POTENTIAL EFFECTS OF WATER WITHDRAWALS ON BLUE CRABS, WHITE SHRIMP, BROWN SHRIMP, AND PINK SHRIMP

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Potential effects of water withdrawals on blue crabs, *Callinectes sapidus*, white shrimp, *Litopenaeus setiferus*, brown shrimp, *Farfantepenaeus aztecus*, and pink shrimp, *Farfantepenaeus duorarum*

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Water withdrawals will alter the hydrology of the St. Johns River, but the river has always been dynamic. The central issue is whether water withdrawals will alter the river's hydrology, and subsequently its ecology, detrimentally and beyond its normal range of variation.

Callinectes sapidus, blue crabs, *Litopenaeus setiferus*, white shrimp, *Farfantepenaeus aztecus*, brown shrimp, and *Farfantepenaeus duorarum*, pink shrimp, represent four valuable species influenced by the hydrology and ecology of the St. Johns River. In fact, the St. Johns River represents a valuable nursery area for these species (Beck et al. 2001; Beck et al. 2003). Key interactions between these species and conditions in the St. Johns River fit with the concept of an overlap between dynamic and stationary habitats (Browder and Moore 1981; Peterson 2003). Physiological tolerances determine important limits, i.e., upstream and downstream boundaries set by salinity, but habitat use and the resulting effects on recruitment, feeding and predation also exert strong influences. In particular, postlarval crabs and shrimp benefit from access to vegetated habitats. Any major alteration in the overlap between zones of suitable salinity and vegetated habitats could alter the abundances and distribution of these valued species significantly. This review of literature pertaining to the biology and ecology of these target taxa provides insights into the effects of water withdrawals by documenting likely responses to changes in salinity, habitats use and recruitment. Such insights can be coupled with the predicted effects of water withdrawals to forecast changes in the ecology and productivity of the St. Johns River.

Distribution, life history and general ecology of blue crabs

In the St. Johns River and elsewhere, blue crabs, *Callinectes sapidus*, provide ecological, social and economic value. This species has supported recreational and commercial fisheries for a considerable period of time (e.g., Tagatz 1965, 1968a), and blue crabs perform a variety of ecological functions, including playing a major role in energy transfer within estuaries (Van den Avyle and Fowler 1984).

The native range of blue crabs extends from Nova Scotia to southern Argentina, with different life history stages occupying shallow oceanic, brackish and fresh waters (Guillory et al. 2001a). Blue crabs also have been introduced along Scandinavian, European and Mediterranean coastlines (Williams 1974; Perry et al. 1984).

Blue crabs typically pass through seven zoeal stages and one megalopal stage, with an occasional eighth zoeal stage that typically does not survive to become a megalopa (Hopkins 1943; Costlow and Bookhout 1959; Van Den Avyle and Fowler 1984). The seven zoeal stages span 31–49 d, and megalopae can molt at 6 d or delay metamorphosis for up to 20 d. First zoeae are approximately 0.25 mm long at hatching, and final zoeae measure about 1.0 mm, although growth rates vary with environmental conditions and availability of food (Sandoz and Rogers 1944). Zoeae live a planktonic existence, with early stages found in nearshore, surface waters and later stages potentially transported over the continental shelf (Darnell 1959; Dittel and Epifanio 1982; Van Den Avyle and Fowler 1984; Guillory et al. 2001a). Based primarily on laboratory observations, zoeae are considered planktivorous filter-feeders, with documented consumption of dinoflagellates, copepod nauplii and sea urchin larvae (Hopkins 1943; Costlow and Bookhout 1959; Darnell 1959; Sulkin and Epifanio 1975). Like juvenile and adult crabs, megalopae, which measure about 1 mm, have pinching claws and points on the tips of their legs

(Churchill 1921; Van Den Avyle and Fowler 1984). Megalopae swim freely, can position themselves to use currents for shoreward transport, and occur in higher numbers near the bottom in nearshore waters or near the mouths of estuaries as they approach metamorphosis (Tagatz 1968b; Blanton et al. 1995, 1999; Ogburn and Forward 2009). Megalopae are omnivorous, and they have been observed to eat pieces of fish, shellfish and aquatic plants (Van Engel 1958).

Juvenile "first crab stages" are primarily benthic and typically 2.5 mm wide (Van den Avyle and Fowler 1984). Subsequent juvenile stages migrate into shallower, fresher water in upper estuaries and rivers as they grow and mature (Fischler and Walburg 1962). Many juveniles complete their migration by autumn and early winter, with males tending to move further upstream than females (Van Engel 1958; Tagatz 1968a; Dudley and Judy 1971; Van Den Avyle and Fowler 1984).

Crabs can develop from hatching to 75 mm carapace width within their first year of life, although on average it takes somewhat longer (Williams 1965; Hines et al. 1987). Male blue crabs reach maturity after 18 or 19 postlarval molts, and females reach maturity after 18 to 20 postlarval molts (Van Engel 1958; Archambault et al. 1990). Sexual maturity in both sexes is closely tied to body size (Millikin and Williams 1984); therefore, food (quantity and quality), temperature, salinity and other environmental factors that influence growth or molting also influence the timing of sexual maturity (Millikin et al. 1980; Cadman and Weinstein 1988). At approximately 90 mm carapace width, males can produce sperm and seminal fluid (Van Engel, 1990), but they typically do not mate until they reach approximately 115 mm carapace width due to competition with larger males (Jivoff 1997). Female blue crabs reach sexual maturity following a terminal or pubertal molt, with hormones regulating this process (Soumoff and Skinner 1983; Quackenbush 1986).

Immature females approaching their terminal molt migrate to lower salinity waters and seek out mature males for mating (Van Engel 1958; Darnell 1959; Tagatz 1968a; Judy and Dudley 1970; Jaworski 1972). Mating takes place throughout the year in the St. Johns River (Tagatz 1968a), but it is restricted to limited periods elsewhere. In Chesapeake Bay, for example, blue crabs mate from May through October (Van Engel 1958; Williams 1965). Mating primarily occurs in relatively low-salinity waters, e.g., upper reaches of estuaries and lower reaches of rivers (Darnell 1959; Williams 1965; Tagatz 1968a). Males compete for females that are ready to molt to maturity (terminal molt at about 2 years of age), and each successful competitor cradles a female upright under his body creating what is called a doubler (Williams 1965; Jivoff 1997). The male frees the female as she casts her exoskeleton and grasps her again when she has molted. He inverts her, presses his ventral surface against hers and introduces sperm into her spermathecae via his copulatory stylets. Copulation may last for several hours. After sperm transfer, the female resumes an upright posture, and the male carries her until the new shell hardens. Males can mate more than once during their last three intermolts, whereas females only mate once (Van Engel 1958; Williams 1965). The sperm supply can fertilize more than one batch of eggs, with egg laying commencing 2–9 months after mating, a second spawning occurring later in the same year, and possibly a third spawning in the succeeding or a third year (Van Engel 1958; Williams 1965). Blue crabs typically live for at most three years (Williams 1965).

After mating, females migrate to lower estuaries, sounds, and nearshore spawning areas (Churchill 1921; Darnell 1959; Fischler and Walburg 1962; Oesterling 1976). Fertilized eggs are extruded as a mass or “sponge” that remains attached to hairlike setae on the female’s abdominal appendages until release of larvae (Van Den Avyle and Fowler 1984). The sponge, containing 700,000–2,000,000 eggs, takes about 2 h to form (Churchill 1921; Williams 1965). Initially, eggs are bright orange, and they become yellow, brown and finally dark brown before hatching (Van Engel 1958). The color changes because yolk is absorbed and dark pigment develops in the eyes of the larvae (Sandoz and Rogers 1944; Van Engel 1958; Costlow 1967). Eggs are about 0.25 mm in diameter, and incubation generally requires 1–2 wk (Churchill 1921). In the St. Johns River and elsewhere in Florida, females that mate in the spring or summer spawn 1–2 months later, and a second spawning is possible (Tagatz 1968a; Steele 1979). A peak in spawning activity occurs from October through December, with some spawning from March through December whenever water temperatures exceed 22°C (Tagatz 1968a; Steele 1979). Spawning seasons tend to become more distinct and significantly shorter in places and during years when temperatures are low probably due to slower growth and maturation (Van Den Avyle and Fowler 1984).

Direct effects on blue crabs via salinity tolerances

The salinity tolerances of blue crabs change throughout their life history (Table 1; Figure 1). Early life history stages, zoeae, inhabit nearshore waters, which probably represents an adaptation that, among other things, reduces benthic predation and increases dispersal (Thorson 1950; Scheltema 1986; Pechenik 1999). Megalopae and juvenile crabs transition into estuarine and riverine habitats. At non-stressful temperatures, crabs can tolerate a wide range of salinities, with individuals occupying and surviving in freshwater (0 ppt) and hypersaline water (≥ 60 ppt), especially if they have time to adapt to changing conditions (Guerin and Stickle 1992; Guillory et al. 2001a). Adult males move furthest upstream because females do not osmoregulate as well and they migrate to higher salinity waters to spawn.

Table 1. Observations relating to the salinity tolerance of *Callinectes sapidus*.

Type Observation	Reference
Field	
Optimal hatching 23–30 ppt	Guillory et al. 2001a
Larvae mostly found in 12–36 ppt	Tagatz 1968a
Some larvae in 9–27 ppt	
Larvae required ≥ 15 ppt	Guillory et al. 2001a
First zoeal molt required ≥ 20 ppt	
Larvae found in 15.8–32.4 ppt	Sandifer 1973
Most larvae in 20–30 ppt	
Megalopae found down to 4 ppt	Millikin and Williams 1984
Most megalopae at ≥ 20 ppt	
Juveniles migrate into lower salinity waters	Van Engel 1958 Sulkin 1977
First instar crabs and juveniles of 3–10 mm carapace width in 15–20 ppt	Millikin and Williams 1984
Juveniles of 10–20 mm carapace width in < 10 ppt	
Juveniles of 20–40 mm carapace width in < 5 ppt	
Juvenile crabs in maximum numbers at < 5 ppt or ~15 ppt	Perry, et al. 1984
Adults reach Lake Harney (305 km up the St. Johns River) in part due to salt springs	Tagatz 1968a
Males more numerous upstream	
One reason for this penetration upstream is the presence of salt springs	Odum 1953
Adults found in freshwater and 60 ppt	Guillory et al. 2001a
Adults survive from 0 ppt to 66.5 ppt if adapted to low or high salinities	Guerin and Stickle 1992
Laboratory	
Temperature and salinity interact	Costlow 1967
Higher temperature reduces tolerance of low salinity	Millikin and Williams 1984
Lower temperature reduces tolerance of high salinity	
Optimum for hatching is 23–28 ppt at 19–29°C	Sandoz and Rogers 1944
Successful hatching recorded at 18 and 26 ppt	Davis 1965
No hatching success at < 20.1 ppt	Millikin and Williams 1984
Hatching and zoeal survival require 22–28 ppt	Van Den Avyle and Fowler 1984
Prezoeae die at low salinity	Van Engel 1958
Zoeae develop best at 20–30 ppt and 25°C	Costlow and Bookhout 1959

Type Observation	Reference
Zoeae less active at < 19 ppt and > 29 ppt, with longer survival at higher salinities	Sandoz and Rogers 1944
Later larvae have narrower salinity tolerances	
Megalopae and crabs tolerate salinities down to 5 ppt	Van Den Avyle and Fowler 1984
Megalopae develop best at 30 ppt and 25°C	Costlow 1967
Megalopae metamorphose by 34 d in 15°C and 20 ppt and by 58 d in 15°C and 40 ppt	Costlow and Bookhout 1959
Salinity not critical for postlarval crabs	Odum 1953 Costlow 1967 Van Den Avyle and Fowler 1984
Crabs survive at 100–1000 ppm Cl and 25–100 ppm Cl	Odum 1953
Juveniles of 20–139 mm carapace width grew on average 13.8–32.0 mm in 7.5–25.8 ppt	Tagatz 1968b
Juveniles of 20–139 mm carapace width grew on average 16.2–31.5 mm in freshwater	
The intermolt interval varied with temperature and size of the pre-molt crab but not salinity	
Juveniles grow and survive in 2–21 ppt	Holland et al. 1971
No change in food conversion rate for 4–40 mm juveniles at 6, 11, 16 and 21 ppt	
Adult crabs tolerate 35.2°C maximum in 36 ppt and 3.2°C minimum in 8.6 ppt	Millikin and Williams 1984
Active transport to resist osmotic stress begins at < 26 ppt	Mantel 1967
Crabs molt in low salinity water	Hines et al. 1987
Numbers of males decrease in salinities > 10 ppt	Van Den Avyle and Fowler 1984
At 7 ppt, females and juveniles less tolerant of 6 and 30°C than males	Tagatz 1969
Prior acclimation at higher temperature moderates response	
Ovigerous females osmoregulate less effectively than males and non-ovigerous females at 10, 20 and 30°C and 1.7, 17 and 34 ppt	Tagatz 1971
Females osmoregulate less effectively than males at 20°C and 10, 20 and 30 ppt	Tan and Van Engel 1966 Millikin and Williams 1984
Females grow equally well at terminal molt in 9, 16 and 27 ppt	Haefner and Shuster 1964
Females grow equally well at terminal molt in 10, 20 and 30 ppt	Haefner 1964
Females grow equally well at terminal molt in > 5 and < 1 ppt	Tagatz 1968b

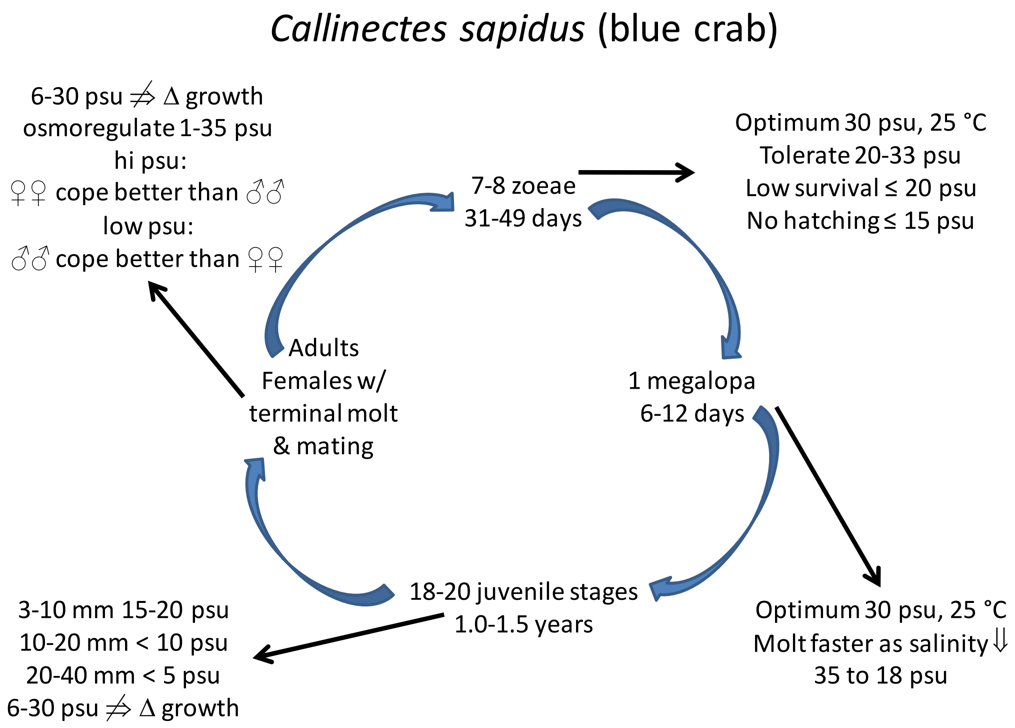

Figure 1. Diagrammatic summary of the life history and approximate salinity tolerances of *Callinectes sapidus*. ♀♀ = females; ♂♂ = males; ↛ = does not yield; ⇓ = decreases

Direct effects of water withdrawals on blue crabs via altered salinity regimes appear unlikely. Larval blue crabs require oceanic salinities, and the broad physiological tolerances of juveniles and adults are unlikely to be exceeded over large expanses of the St. Johns River. Overall, the key to sustaining blue crab populations in the St. Johns River is likely to be the maintenance of a range of salinity regimes. Importantly, these regimes need to overlap suitable habitat because blue crabs garner improved refuge and foraging in certain habitats.

Indirect effects on blue crabs via habitat alteration

Callinectes sapidus occupies and partitions a variety of habitats throughout its life history, with habitat use by the estuarine juvenile and adult stages most relevant here (Hines et al. 1987; Hines 2003). Juvenile and adult blue crabs are found on soft substrates (Perry et al. 1984; Tsou and Matheson 2002), but many studies indicate that densities tend to be higher in or near vegetated habitats (Zimmerman et al. 2000; Table 2). The comparative value of submerged aquatic vegetation and saltmarsh varies among regions, with this value partially determined by i) potential to intercept the supply of settlers; ii) density dependent interactions if the number of settlers saturates available space; iii) inundation schedules; iv) variation in temperature, salinity and other physical factors; and iv) habitat complexity (Heck and Thoman 1984; Perry et al. 1984; Orth and van Montfrans 1987, 1990; Mense and Wenner 1989; Thomas et al. 1990; Minello and Webb 1997; Spitzer et al. 2003; Stockhausen and Lipcius 2003). Structural complexity at several spatial scales may affect habitat use, e.g., increased density of shoots and increased length of vegetation–water interfaces in reticulated marshes (Wilson et al. 1990; Etherington and Eggleston 2000, 2003; Orth and van Montfrans 2002; Minello et al. 2008). A meta-analysis of density data for multiple species of nekton indicated that decapod crustaceans, including blue crabs, along the Gulf coast tended to be associated with vegetated habitats more strongly than along the Atlantic coast (Minello et al. 2003). In fact, annual production estimates of 170 kg ha^{-1} of marsh exceeded those for unvegetated habitat by over 8× (Minello et al. 2008). Furthermore, modeling based on the loss of 20% of total coverage of submerged aquatic vegetation in Mobile Bay predicted less than 60% chance of sustaining blue crab harvest if the loss occurred in one 55.2 km^2 cell and less than 70% chance if the loss spread across multiple cells (Jordan et al. 2009).

Table 2. Examples of differences in abundance of blue crabs in three habitats. SAV = various species of submerged aquatic vegetation other than marsh plants

Mean density (number m^{-2})			Reference
Marsh edge	SAV	Unvegetated	
8.5	—	1.0	Zimmerman and Minello 1984
6.0	—	2.5	Thomas et al. 1990
4.2	3.7	0.4	Zimmerman et al. 1990a
10.8	4.0	1.9	Zimmerman et al. 1990b
4.6	—	0.0	Minello et al. 1991
8.7	—	0.5	Minello and Webb 1997 (autumn)
6.8	—	0.4	Minello and Webb 1997 (spring)
11.1	7.5	0.4	Rozas and Minello 1998 (autumn)
10.3	2.5	0.1	Rozas and Minello 1998 (spring)

One key reason that patches of complex, vegetated habitat may yield more crabs, especially early juveniles, is that they limit predation, including density dependent cannibalism (Heck and Wilson 1987; Pile et al. 1996; Guillory et al. 2001b and references therein; Hovel and Lipcius 2001, 2002). Benefits accrue primarily to early instars, in part, because smaller crabs are prey for a wider variety of animals and they molt more frequently, with the risk of predation and cannibalism being greater for soft crabs (Orth and van Montfrans 1987, 2002; Thomas et al. 1990; Steele and Bert 1994; Heck and Coen 1995; Pile et al. 1996; Ryer et al. 1997; Hewitt 2008). Theoretically, predation pressure of 12% d^{-1} can reduce numbers of blue crabs by two orders of magnitude (Heck and Coen 1995). In fact, cannibalism and other density dependent feedbacks influence stock-recruitment relationships that explained up to 73% of the variation in data relating spawning stocks and recruitment (Lipcius and Van Engel 1990).

Loss of vegetation may not decimate blue crab populations if crabs can access shallow water that precludes larger predators, soft sediments, oyster reefs or other alternative habitats (Hines et al. 1987; Mense and Wenner 1989; Zimmerman et al. 1989; Wolcott and Hines 1990; Steele and Bert 1994; Dittel et al. 1995; Hines and Ruiz 1995; Tsou and Matheson 2002; Lipcius 2003; Rakocinski et al. 2003). In addition, improved documentation of emigration from vegetated habitats may reduce estimates of mortality (Etherington et al. 2003). In fact, abundances may increase during the initial stages of habitat loss because fragmentation extends the highly productive vegetation–water interface leading to increased abundances (Zimmerman et al. 2000). Eventually, patches become too small to support high abundances (Zimmerman et al. 2000).

Access to food represents a second key influence linked to habitats. Blue crabs are omnivorous and capable of feeding on a variety of prey if they are available (Laughlin 1982). Nevertheless, access to feeding areas influences foraging success, with access to marshes and other emergent vegetation more dependent on tides than access to submerged aquatic vegetation (Ryer 1987; van Montfrans et al. 1991). At small spatial scales, food availability may dominate salinity as an influence on the distribution and abundance of blue crabs (Seitz et al. 2003).

In the lower St. Johns River, fisheries independent monitoring with 21.3 and 183 m seines provided little evidence of a strong association between blue crabs and any particular habitat, including vegetation (MacDonald et al. 2009). In fact, fewer blue crabs were caught in 21.3 m seines deployed over vegetation (approximate back-transformed means and 95% confidence limits = 2.0 crabs 100 m^{-2} and 1.8–2.2 crabs 100 m^{-2} for vegetated sediment and 2.7 crabs 100 m^{-2} and 2.4–3.0 crabs 100 m^{-2} for unvegetated sediment). The larger seine did capture more blue crabs in vegetated areas, but the difference was small (approximate back-transformed means and 95% confidence limits = 1.6 and 1.3–2.0 crabs 100 m^{-2} for vegetated sediment and 1.2 and 1.1–1.3 crabs 100 m^{-2} for unvegetated sediment).

Indirect effects on blue crabs via alteration of settlement and recruitment

The exact mechanism by which *Callinectes sapidus* megalopae return to estuaries is not fully understood, but a range of factors influence this return, including river discharge, tidal range, the effects of wind-driven surface currents, lunar phase, and vertical migrations (McConaugha et al. 1983; Johnson et al. 1984; Johnson 1985; Goodrich et al. 1989; Johnson and Hester 1989; Johnson and Hess 1990; Boylan and Wenner 1993; Blanton et al. 1995, 1999, 2001; Mense et al. 1995; Epifanio 1995, 2003; Johnson 1995; Olmi 1995; Perry et al. 1995; Rabalais et al. 1995; Morgan et al. 1996; Garvine et al. 1997; Blanton et al. 1999; Roman and Boicourt 1999; Etherington and Eggleston 2000, 2003; Epifanio and Garvine 2001; Hasek and Rabalais 2001; Perry et al. 2003; Forward et al. 2004; Ogburn and Forward 2009). As a consequence, postlarval abundance varies considerably and episodically within and among years and sites (Mense and Wenner 1989; Olmi et al. 1990; van Montfrans et al. 1990; Boylan and Wenner 1993; Olmi 1995; Perry et al. 1995, 2003; Rabalais et al. 1995; van Montfrans et al. 1995; Morgan et al. 1996; Pardieck et al. 1999; Hasek and Rabalais 2001; Spitzer et al. 2003).

Once in an estuary, the timing and distribution of settlement by megalopae also may be influenced by a variety of factors, including an endogenous rhythm, salinity, turbulent kinetic energy, light, physical or chemical cues from vegetation, humic acids, and chemical cues from potential predators (Latz and Forward 1977; Sulkin and Van Heukelem 1986; Forward et al. 1994, 1996, 1997, 2003a; Forward and Rittschof 1994; Wolcott and De Vries 1994; Welch et al. 1997, 1999; Welch and Forward 2001; van Montfrans et al. 2003). In combination, these influences generate a form of selective tidal-stream transport termed nocturnal flood tide transport, which carries megalopae further into estuaries at night (Dittel and Epifanio 1982; Brookins and Epifanio 1985; Mense and Wenner 1989; Little and Epifanio 1991; Olmi 1994; Tankersley et al. 1998; Forward et al. 2003b; Gibson 2003). The currently accepted model has megalopae i) maintaining their positions on the substratum during daytime and nocturnal ebb tides; ii) ascending as salinity rises during nocturnal flood tides; iii) swimming in response to turbulence, which keeps them in the water column during transport into the estuary; and iv) settling as turbulence declines at the end of the flood tide, with active selection among habitats.

Thus, flow and salinity play critical roles in sustaining healthy populations of *Callinectes sapidus*. Determining the exact form and magnitude of their influence on blue crabs in the St. Johns River would require further investigations because evidence suggests spatial and temporal variation (Wilber 1994; Miller 2003; MacDonald et al. 2009). For example, flow from the Apalachicola River, but not four other nearby rivers, was positively correlated with local harvests of blue crabs in the following year, with slightly stronger correlations ($r^2 = 0.32–0.52$) for data from certain periods of time (Wilber 1994). In shallow waters of the Suwannee River estuary, blue crab abundances were negatively correlated with salinity, implying higher numbers at higher flows (Tsou and Matheson 2002). In addition, fisheries independent monitoring in the lower St. Johns River identified several different responses to flow (MacDonald et al. 2009). In the mainstem, crabs of all sizes moved downstream at higher flows, and small crabs (≤ 50 mm carapace width) exhibited peak abundances when average flows over 90 d reached 8 cfs. Overall, fewer crabs of all sizes were caught in the mainstem and backwater reaches as flows increased from approximately 7 to 9 cfs. A targeted investigation of responses to variation in flow and the resulting differences in salinity over different habitats would improve insights gained from this sampling that was designed to identify long-term, broad-scale trends.

In summary, information on habitat use and recruitment could be assembled to make predictions of changes in blue crab abundances once changes in habitats have been identified (Zimmerman 2000). Any predictions could be refined by targeted studies in the St. Johns River, and all predictions should be evaluated by ongoing monitoring.

Distribution, life history and ecology of three penaeid shrimp

Three species of shrimp support commercial and recreational fishing on the east coast of Florida (Pérez Farfante 1969; Bielsa et al. 1983; Muncy 1984; Larson et al. 1989). In the St. Johns River, white shrimp, *Litopenaeus setiferus*, and brown shrimp *Farfantepenaeus aztecus*, are more common than pink shrimp, *Farfantepenaeus duorarum* (Joyce 1965; Pérez Farfante and Kensley 1997).

All three species have fairly broad distributions (Pérez Farfante 1969). White shrimp, *Litopenaeus setiferus*, range from Fire Island, New York to Saint Lucie Inlet, but they do not occur around the southern tip of Florida or north along the Gulf coast to about the mouth of the Ochlockonee River. Brown shrimp *Farfantepenaeus aztecus* are found from Martha's Vineyard, Massachusetts to the Florida Keys, are absent between Sanibel Island and Apalachicola Bay, and then, are found again from Apalachicola Bay to the northwest coast of the Yucatan. Pink shrimp, *Farfantepenaeus duorarum*, occur from lower Chesapeake Bay to the Florida Keys, from the Tortugas along the Gulf coast of the United States and Mexico to the Yucatan, and in the Bermuda Islands.

All three species pass through a series of larval stages that are subjected to transport by currents in nearshore waters before returning to estuaries as postlarvae or juveniles (Pearson 1939; Munro et al. 1968; Pérez Farfante 1969; Bielsa et al. 1983; Muncy 1984; Larson et al. 1989). Shrimp pass through five naupliar stages (0.3–0.6 mm long), three protozoeal stages (0.8–2.6 mm long) and two mysis stages (3.2–4.4 mm long). Nauplii utilize yolk, and protozoeae and mysis feed on phytoplankton and zooplankton. At temperatures of 24–32°C, larval development takes 11–17 d. The return to estuaries primarily involves the second of two postlarval stages (4–6 mm long), and these instars travel upstream for less than a month before settling to the bottom and molting to become juveniles (Weymouth et al. 1933; Anderson et al. 1949; Williams 1955a; Baxter and Renfro 1961; Joyce 1965; Pérez Farfante 1969; Bielsa et al. 1983; Muncy 1984; Larson et al. 1989; Weathers et al. 2003). Postlarvae can penetrate substantial distances into estuaries, with specimens captured 50 km from the mouth of the St. Johns River (Joyce 1965).

Small juvenile shrimp tend to move further upstream (Joyce 1965; Pérez Farfante 1969; Muncy 1984; Larson et al. 1989). White shrimp can travel over 200 km from the coast (Joyce 1965), whereas brown and pink shrimp typically do not penetrate as far into freshwater (Pérez Farfante 1969). All three species are omnivores that feed on a variety of plants and animals, including detritus (Weymouth et al. 1933; Williams 1955a; Bielsa et al. 1983; Muncy 1984; Larson et al. 1989; Weathers et al. 2003). At temperatures around 25°C, their total lengths increase by approximately 20–65 mm month^{-1} (Williams 1955a; Iversen and Idyll 1960; St. Amant et al. 1965; Zein–Eldin and Griffith 1966; Pérez Farfante 1969; Knudsen et al. 1977). Sexual differentiation begins around 50 mm total length, sexual maturity is achieved at 114–140 mm total length, growth slows at around 100 mm total length, and females grow larger than males (Williams 1955a; Fontaine and Neal 1971; Weathers et al. 2003).

Maturing shrimp move back toward the mouths of estuaries in preparation for spawning, and they become part of commercial catches at around 90 mm total length (Weymouth et al. 1933; Weathers et al. 2003). Mature shrimp move and spawn in nearshore coastal waters, with large numbers remaining at 20–50 m depth and some spawning taking place at up to 110 m (Lindner and Anderson 1956; Pérez Farfante 1969; Baxter and Holloway 1981; Bielsa et al. 1983; Muncy 1984; Larson et al. 1989). During mating, males attach a spermatophore that is carried by females until they spawn 500,000–1,000,000, eggs that hatch within 24 h (Weymouth et al. 1933; Anderson 1956; Pérez Farfante 1969; Bielsa et al. 1983; Muncy 1984; Larson et al.

1989; Weathers et al. 2003). The demersal eggs are semi-buoyant, non-adhesive and approximately 0.23–0.33 mm in diameter (Bielsa et al. 1983; Muncy 1984; Larson et al. 1989).

A variety of predators feed on white, brown and pink shrimp, including fish and other crustaceans, and like other shrimp, they experience relatively high natural and fishing mortality, which translates into a life span of 12–16 months (Berry 1970; Bielsa et al. 1983; Muncy 1984; Larson et al. 1989). The magnitude of predation pressure demonstrates that these three species of shrimp play an important role in transferring primary and secondary production to higher trophic levels.

Along northeast Florida and in the St. Johns River, the timing of life history events and the distribution of the three species vary (Table 3; Joyce 1965). In general, white shrimp use more of the river for a longer period of time.

Table 3. Characteristics of the life histories and distributions of *Litopenaeus setiferus*, *Farfantepenaeus aztecus* and *Farfantepenaeus duorarum* (Joyce 1965).

Characteristic	*Litopenaeus setiferus*	*Farfantepenaeus aztecus*	*Farfantepenaeus duorarum*
Peak spawning	May and June	March	June and July
Appearance in river	late June	early May	late June
Maximum incursion	217 km	133 km	83 km
Peak catch in river	July and August	June and July	July through October
Absence from river	December onward	August onward	April onward
Peak catch offshore	December and January	July	March and April

Direct effects of salinity on three species of penaeid shrimp

Similar to blue crabs, the salinity tolerances of white, brown and pink shrimp change throughout their life history (Table 4; Figure 2). Nauplii, protozoeae and mysis stages inhabit nearshore waters where they disperse. Second postlarvae and juveniles transition into estuarine and riverine habitats. At non-stressful temperatures, shrimp can tolerate a wide range of salinities, with individuals surviving in freshwater (0 ppt) and hypersaline water (69 ppt), especially if they have time to adapt to the conditions (Table 4).

Table 4. Observations relating to the salinity tolerances of *Litopenaeus setiferus* (white shrimp), *Farfantepenaeus aztecus* (brown shrimp) and *Farfantepenaeus duorarum* (pink shrimp).

Type Observation	Reference
Field	
Larval, early post-larval, subadult and adult pink shrimp in 36.15–37.73 ppt	Pérez Farfante 1969
Young white shrimp in < 10 ppt	Pérez Farfante 1969 Gunter 1961 Gunter et al. 1964
Young white shrimp in 0.42 ppt	Pérez Farfante 1969
Young white shrimp in 0.26 ppt	Joyce 1965
Small white shrimp in 47.96 ppt	Pérez Farfante 1969 Gunter 1961
Postlarvae, juvenile and early subadult pink shrimp in 0–47 ppt	
Pink shrimp 80.5 km up the St. Johns River in almost fresh water	Joyce 1965
Pink shrimp in ≥ 18 ppt	Gunter et al. 1964
Brown shrimp in 10–20 ppt	
White shrimp in < 10 ppt	
Juvenile (28–38 mm total length) brown shrimp in 0.22–0.36 ppt	Pérez Farfante 1969
Juvenile (28–38 mm total length) brown shrimp in 0.0–1.0 ppt	Gunter et al. 1964
Brown shrimp in 69 ppt	Pérez Farfante 1969
More white shrimp than brown shrimp if salinity low	Williams 1955b
Brown shrimp most abundant in 10–30 ppt	Gunter et al. 1964
Greater numbers of brown shrimp above 20 ppt than below 10 ppt	
Brown shrimp collected in 0.2 ppt	Browder et al. 2002
Landings of brown shrimp low after low temperatures and salinities	
Commercial catches decrease if brown shrimp recruit to < 8 ppt and < 20°C	St. Amant et al. 1965
Commercial catches increase if brown shrimp recruit to 15 ppt and > 20°C	
White, brown and pink shrimp tolerate from 0.00–0.22 ppt up to 69 ppt	Pérez Farfante 1969
Abundances drop above 45 ppt	
Along the northern Gulf coast, white shrimp tolerate salinities down to 0.42 ppt	
Along the northern Gulf coast, brown shrimp tolerate salinities down to 0.80 ppt	
Along the northern Gulf coast, pink shrimp tolerate salinities down to 2.5 ppt	
Maximum abundances of white shrimp at < 10 ppt	
Maximum abundances of brown shrimp at 10–20 ppt	
Maximum abundances of pink shrimp at ≥ 18 ppt	

Type Observation	Reference
Brown shrimp postlarvae collected in 0.1–34.9 ppt	Williams and Deubler 1968
White shrimp postlarvae collected in 0.5–36.7 ppt	
Brown shrimp postlarvae collected in 0–45 ppt, with no evidence of a relationship	Zein–Eldin and Renaud 1986
Brown shrimp juveniles collected in 0–69 ppt, with good growth at 2–40 ppt	
Brown shrimp adults survive in 2–35 ppt in ponds	
White shrimp postlarvae collected in 0.4–37.4 ppt, with good growth at 25 ppt	
White shrimp juveniles collected in 0–38 ppt, with no evidence of a relationship	
White shrimp adults survive in 2–35 ppt in ponds	
Pink shrimp taken at 3.9 ppt	Darnell and Williams 1956
Pink shrimp taken at 2.7 ppt	Hoese 1960
Laboratory	
Hatching and survival of larval brown shrimp poor below 27 ppt and above 35 ppt	Cook and Murphy 1969
Post-larval brown shrimp survive 2–40 ppt	Zein–Eldin 1963
50% of white shrimp postlarvae die at 8 ppt within 2 h	Rosas et al. 1999
Postlarval brown shrimp grow best at 25 ppt versus 5, 10 or 40 ppt	Zein–Eldin 1962
All but 5% of brown shrimp juveniles survive 5, 25 and 40 ppt at 12°, 25° and 34°C	Aldrich 1964
Brown shrimp postlarvae grow in 2–40 ppt with less tolerance at extreme temperatures	Zein–Eldin 1964
Brown shrimp growth affected by temperature but not salinity	Zein–Eldin 1966
Mixed groups of brown, white and pink shrimp postlarvae grow and survive in 2–40 ppt over 28 d	Zein–Eldin 1963
Juvenile white shrimp reared at 17.6–33.2 ppt	Pérez Farfante 1969
White shrimp reared at 18.5–34.0 ppt	Muncy 1984
Pink shrimp survive 2–55 ppt when at 15–33°C	Browder et al. 2002
Outside 20–30°C salinity tolerance narrows	
Acclimation helps at 55 ppt but not 5 or 10 ppt	
Growth rate maximum at 30 ppt	
Responses to salinity, temperature and predation modeled, with the appropriate regression coefficients	
Brown shrimp convulse and are disoriented at salinities below 2 ppt	
Brown shrimp maintain ionic balance at 69 ppt	Williams 1960
Maximum salinity tolerance for brown shrimp at 26°C	Browder et al. 2002
Maximum temperature tolerance for brown shrimp at 8.5–17.0 ppt	
Salinity tolerance reduced below 20°C	
Tolerance to salinities below 10 ppt reduced at < 15°C for brown shrimp	Zein–Eldin and Aldrich 1965
Brown and pink shrimp hypotonic in 30–34 ppt and tend to hypertonic in 10–30 ppt	Williams 1960
Early stage postlarvae of white shrimp grow best at 30–40 ppt	

Type Observation	Reference
Later stage postlarvae of white shrimp grow best at 10 ppt	
White shrimp osmoregulate more effectively at 4–5 ppt	Zein–Eldin and Aldrich 1965
Brown shrimp osmoregulate more effectively at 60 ppt	
Brown shrimp survive up to 69 ppt at 25° or 30°C	Aldrich 1963
Less salinity tolerance at lower temperatures	
Juvenile brown shrimp survive transfer from 25 and 90 ppt (near the lethal limit) to 8–88 ppt	Aldrich 1964
Juvenile brown shrimp exhibit an acclimation effect	
80–100% of brown shrimp survive and grow over 24 h in 3–41 ppt across temperatures from 7–35°C	Zein–Eldin and Aldrich 1965
80–100% of brown shrimp survive and grow over 28 d in 5–35 ppt across temperatures from 10–32°C	
100% mortality in 5 d at 2 ppt and 11°C	
Growth affected more by temperature than salinity	

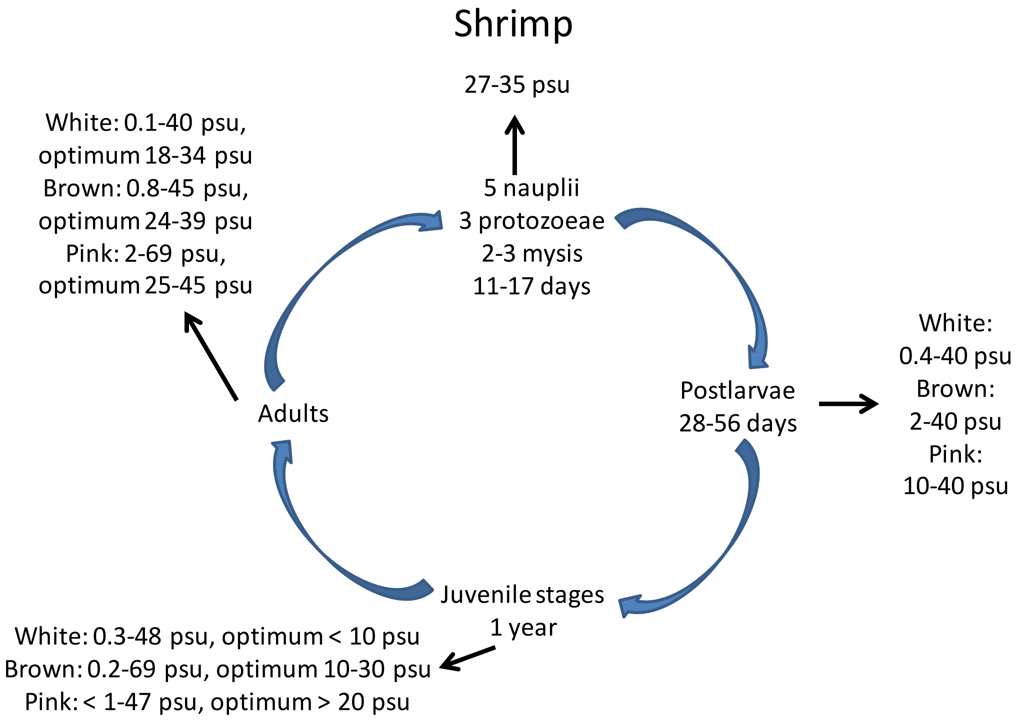

Figure 2. Diagrammatic summary of the life histories and approximate salinity tolerances of *Litopenaeus setiferus* (white shrimp), *Farfantepenaeus aztecus* (brown shrimp) and *Farfantepenaeus duorarum* (pink shrimp).

As for blue crabs, the distribution of larval stages and the salinity tolerances of juvenile and adult instars reduce the likelihood of direct adverse impacts from changes in salinity due to water withdrawals. Again, the key to sustaining shrimp populations is likely to be the maintenance of a range of salinity regimes that overlap suitable habitats.

Indirect effects on three species of penaeid shrimp via habitat alteration

The three species of shrimp inhabit similar substrates. Inshore, abundances of white and brown shrimp tend to be higher where there is a muddy or peaty substrate with refuge provided by decaying organic matter or vegetation, although these shrimp do inhabit sand or clay substrates (Williams 1955a, b, 1959; Pérez Farfante 1969; Tsou and Matheson 2002). Offshore, adult white shrimp are captured in greatest numbers from muddy and silty bottoms, although they do occur on clay, sand and shell fragments (Springer and Bullis 1954; Kutkuhn 1962).

White shrimp burrow, but they do so less often than brown or pink shrimp (Williams 1958; Aldrich et al. 1968). Higher numbers of pink shrimp inhabit firmer mud and silt substrates, often where there are coral or shell fragments (Springer and Bullis 1954; Gunter 1956; Williams 1958). This association with firmer substrates may explain the absence of pink shrimp along stretches of the Gulf coast dominated by muddy or silty substrates (Pérez Farfante 1969).

The presence of various types of inshore vegetation leads to increased abundances of white, brown and pink shrimp, although limited sampling hampers an assessment of the value of submerged aquatic vegetation, including *Vallisneria americana*, the dominant macrophyte in the St. Johns River (Zimmerman et al. 1984; Table 5). In addition, the exact form and magnitude of the relationship between shrimp abundance and habitat extent and quality remains uncertain, although empirical modeling supports the concept that vegetation represents a valuable habitat (Turner 1977; Minello et al. 2008). Direct comparisons of annual production for marsh and unvegetated habitats highlighted the importance of maintaining a link between salinity and suitable habitats (Minello et al. 2008). Marsh yielded 2.2 × 106 kg ha^{-1} of brown shrimp and 1.9 × 106 kg ha^{-1} of white shrimp, with these values being 3.1 and 2.5× higher than estimates for unvegetated habitats (Minello et al. 2008). Uncertainty arises from undocumented sampling efficiencies across habitats and from some equivocal results. For example, small patches of seagrass harbored less pink shrimp in total, but numbers weighted for coverage were more similar (Murphey and Fonseca 1995). In another case, oyster reefs harbored reasonable numbers of white, brown and pink shrimp (Zimmerman et al. 1989). In fact, fisheries independent monitoring in the lower St. Johns River yielded larger numbers of white shrimp from a variety soft bottoms with no indication that shrimp selected vegetation (MacDonald et al. 2009). Additional uncertainty is generated by the observation that an increase in the extent of the vegetation–water interface may lead to increased abundances of shrimp until patches become too fragmented (Zimmerman et al. 2000). In summary, any change in salinity that adversely affects submerged aquatic vegetation or marshes could adversely affect shrimp populations, and an estimate of the effect can be calculated using the area lost, with models from the literature providing an initial estimate that can be refined based on the results of a targeted study of habitat use in the St. Johns River.

Table 5. Examples of differences in abundances of white, brown and pink shrimp in three habitats. SAV = various species of submerged aquatic vegetation other than marsh plants

Shrimp	Mean density (number m^{-2})			Reference
	Marsh edge	SAV	Unvegetated	
White	26.3	—	11.7	Zimmerman and Minello 1984
	4.2	—	0.3	Zimmerman et al. 1989
	1.6	0.4	1.5	Zimmerman et al. 1990a
	4.4	0.4	0.8	Zimmerman et al. 1990b
	26.7	—	6.0	Minello and Webb 1997
	4.2	1.9	0.0	Rozas and Minello 1998 (autumn)
	5.5	0.5	1.5	Minello 1999
Brown	24.9	—	4.0	Zimmerman and Minello 1984
	9.6	—	1.1	Zimmerman et al. 1989
	5.0	3.7	1.7	Zimmerman et al. 1990a
	5.0	4.0	1.2	Zimmerman et al. 1990b
	9.2	—	0.4	Minello et al. 1991
	12.0	—	3.3	Minello and Webb 1997
	4.5	5.3	0.5	Rozas and Minello 1998 (autumn)
	4.5	11.3	0.7	Rozas and Minello 1998 (spring)
	7.5	7.3	2.6	Minello 1999
Pink	0.2	0.8	0.1	Zimmerman et al. 1990a
	4.8	2.7	0.5	Zimmerman et al. 1990b
	1.3	2.6	0.1	Rozas and Minello 1998 (autumn)
	1.6	1.0	0.5	Minello 1999

Indirect effects on three species of penaeid shrimp via settlement and recruitment

Penaeid shrimp broadcast their eggs on the continental shelf unlike blue crabs that brood their eggs. Thus, ocean currents can transport both eggs and larvae away from the spawning grounds, which means later stage larvae and postlarvae must return (Blanton et al. 1999). The mechanisms that concentrate shrimp larvae near the mouths of estuaries remain poorly understood, but one mechanism may involve a change from diurnal vertical migration to tidally moderated migration in shallow water where changes in pressure caused by tides represent a significant fraction of the total pressure (Rothlisberg et al. 1995). In addition, tidal and wind-driven flow can advect larvae from a variety of initial positions on the continental shelf near or into an estuary (Wenner et al. 1998; Blanton et al. 1999, 2001; Criales 2010). Postlarvae of penaeids facilitate landward transport by engaging in diel-tidal vertical migration, i.e., upward swimming on flood tides at night and sinking during all ebb tides and throughout the day, as well as by following gradients in salinity, temperature and other environmental cues (Foxon 1934; Dakin 1938; Pearson 1939; Hughes 1969, 1972; Matthews et al. 1991; Wenner et al. 2005; Criales et al. 2011). As a result, nocturnal spring tides may yield pulses in recruitment, although gear avoidance during the day and other variations in sampling efficiency need to be considered (Williams and Deubler 1968; Roessler and Reher 1971; DeLancey et al. 1994). Overall, postlarval abundance remains difficult to predict reliably (Haas et al. 2001).

Once in estuaries, physiological tolerances, especially the combined effects of salinity, temperature and dissolved oxygen interact with availability of vegetated habitat to affect postlarval survival significantly (Mulholland 1984; Kenyon et al. 1995; Clark et al. 1999; Browder et al. 2002; DeLancey et al. 2008). In particular, historical production of shrimp relates to both historical rainfall patterns, most likely reflecting differences in salinity, and changes in the length of the interface between marshes and wetlands (Gunter and Hildebrand 1954; Gunter et al. 1964; Browder et al. 1989; Haas et al. 2004). In the shallow waters of the Suwannee River estuary, brown shrimp abundances were higher at low salinity, which related to higher flows (Tsou and Matheson 2002). On small and large scales, vegetated habitat plays a critical role, with production estimated at over 100 kg ha^{-1} (Minello et al. 2008). In fact, juvenile abundance may represent a useful, although imprecise, predictor of adult abundance (Baxter 1963; Baxter and Sullivan 1986).

In the lower St. Johns River, fisheries independent monitoring highlighted several different responses to flow by shrimp (MacDonald et al. 2009). In the mainstem, white and brown shrimp ≤ 50 mm long moved downstream at higher flows. Brown shrimp exhibited peak abundances when average flows over 60 d that included their recruitment period reached 8.0–8.2 cfs. Targeted investigation of responses to variation in flow and the resulting differences in salinity would improve insights gained from sampling designed to identify long-term, broad-scale trends.

Although likely to be limited in precision, habitat suitability models and other similar models could be applied to assess the overall likelihood of changes in shrimp populations once changes in hydrology and habitats from water withdrawals have been predicted (Turner and Brody 1983; Mulholland 1984; Browder et al. 1989; Baker et al. 2008; Smith et al. 2010). These models draw on data and expert opinion to characterize responses of animals to variations in environmental conditions and habitats.

Summary

Reviewing the literature related to *Callinectes sapidus*, *Litopenaeus setiferus*, *Farfantepenaeus aztecus* and *Farfantepenaeus duorarum* confirmed the importance of these species in the St. Johns River. The distribution of larvae and broad salinity tolerances of postlarvae, juveniles and adults suggested that water withdrawals and associated changes in salinity are unlikely to affect these species directly. Changes in relationships between habitats and salinity, loss of vegetated habitat, and changes in recruitment resulting from changes in habitats or environmental cues followed by postlarvae remain potential concerns. Existing models can be applied to estimate such effects once the outcomes from water withdrawal scenarios have been elucidated. Targeted investigations could refine these estimates, and ongoing monitoring should be implemented to evaluate the accuracy of any estimates, assess the success of management strategies, and guide adaptations to promote the sustainable use of the St. Johns River and the natural resources it supports.

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