration of any species. Among environmental factors that may act as migratory cues, river flow as induced by precipitation predominates among eel species (Table 1). The actual sensory cues that trigger migration associated with increased flow may involve factors related to flow events, primarily precipitation, turbidity, olfactory cues, or low atmospheric pressure, rather than flow per se. Other factors [e.g., increased light intensity, both at diurnal and nocturnal (lunar) levels] may inhibit migration, either before eels begin downstream movements or while in transit. Few studies have investigated environmental cues in the laboratory (Boëtius 1967; Hain 1975), and although lunar rhythms in activity of silver-phase eels have been detected, other factors have not been fully evaluated under controlled conditions.

3. Rates of Migration

Rates of downstream migration of eels may be rapid in large rivers (Table 2), and have been measured at or near average river velocities [average, 2.7–3.9 km/h for *A. anguilla* (Tesch 1994) and 1.5–4.7 km/h for *A. rostrata* (A. Haro, unpublished data)], as evidenced by telemetry. Downstream movement may therefore involve passive drifting or active swimming in a downstream direction and has been noted to occur at all levels in the water column (Tesch 1994; Parker and McCleave 1997; Haro and Castro-Santos 2000). Telemetered migrants usually stop movement during the day and move to the bottom or suitable cover, although migration may

Table 1. Summary of studies documenting potential factors known to influence downstream migration behavior in *Anguilla*

Study	Species	Environmental Factor					Experiment type	Data type
		Flow	Water temperature	Lunar phase	Rainfall	Other		
Frost 1950	*A. anguilla*	A (+)		A (+, dark)		wind (+)	Field	Weir
Lowe 1952	*A. anguilla*	A (+)	A (*)	A (+, dark)			Field and lab	Weir, activity in tank
Deelder 1954	*A. anguilla*	A (+)		A (+, dark)		microseisms (+)	Field	Weir
Boëtius 1967	*A. anguilla*			A (+, dark)			Lab	Activity in tank
Haraldstad et al. 1985	*A. anguilla*	A (+)	A (*)			low light intensity (+)	Field	Weir
Hvidsten 1985	*A. anguilla*	C (+)		C (+, dark)		barometric pressure (−)	Field	Weir
Vøllestad et al. 1986	*A. anguilla*	C (+)	†				Field	Weir
Pursiainen and Tulonen 1986	*A. anguilla*	A (+)		A (+, dark)	A (+)		Field	Weir
Poole et al. 1990	*A. anguilla*	A (+)		A (+, dark)			Field	Weir
Hansen et al. 1995	*A. anguilla*	A (+)	A			photoperiod (primer)	Field	Weir
Durif et al., in press	*A. anguilla*	C (+)				turbidity (+), conductivity (+)	Field	Weir, telemetry
B. Adam, unpublished data	*A. anguilla*	A (+)					Lab	Activity in tank
Therrien and Verrault 1998	*A. rostrata*	A (+)	A (*)				Field	Weir
Smith and Saunders 1955	*A. rostrata*	A (+)			A (+)		Field	Weir
Haro et al. 2002	*A. rostrata*				C (+)		Field	Weir
Todd 1981	*A. dieffenbachii*	A (+)		A (+, dark)	A (+)		Field	Weir
	A. australis	A (+)		A (+, dark)	A (+)		Field	Weir
Sloane 1984	*A. australis*		C (+)				Field	Weir
Boubée et al. 2001	*A. dieffenbachii*	A (+)	A (*)		A (+)		Field	Weir, telemetry
	A. australis	A (+)	A (*)		A (+)		Field	Weir, telemetry
J. Aoyama, unpublished data	*A. japonica*	A (+)	A (*)	A (+, dark)			Field	Weir

A, observed association between factor and downstream movement; C, statistical correlation between factor and movement
Sign in parentheses indicates a positive or negative relationship; *, temperature decrease, rather than absolute temperature; †, maximum activity at an intermediate temperature (9°C); dark, darker lunar phases (e.g., quarter moon, new moon)

continue during daylight hours under heavily overcast conditions or when the water is turbid. Delays in downstream migration may occur when passing through lakes (Vøllestad et al. 1986) or within impoundments created by dams (Haro and Castro-Santos 2000). Delays may also occur at hydroelectric projects, where eels can spend considerable time in search of an exit to a forebay intake rather than pass through trashracks or other obstructions (Haro and Castro-Santos 2000). Eels also avoid illuminated areas during downstream migration at night (Lowe 1952; Hadderingh et al. 1999). Migration may pause when eels reach estuarine or tidal environments or be modulated by tidal transport (Parker and McCleave 1997). There is some evidence that silver-phase eels may not complete downstream migration in one season, and may resume migration after the winter months in the spring (Tesch 1977) or subsequent fall (Vøllestad et al. 1986).

4. Conclusions

Current knowledge of downstream movement in silver-phase *Anguilla* is based to a large extent on studies of temperate and subtropical species, primarily *A. anguilla* and *A. rostrata*, and to a lesser extent on *A. australis* and *A. dieffenbachii*. Downstream migration in tropical *Anguilla* is not well documented; migration strategies, timing, and mechanisms may be different for these species.

Characterization of eel downstream migration has been highly dependent on weir and trap data. The intermittent and irregular nature of catches as quantified by these intercept methods suggests that downstream movements are rapid and strongly coupled with environmental factors, primarily those factors related to precipitation and resulting increases in river flow. Movement during increased flow events could be viewed as adaptive for outmigrant eels in that it minimizes transit time through the watershed and potentially reduces encounters with natural obstructions (i.e., debris or shallow river runs) or predators that could make downstream migration during low flow more energetically arduous or hazardous. However, whether eels migrate downstream without stopping once they have been motivated to emigrate, or move only during periods when environmental conditions permit, is less well understood. In long or heavily dammed river systems, periods of downstream movement may be less peaked and not as strongly correlated to environmental conditions as in smaller or tributary systems (Fig. 3). Silver-phase eels may also take more than one migratory season to emigrate from freshwater and may have a flexible maturation process that can accommodate delays in emigration of silver-phase eels of up to several years (Svedäng and Wickström 1997). Future studies involving continuous, long-term tracking of individuals (e.g., telemetry) or controlled laboratory tests of environmental influences on maturation, metamorphosis, and migratory activity would help to clarify these behavioral traits.

Better knowledge of timing and environmental influences on downstream migration in *Anguilla* is especially important for efforts in protecting eels from mor-

Table 2. Rates of downstream migration of silver-phase *Anguilla* in rivers estimated using mark-recapture and telemetry methods

Species	Rate (km/day)	Method	Study
A. anguilla	0.1–0.3	Mark-recapture	Haraldstadt et al. 1985
A. anguilla	65–94	Telemetry	Tesch 1994
A. australis	52	Telemetry	Watene et al. 2002
A. rostrata	10.3	Telemetry	Desrochers 2001
A. rostrata	4–69	Telemetry	A. Haro, unpublished data

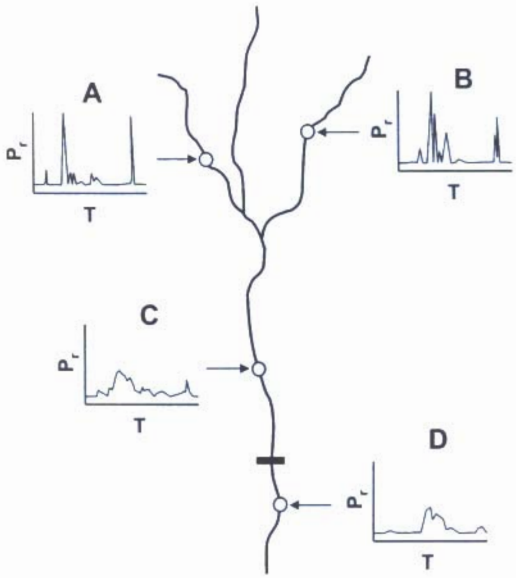

Fig. 3A–D. Potential scenario for variation of silver-phase eel run timing within a large watershed, expressed in plots as proportion of the run (P_r) as a function of time (T). Runs in tributaries (**A**,**B**) are strongly peaked and intermittent, and closely linked with precipitation/flow events; tributaries that are geographically close to one another exhibit similar run timing curves. In the river mainstem (**C**), peaks in downstream movement may be more damped. Below dams or other obstructions to downstream movement (**D**), peaks of movement may be delayed

tality, injury, and delay at dams and hydroelectric projects. Because pulses of downstream migration are linked with precipitation and flow events, it may be possible to predict periods when these pulses occur from meteorological or upstream flow conditions. Modification of project operations (e.g., increased spill) during predictable periods of downstream migration may appreciably reduce entrainment mortality and enhance spawner escapement.

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