

Comparing Early Life History Strategies of *Pomatomus saltatrix*: a Global Approach

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Abstract. *Pomatomus saltatrix* (Pisces: Pomatomidae) is a highly migratory, continental-shelf species with a worldwide subtropical distribution including the eastern coast of North America, the Gulf of Mexico, Mediterranean Sea, Black Sea, north-western Africa, the eastern coast of South America, the south-eastern coast of South Africa, and the south-eastern and south-western coasts of Australia. This paper summarizes available life history information from the different regions where *P. saltatrix* occurs, with a focus on the early life history. The basic physical oceanography of these regions is also reviewed to elucidate patterns in larval transport. Comparison of these populations suggests that there are commonalities: adults migrate to spawning grounds; eggs and larvae are typically advected along-shore to juvenile nursery habitats; juveniles recruit to inshore habitats at a similar size, and there they grow rapidly and are mainly piscivorous, feeding primarily on atherinids and engraulids. There are also a number of life history traits that are quite variable among populations: the number of annual reproductive peaks, the number of juvenile cohorts, adult growth patterns and reproductive parameters. Comparison of these life history patterns leads to several non-exclusive hypotheses as to the adaptive significance of variations in life history traits. The goal is to identify areas where more research is needed to assess the degree to which populations of a global species are adapted to their local environment.

Introduction

Pomatomus saltatrix is a highly migratory, continental-shelf species with a worldwide subtropical distribution (LeGall 1934; Briggs 1960; van der Elst 1976; Champagnat 1983) (Fig. 1). Commercial and recreational fisheries exist for this species throughout its range: western North Atlantic, including both the eastern coast of the United States and northern Gulf of Mexico (Oliver *et al.* 1989; Pottern *et al.* 1989; Anon. 1993); the Mediterranean (Ktari and Kedidi 1977; Sabates and Martin 1993); the Sea of Marmara and the Black Sea (Ivanov and Beverton 1985; Kocatas *et al.* 1993); western South Atlantic (Krug and Haimovici 1991; Haimovici and Krug 1996); north-western Africa (Champagnat 1983; Samba and Laloe 1991), extending out to the Azores (Santos and Nash 1995); southern Africa (van der Elst 1976; Coetzee and Baird 1981); eastern and western Australia (Pollock 1984; Lenanton and Potter 1987; Lenanton *et al.* 1996; Zeller *et al.* 1996).

The basic life history of *P. saltatrix* is similar to that of many coastal pelagic species. During annual migrations along continental shelves, adults spawn large numbers of small eggs (Table 1). Eggs hatch in about 48 h and the yolk is absorbed in another 24 to 48 h (Salekhova 1959; Deuel *et al.* 1966). Flexion occurs at about 10 days and 4–6 mm standard length (SL) (Norcross *et al.* 1974; Hare and Cowen 1994) and larvae transform into pelagic juveniles at about 18

to 25 days and 10–12 mm SL (Hare and Cowen 1994). Juveniles remain oceanic for an additional 15 to 45 days before recruiting to nearshore habitats at 40–80 mm fork length (FL) (Nyman and Conover 1988; McBride and Conover 1991).

The purpose of this paper is to review the current state of knowledge pertaining to the life history of *P. saltatrix* throughout its global range, with particular emphasis on the early life history stages (i.e. eggs, larvae and juveniles). It first summarizes available life history information from the different regions where *P. saltatrix* populations occur and then reviews the basic physical oceanography of these regions to provide an additional basis for comparing populations. In this summary, populations of the Northern and Southern Hemispheres are separated to facilitate discussions of differences in seasons and the effect of Coriolis. The aim is to elucidate the similarities and differences between populations and to suggest areas where more research is needed for a better understanding of the biology of this economically important species.

Northern Hemisphere Populations

Western North Atlantic

The population of *P. saltatrix* (bluefish) along the eastern coast of North America, which ranges from 25°N to 43°N, has been studied for at least 150 years (Ayres 1852; Atwood

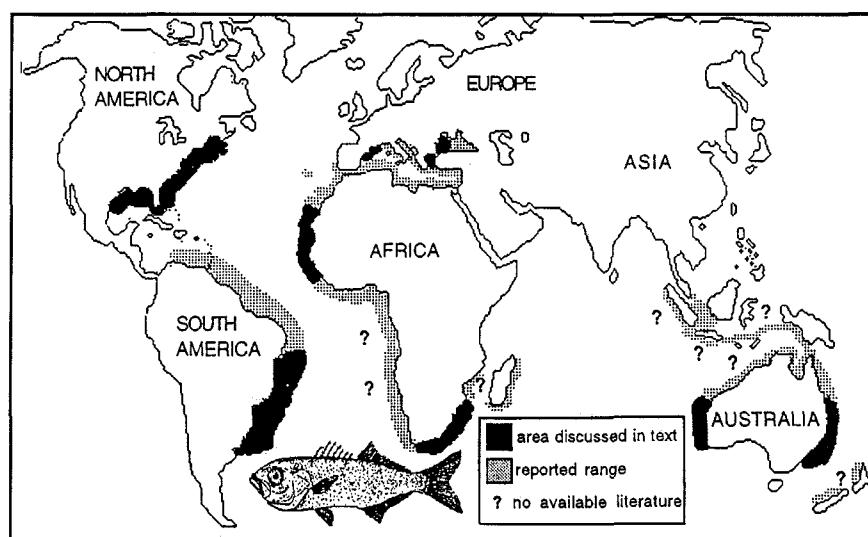


Fig. 1. Worldwide distribution of *P. saltatrix*. Specific locations are indicated in the text.

1869; Baird 1873). *P. saltatrix* is heavily exploited throughout this range, often accounting for the greatest catch by weight in the recreational fishery (Pottern *et al.* 1989; Anon. 1993). In the commercial fishery, *P. saltatrix* is less important, ranking about 20th by weight for finfish during the 1980s (Anon. 1988).

The general patterns of spawning within the South Atlantic Bight (SAB; Cape Canaveral, Florida, to Cape Hatteras, North Carolina) and Middle Atlantic Bight (MAB; Cape Hatteras to Cape Cod, Massachusetts) are known, but the specific temporal and spatial nature of spawning remains at issue. Adults migrate northwards from wintering grounds off eastern Florida in the spring and return in the autumn (Lund and Maltezos 1970; Richards 1976; Wilk 1977; Chiarella and Conover 1990), although there is evidence that some fish overwinter south of New England at the shelf break (Wilk 1977).

Spawning occurs in spring (March to May) and autumn (September to November) in the SAB (Kendall and Walford 1979; Collins and Stender 1987; Hare and Cowen 1993) and in summer (May to August) in the MAB (Norcross *et al.*

1974; Kendall and Walford 1979; Kendall and Naplin 1981; Chiarella and Conover 1990; Hare and Cowen 1993; Smith *et al.* 1994). One hypothesis proposes that spawning in the separate regions (i.e. MAB and SAB) and seasons (i.e. spring, summer, autumn) is temporally and spatially distinct (Kendall and Walford 1979; Nyman and Conover 1988; Chiarella and Conover 1990; McBride and Conover 1991; Juanes and Conover 1995), and a second hypothesis proposes that spawning is continuous and protracted (Hare and Cowen 1993; Smith *et al.* 1994).

The patterns of recruitment in the western North Atlantic are also generally known. SAB spring-spawned fish recruit predominantly to MAB nearshore habitats (Nyman and Conover 1988; McBride and Conover 1991), 500 to 1500 km north of their spawning grounds. Some spring-spawned fish enter SAB estuaries, but in apparently much lower numbers than those entering MAB estuaries (McBride *et al.* 1993). MAB summer-spawned juveniles utilize primarily estuaries in the MAB (McBride and Conover 1991). SAB autumn-spawned fish apparently recruit to SAB estuaries but are much less abundant than the spring- and summer-

Table 1. References: ¹Sabates and Martin 1993. ²Norcross *et al.* 1974. ³Kendall and Walford 1979. ⁴Borcea 1929, 1933. ⁵Thomson 1957b; Steckis personal communication. ⁶Finucane *et al.* 1980; Ditty and Shaw 1995. ⁷Collins and Stender 1987. ⁸Oliver *et al.* 1989; Wilk 1977. ⁹Conand 1975. ¹⁰Kedidi 1975. ¹¹Champagnat 1983. ¹²van der Elst 1976. ¹³Thomson 1957a. ¹⁴Barger 1990. ¹⁵Haimovici and Krug 1992. ¹⁶Krug and Haimovici 1989. ¹⁷Bennett 1989b, 1989c. ¹⁸Bennett 1989a. ¹⁹Smale 1984. ²⁰Smale and Kok 1983. ²¹Bade 1977. ²²Blaber and Blaber 1980. ²³Anon. 1981. ²⁴Gordina and Klimova 1996. ²⁵Salekhova 1959. ²⁶Zaitsev 1964. ²⁷Porumb 1968, 1971. ²⁸Oven 1957. ²⁹Turgan 1959. ³⁰Deuel *et al.* 1966. ³¹Lassiter 1962. ³²Lenanton 1977. ³³McBride and Conover 1991; McBride *et al.* 1993; McBride *et al.* 1995. ³⁴Juanes *et al.* 1993, 1994; Juanes and Conover 1994a, 1995. ³⁵Friedland *et al.* 1988; Creaser and Perkins 1994. ³⁶Beckley and Connell 1996. ³⁷Miskiewicz *et al.* 1996. ³⁸Muelbert and Sinque 1996. ³⁹Hare and Cowen 1994.

^aAll measurements in mm. ^bTL, total length; SL, standard length; FL, fork length; ?L, unknown length measurement. ^cP, piscivorous diet; C, crustacean diet. ^dFirst number is for spring-spawned fish, the second for summer-spawned fish. ^eA third minor autumn–winter recruitment occurs in the South Atlantic Bight. ^fIt is unclear whether these represent one continuous extended spawning event or discrete events. ^gThe following are parameters for the von Bertalanffy growth model: *K*, Brody growth coefficient; *L*_∞, asymptotic length; *t*₀, theoretical age when length is 0 mm.

Table 1. Comparison of biological traits of different *Pomatomus saltatrix* populations^{a,b}

Traits	Location of bluefish population								
	East coast USA	Gulf of Mexico	North-west Africa	Black Sea	Mediterranean	South America	South Africa	Eastern Australia	Western Australia
Common name	Bluefish	Bluefish	Tassergal	Lufar	Anjora	Enchova	Elf	Tailor	Tailor
Temperature at larval appearance (°C)	18–26 ^{2,3}	21.7–26.9 ⁶		20–26 ²⁴	18–26 ¹	21–26 ³⁸	>22 ³⁶	>22 ³⁷	
Salinity at larval appearance (PSS)	26.6–38 ^{2,3}	>30 ⁶		17–18 ²⁴	31.8–38.01 ¹	29–36.5 ³⁸			
Spawning times	Mar–May/Jun–Aug/ Sep–Nov ^{2,3,7,f}	Apr/Oct–Nov ⁶	May–Jul/ Oct–Nov ^{9,11}	June–Sep ²⁴	Jul–Aug ^{1,10}	Nov–Mar ¹⁵	Sep–Mar ^{12,36}	Sep–Nov/ Jan–May ^{21,37}	April ⁵
Egg diameter (mm)	0.90–1.20 ³⁰		0.69–0.97 ⁹	0.80–1.1 ²⁵			0.77 ¹²		0.75 ⁵
Fecundity	6–14 × 10 ⁵ FL = 528–584 ³¹		3.52 × 10 ⁶ TL ^{3,99,11}	427207–1207165 ?L=370–450 ²⁵		6.20 × 10 ⁻⁵ TL ^{3,84} TL = 410–570 ¹⁵	7.32 × 10 ⁻⁹ TL ^{4,65} TL = 320–760 ¹²	3.7–12.4 × 10 ⁵ FL = 307–537 ²¹	3.75–5.0 × 10 ⁵ FL=345–385 ⁵
Minimum larval size (mm)	2.2 SL ³	1.8 SL ⁶				3 SL ³⁸	2.8 SL ³⁶		
Larval growth rate	0.3–0.8 mm/day ^{30,39}			0.30 mm/day ²⁵					
Juvenile growth rate	0.9–2.1 mm/day ^{33,34}							0.75–1.3 mm/day ²³	
Larval/juvenile transition	18–25 days ³⁹								
No. recruits	2 ^{33,e}		2 ¹¹	1 ^{27–29}			2 ^{12,36}	2 ^{21–23}	
Recruitment size (mm)	30–70 TL ^{33,34}			30–60 ?L ^{26,27,28}			40–80 TL ^{12,17,20}	30–60 FL ^{21,23}	>50 TL ³²
Recruitment date	May–Jun/Aug– Sep/Oct–Jan ^{33,34}	Dec–Jan/Aug –Sep ¹¹	July–Aug ^{4,27,28}				Sep–Dec ^{20/} Dec–Mar ^{12,17,19}	Dec–Feb/ Jun–Aug ^{21–23}	
Young-of-year diet ^c	P ^{34,35}			P ^{27,28}		P ¹⁵	P ^{18,19/C} ²⁰	P ^{21–23}	P ¹³
Length at maturity (mm)	450 FL ⁸	>300 FL ⁶	430 TL ⁹	300–370 ?L ²⁹	320 SL ¹⁰	350 TL ¹⁵	250 TL ¹²	270 FL ²¹	325–350 TL ^{5,6}
K^g	0.103, 0.342 ^{31,d} 0.096 ¹⁴	0.18 ¹⁴	0.178 ¹¹			0.387 ¹⁶	0.197 ¹²	0.163 ²¹	
L_{∞}^g	1285, 675 ^{31,d} 1099 ¹⁴	944 ¹⁴	1044 ¹¹			662 ¹⁶	840 ¹²	727 ²¹	
t_0^g	1.366, 0.249 ^{31,d} 2.493 ¹⁴	1.033 ¹⁴	0.5275 ¹¹			0.321 ¹⁶	0.321 ¹²	0.409 ²¹	

spawned fish (McBride *et al.* 1993). Juveniles remain in these nearshore nursery areas throughout the summer and leave as temperatures decline below 15°C in the autumn.

There are apparently several growth phases in the early life history of *P. saltatrix* along the eastern coast of the United States (Figs 2A and 2B). During the larval and pelagic juvenile stages, growth is apparently exponential, with growth rate increasing from 0.3 mm day⁻¹ at hatching to 0.8 mm day⁻¹ at the larval–juvenile transition (Hare and

Cowen 1994, 1995). Following estuarine entrance, growth is approximately linear, with rates ranging from 0.9 to 2 mm day⁻¹ (McBride and Conover 1991; Juanes *et al.* 1993) (see Figs 2A and 2B).

P. saltatrix undergoes an ontogenetic shift in the diet associated with the transition from oceanic to coastal habitats. Before entry to the estuary, at sizes <40 mm SL, pelagic juveniles feed predominantly on copepods (Kendall and Naplin 1981; Marks and Conover 1993). After entry to the estuary, juveniles feed primarily on locally abundant fishes (*Menidia menidia*, *Anchoa mitchilli* and *Morone saxatilis*; Friedland *et al.* 1988; Juanes *et al.* 1993; Creaser and Perkins 1994) and show strong size selectivity but no species selectivity (Juanes *et al.* 1993; Juanes and Conover 1994b). An increase in growth rate co-occurs with the shift from planktivory to piscivory and from oceanic to estuarine habitats (Marks and Conover 1993; Juanes and Conover 1994a), and high juvenile growth is supported by large consumption rates and rapid gastric evacuation rates (Juanes and Conover 1994a; Buckel *et al.* 1995; Buckel and Conover 1996).

In northern MAB estuaries, spring- and summer-spawned *P. saltatrix* juveniles recruit as two distinct cohorts. This observation has been used as evidence for the hypothesis that *P. saltatrix* spawns in temporally and spatially distinct episodes (Nyman and Conover 1988; McBride and Conover 1991). Hare and Cowen (1993), however, proposed that spawning is continuous and that fish spawned in the southern MAB during late May and early June have a higher probability of being in the Slope Sea (the region between the Gulf Stream and the MAB shelf edge) at the time they normally enter nearshore habitats; these fish may have a lower probability of recruitment, thereby creating the appearance of two distinct spring- and summer-spawned cohorts. Smith *et al.* (1994) also proposed that *P. saltatrix* spawns continuously but hypothesized that fish spawned in the southern MAB during late May and early June recruit to nearby estuaries (e.g. Chesapeake Bay and Pamlico Sound), thereby creating the appearance of the two distinct cohorts in northern MAB estuaries. In estuaries in the southern Gulf of Maine, distinct cohorts were not observed (Creaser and Perkins 1994); birthdates ranged from late February through mid June. In SAB estuaries, both cohorts are collected, the spring-spawned cohort probably recruiting directly to the estuaries and the summer-spawned cohort probably using SAB estuaries during the southward migration in the autumn (McBride *et al.* 1993).

The physical oceanographic regimes of the South and Middle Atlantic Bights are very different. In the SAB, the Gulf Stream (a western boundary current) flows along the shelf edge and has a major influence on shelf circulation (Atkinson *et al.* 1985; Pietrafesa 1989). At Cape Hatteras, the Gulf Stream diverges from the shelf and is 100–300 km

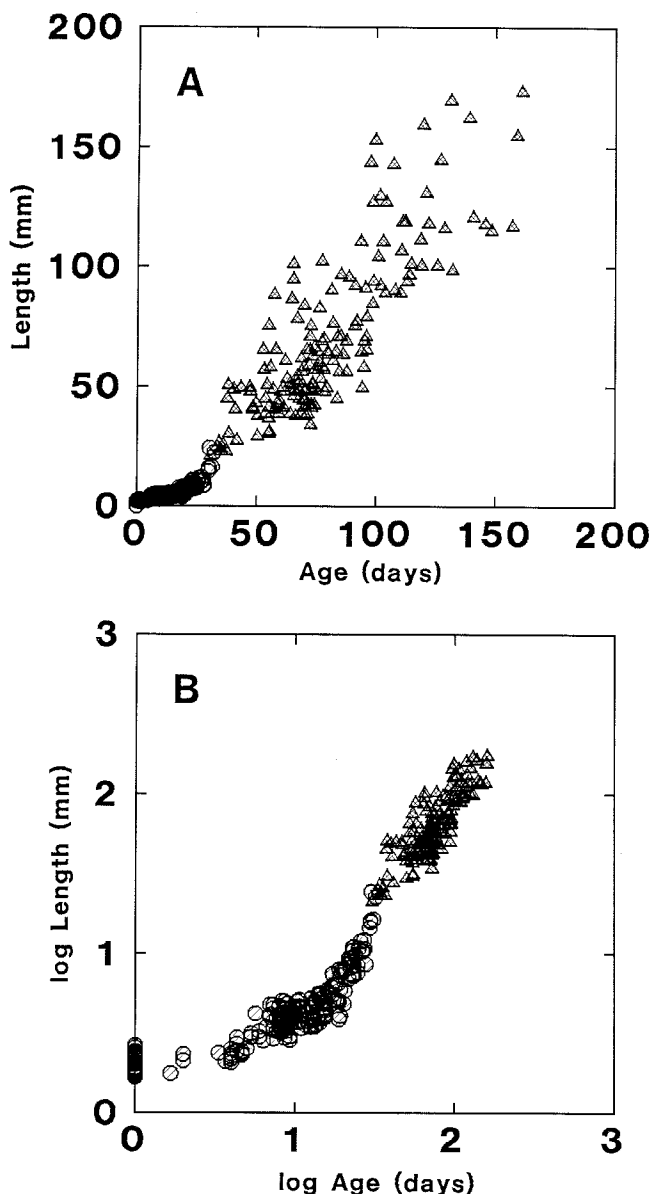


Fig. 2. Length–age relationships for western Atlantic *P. saltatrix* larvae and juveniles: (○) oceanic stages (larvae and pelagic juveniles) (data from Hare and Cowen 1995); (▲) estuarine stages (juveniles) (data from McBride 1989). Both (A) non-transformed and (B) log-transformed data are provided to clearly show the length–age relationship for both younger and older fish.

offshore of the middle and northern MAB shelf edge (Stommel 1965; Halliwell and Mooers 1979). As a consequence, the Gulf Stream has little direct influence on MAB shelf flow, which is generally along-shelf towards the south-west (Bumpus 1973; Epifanio *et al.* 1989). In the southern MAB, shelf water is entrained into Gulf Stream flows (Ford *et al.* 1952; Fisher 1972).

Hare and Cowen (in press) have proposed that most spring-spawned larvae are advected out of the SAB towards the north-east in association with the Gulf Stream (see also Kendall and Walford 1979). They hypothesize that larvae are then transported across the Slope Sea in association with warm-core ring streamers but that discharges of Gulf Stream water may advect some larvae across the Slope Sea and some more developed individuals (e.g. pelagic juveniles) may actively swim across the Slope Sea. Once at the MAB shelf edge, pelagic juveniles accumulate at the surface shelf/slope temperature front and, when this front breaks down, apparently swim across the shelf to nearshore habitats (see also Shima 1989). This scenario of larval transport suggests that recruitment magnitude of SAB-spawned *P. saltatrix* to nearshore habitats in the MAB is largely determined by warm-core ring streamer activity and that the timing of estuarine entrance is determined by the timing of the breakdown of the surface shelf/slope temperature front.

On the MAB shelf, spawning progresses northwards as the summer progresses (Hare and Cowen 1993; Smith *et al.* 1994). Larvae spawned in the southern MAB earlier in the summer may be advected off the shelf into either the Slope Sea or the Gulf Stream (Norcross *et al.* 1974; Hare and Cowen 1993, in press). However, Smith *et al.* (1994) proposed that larvae spawned in the southern MAB may recruit to nearby estuaries. Larvae spawned further north in the MAB are probably advected along the shelf to the south-west, but summertime south-westerly winds may reverse this average flow, causing the retention of larvae in the MAB (see Epifanio *et al.* 1989), similar to the pattern seen for other summer-spawned larvae (Malchoff 1993).

Gulf of Mexico

In the Gulf of Mexico (GOM), *P. saltatrix* ranges from 26°N to 30°N and forms the basis for a recreational fishery (Wilk 1977; Holliday 1986). Adult growth rate is similar between *P. saltatrix* populations in the western North Atlantic and the GOM (Barger 1990). Juveniles are abundant in coastal waters and estuaries along the northern GOM coast throughout the year but highest abundances occur in the spring and summer (Williams *et al.* 1990; Czaplá *et al.* 1991; Nelson *et al.* 1992). As on the eastern coast of North America, a large proportion of the juvenile diet is made up of locally abundant fishes (Naughton and Saloman 1984). Other data on juvenile size, birthdate and growth are lacking,

as is comparative information on recruitment patterns to various estuarine systems in the GOM.

Spawning in the GOM is bimodal, occurring in the spring and autumn (Barger *et al.* 1978; Finucane *et al.* 1980; Ditty and Shaw 1995). In April and May, large numbers of larvae have been collected on the central and northern GOM shelf in the vicinity of the Mississippi River plume (Ditty and Shaw 1995). Larvae are also found on the northern and western GOM shelf in November (Barger *et al.* 1978) and along the entire northern GOM shelf in October and November (Ditty and Shaw 1995).

In physical oceanography, the Gulf of Mexico is more similar to the MAB shelf than the SAB shelf. The Loop Current, which is part of the Gulf Stream system, typically occurs well offshore of the northern GOM shelf and does not directly affect shelf circulation (Vukovich *et al.* 1979; P. Hamilton 1992). Flow on the shelf is dominated by discharge from the Mississippi River (Wiseman and Kelly 1994) and is influenced by the bathymetry of the delta (Dinnel and Wiseman 1986). On the inner shelf, flow is generally westward, whereas on the outer shelf, flow is eastward (Shaw *et al.* 1985). Drift bottles released in the Mississippi outflow region (the area where large numbers of *P. saltatrix* larvae were collected by Ditty and Shaw 1995) were recovered in both the eastern and western areas of the northern GOM (Chew *et al.* 1962). When coupled with the appearance of juveniles in estuaries along the entire northern GOM coast, the physical oceanographic data suggest that larvae do not undergo directed transport along the shelf but experience perhaps a reciprocating flow regime that acts to retain larvae near spawning areas. This, however, is speculation and awaits more complete data on the distribution of *P. saltatrix* early life history stages in conjunction with physical oceanographic data.

Mediterranean Sea

P. saltatrix (local common names: anjora, anchoa de banco, tassergal) is distributed throughout the Mediterranean but is more abundant in the southern and eastern Mediterranean (Tortonese 1954; Sabates and Martin 1993). In the western Mediterranean, *P. saltatrix* ranges from 35°N to 45°N. In the northern part of this range, adults are captured as by-catch in various gears, with highest catches from May to December and lowest catches from February to April (Sabates and Martin 1993). Juveniles are reported from coastal areas in the southern Mediterranean (Ninni 1932; Ktari and Kedidi 1977; Arias and Drake 1990), but detailed data on the recruitment of juveniles is lacking.

Spawning in the Mediterranean has been reported to occur in spring and summer (Sparta 1963; Tortonese 1984). Along the north-western Mediterranean coast (42°N to 45°N), larvae have been collected in July and September (no sampling in August), predominantly on the middle shelf

(water depth 25 to 100 m) (Sabates and Martin 1993). Sampling by Sabates and Martin (1993) was at the northern limit of *P. saltatrix* distribution and they suggested that spawning in more southerly regions occurs over a longer time. The data of Sabates and Martin (1993) also suggest onshore movement of larger (>8 mm) larvae.

The physical oceanography of the Mediterranean is complex, and given the limited knowledge of the early life history of *P. saltatrix* in this region, it is premature to consider larval transport on the scale of the whole basin. The north-western Mediterranean shelf, however, is similar to the northern GOM shelf and the MAB shelf in that the flow is not influenced by a strong boundary current and shelf waters are separated from offshore waters by a temperature and salinity front (Font *et al.* 1990; Wang *et al.* 1988; Sabates 1990; Sabates and Martin 1993). Although the flow direction on the northern GOM and MAB shelves is variable during the reproductive season of *P. saltatrix*, the flow on the north-western Mediterranean shelf is nearly unidirectional towards the south-west in the summer (Font *et al.* 1990; Salat *et al.* 1992). However, freshwater input from the Ebro River may produce small gyres (Font *et al.* 1990) that could retain larvae in the vicinity of the delta (Sabates and Martin 1993). In addition, there are inertial motions that may complicate the average flow regime (Font *et al.* 1990; Salat *et al.* 1992). Future work should resolve the question of whether larvae are retained in the vicinity of the Ebro River and should examine the fate of larvae that are carried to the south-west with the time-averaged flow. Information on the location of juvenile habitats along the north-eastern coast of Spain would also shed light on larval transport processes.

Black Sea

Adults of *P. saltatrix* (local common name: lufar) overwinter in the eastern Mediterranean, primarily in the Sea of Marmara and Aegean Sea (36°N to 40°N). They then migrate through the Bosphorus towards the Black Sea in spring (Turgan 1959; Kolarov 1964). Spawning occurs from June to September, primarily on the western and north-western shelf along the Bulgarian and Ukrainian coasts (41°N to 47°N) (Borcea 1929, 1933, 1936; Turgan 1959; Ivanov and Beverton 1985; Gordina and Klimova 1996). Eggs and larvae are transported towards the south-west and recruit to coastal areas in Bulgaria and Romania in the late summer (Borcea 1929, 1933, 1936; Porumb 1968, 1971). Juveniles feed on locally abundant fishes (e.g. *Engraulis ponticus*, *Atherina mochon*, *Trachurus mediterraneus*) (Borcea 1933; Oven 1957; Kolarov 1964; Porumb 1968, 1971; Ivanov and Beverton 1985) and grow by up to 2 mm day⁻¹ (Porumb and Porumb 1959).

The hypothesis that larvae in the Black Sea are transported along the western shelf to the south is well

supported by physical data. Surface circulation in the Black Sea is cyclonic with two or more central gyres (Sorokin 1983). Along the western and north-western shelf, flow is towards the south-west (Tolmazin 1985), but variation in this average flow is caused by wind-forcing and freshwater runoff (Sorokin 1983; Tolmazin 1985). This system is similar to those of the continental shelves of the MAB and north-western Mediterranean, in that average flow is relatively slow towards the equator, but reversals in this flow are observed owing to wind- and buoyancy-forcing. In addition, the system is similar to that of the north-western Mediterranean in that there is no influence of a strong boundary current on the flow dynamics on the shelf.

North-western Africa

Fisheries for *P. saltatrix* (local common name: tassergal) off north-western Africa were important between 1975 and 1983 with annual catches of 2500 to 4200 tons, but catches have declined since 1983, reaching a low of 200 tons in 1987 (Samba and Laloe 1991). The major spawning grounds are found in frontal zones off the southern Mauritanian coast (17°N to 22°N) from May to July (Conand and Franqueville 1973; Conand 1975, 1976; Champagnat 1983). There is evidence for a second spawning further south, off northern Senegal (15°N to 17°N) in October and November, involving younger individuals (2–3 years old, >35 cm FL) (Champagnat 1983). Juveniles are believed to enter the many estuaries south of the spawning grounds in southern Senegal, Gambia and northern Guinea (12°N to 15°N). Recruitment of juveniles is in two peaks: December to January and August to September (Champagnat 1983).

The north-western coast of Africa is a region with an eastern boundary current and upwelling. South of 20°N, upwelling occurs essentially during winter and spring and shelf flow is to the south. In late spring, the upwelling area shifts northward, and in the area of *P. saltatrix* spawning northward-flowing currents predominate on the shelf into the summer. In autumn, upwelling and southward flows return (Badan-Dangon 1982; Mittelstaedt 1982). The mechanisms of apparent southward larval transport are unclear but may relate to the cross-shelf structure of along-shelf flow and the complex geomorphology of the coastline (see Mittelstaedt 1982). Recruitment success of other species in this system has been positively linked with upwelling intensity, the hypothesized cause being physical control of the larval feeding environment (e.g. Cury and Roy 1989). Along the western North American coast (another region with an eastern boundary current), upwelling has been negatively linked to recruitment through offshore advective loss of larvae (e.g. Parrish *et al.* 1981; Fiedler 1986). These contrary hypotheses should be examined with regard to larval survival and nearshore recruitment along the north-western coast of Africa.

Southern Hemisphere Populations

Western South Atlantic

Off the eastern coast of South America, *P. saltatrix* (common names: enchova, anchoa de banco) has a wide distribution. Adults have been reported from Colombia (Fowler 1954), Venezuela (Lund 1961; Cervigon 1966), Brazil (Rego *et al.* 1982; Haimovici and Krug 1996), Uruguay (Goberna 1987; Nion and Rios 1991) and Argentina (Hansen 1988; Perier 1995), although they appear to be more abundant south of Rio de Janeiro (23°S). Spawning apparently occurs predominantly south of 32°S during the austral summer (January/February) but may extend northward (towards the equator) as the year progresses (March/April) (Muelbert and Sinque 1996). Juveniles recruit to estuaries in Brazil south of Rio Grande and in northern Argentina (Perier 1995), implying southward transport of larvae. Once in estuaries, juvenile diet is predominantly composed of local fishes (*Engraulis anchoita*, *Anchoa marinii* and *Mugil* sp.) (Haimovici and Krug 1992).

In physical oceanography, the eastern South American coast is similar to the SAB portion of the eastern North American coast; a strong western boundary current (the Brazil Current) flows poleward along the shelf edge. Unlike the Gulf Stream, the point of separation of this western boundary current is not fixed and varies owing to interactions with the cold, northwards-flowing Malvinas Current. The average position of the Brazil–Malvinas Confluence is 35–8°S but is more to the south in summer and to the north in winter (see Legeckis and Gordon 1982; Olson *et al.* 1988; Provost *et al.* 1992). Muelbert and Sinque (1996) suggest that *P. saltatrix* larvae are distributed in warmer shelf water and the associated Brazil Current. Larvae are presumably transported to the south in these warm water masses, but to recruit to estuaries south of the Brazil–Malvinas Confluence, larvae would need to move against the northward-flowing Malvinas Current. Thus, the transport routes of *P. saltatrix* remain unresolved owing to the relative lack of larvae in ichthyoplankton collections and the complexity of the physical regime.

South-eastern Africa

In eastern South Africa, adults of *P. saltatrix* (common names: elf, shad) migrate northwards towards KwaZulu–Natal in the winter, spawning north of 31°S, off Durban, in the austral spring and summer (October to March) (van der Elst 1976; Beckley and Connell 1996). Juveniles recruit mainly to coastal bays, and to a lesser extent, estuaries south of the spawning grounds from December to March (van der Elst 1976; Smale and Kok 1983; Smale 1984; Wallace *et al.* 1984; Bennett 1989c), indicating southward transport of larvae, but the fate of larvae spawned in February and March is unclear. Juveniles are predominantly piscivorous,

focusing on atherinids (*Atherine* (= *Hepsetia*) *breviceps*), clupeids (*Gilchristella aestuarius*, *Etrumeus teres*) and engraulids (*Engraulis capensis*) (Smale and Kok 1983; Marais 1984; Smale 1984, 1986; Bennett 1989a). Juvenile growth is rapid; typically fish are 250 mm FL at age 1 year (van der Elst 1976). There is little information regarding *P. saltatrix* north of South Africa, but it is also reported from Madagascar and north to Mozambique (van der Elst 1976).

Unlike other systems in which *P. saltatrix* reproduces, along eastern South Africa the continental shelf is quite narrow (<10 km) and is influenced by a strong poleward-flowing western boundary current (the Agulhas Current) (Lutjeharms 1981). South of Port Alfred (34°S), owing to a widening of the shelf (to about 200 km), the influence of the Agulhas Current on shelf circulation decreases and the effect of wind-forcing becomes more important. Beckley and Connell (1996) report on larvae on the eastern South African coast. Though few larvae were collected ($n = 10$), all were on the continental shelf. Those authors hypothesize that southward larval transport does not occur in the Agulhas Current. Rather, they suggest that larvae are transported in shelf currents, which are predominantly south-westward owing to the influence of the Agulhas Current. Beckley and Connell discuss studies that have observed reversals (i.e. north-east flows) in shelf currents as a result of wind and barotropic forcing (Schumann 1987, 1988). The effects of current reversals on larval transport are unknown, as are the specific mechanisms of southward larval transport, primarily because of the lack of larvae in ichthyoplankton collections.

Western Australia

The current state of knowledge regarding *P. saltatrix* (common name: tailor) along the western coast of Australia is reviewed by Lenanton *et al.* (1996). Total catches are low (<1000 t), leading to the suggestion that the population is small. Spawning occurs in late spring (October–November) and autumn (March–April), with spring spawning occurring in the central portion of the range and autumn spawning in the southern portion of the range. Larval sampling has not been intense along this coast, and to date no *P. saltatrix* larvae have been collected. Juvenile nursery habitats are coastal, including estuarine areas along the southern west coast. Juveniles feed predominantly on other fishes (Thomson 1957a).

Unlike other eastern boundary currents, the Leeuwin Current flows poleward, transporting warm water southward, along the continental shelf edge (Pearce and Griffiths 1991). This oceanographic system is similar to that of the eastern coast of South Africa in that a major ocean current flows along the shelf edge throughout the range of *P. saltatrix*. However, the spawning period does not appear to coincide with major periods of strong Leeuwin Current

flow. Again as in eastern South Africa, larvae may be transported to coastal nursery areas by wind-driven shelf flow. However, this transport may be towards the north, in the direction opposite to the Leeuwin Current (Lenanton *et al.* 1996).

Eastern Australia

As in other areas of the world, *P. saltatrix* is a popular sportfish along the eastern coast of Australia. The species ranges from 24°S to 40°S but is rare south of 38°S. In late winter/early spring, adults migrate northwards to spawn (Bade 1977; Pollock 1984; Zeller *et al.* 1996). The nature of spawning is unresolved (see Miskiewicz *et al.* 1996; Zeller *et al.* 1996) but reportedly occurs in the spring and summer in the northern portion of the range. Juveniles utilize estuarine nursery habitats in both the northern and southern portions of the range. Two juvenile recruitment periods are evident: December to February and June to August (Bade 1977; Blaber and Blaber 1980; Anon. 1981; Morton *et al.* 1993). Fish represent the major dietary component of estuarine juveniles (Thomson 1959; Bade 1977; Blaber and Blaber 1980; Anon. 1981). Juvenile growth rates have been estimated at 0.8–1.3 mm day⁻¹, and summer-recruiting individuals reach about 220 mm FL at age 1 year (Bade 1977; Anon. 1981).

The physical regime along the eastern coast of Australia is similar to that of eastern South America. A warm western boundary current, the East Australian Current, flows to the south along the shelf break (Mulhearn 1988; L. J. Hamilton 1992). Cold water moves northward along the south-eastern Australian coast, and where these two water masses meet, the East Australian Current separates from the coast and flows eastward towards New Zealand (Nilsson and Cresswell 1981; Mulhearn 1987; L. J. Hamilton 1992). *P. saltatrix* larvae spawned in the northern part of the range are apparently advected southwards on the shelf in flow driven by the East Australian Current (Miskiewicz *et al.* 1996). The mechanisms of larval transport, however, remain unclear and the role of transport in influencing recruitment patterns has not been investigated.

Life History Similarities, Differences and Hypotheses

Examination of the available global information for *P. saltatrix* populations suggests that there are some commonalities. Adults typically migrate to spawning grounds or spawn during annual migrations. There seems to be a component of along-shore advection in the transport of eggs and larvae to juvenile nursery habitats. Juveniles recruit to inshore habitats, either coastal or estuarine, at between 30 and 80 mm total length (TL). Juvenile diets are mainly piscivorous, focusing on atherinids and engraulids, which perhaps reflects the general abundance of these groups in coastal waters (Haedrich 1983; Day *et al.* 1989).

Basic early life history features seem to be similar. *P. saltatrix* broadcast-spawns small eggs that go through a larval and pelagic juvenile stage before recruiting to juvenile nursery habitats (Salekhova 1959; Deuel *et al.* 1966; Norcross *et al.* 1974). Where examined, these stages seem to be strongly associated with surface waters (Kendall and Naplin 1981; Powles 1981; Shima 1989; Sabatés and Martin 1993). There are, however, no comparative data regarding larval growth and development rates (see Hare and Cowen 1994, 1995), except that juveniles seem to recruit to nursery habitats at similar sizes (Table 1). In addition, Hare and Cowen (1995) propose that pelagic juveniles actively swim across the Middle Atlantic Bight shelf. The ability of pelagic juvenile fishes to actively swim has recently been studied (see Stobutzki and Bellwood 1994; Leis *et al.* 1996) and this aspect of *P. saltatrix* early life history needs to be investigated further.

There are several life history traits that appear to be quite variable from population to population. These differences include the presumed number of annual reproductive peaks, the number of juvenile cohorts, adult growth patterns and reproductive parameters (Table 1). Spawning season is estimated to occur over two to nine months, although in many areas spawning generally coincides with spring and autumn (Table 1). Part of the variability implied here, however, may result from the latitudinal scale of larval sampling conducted to date. For example, in the north-western Mediterranean, where spawning occurs during two months, studies have been conducted only in the northern portion of the range. In addition, spawning by the population may occur as multiple distinct events or continuously over a protracted period (Table 1). Distinct juvenile cohorts have been observed in most systems (Table 1) and the relationship between these cohorts, the pattern of spawning, and larval transport processes needs to be examined in greater detail in all systems. Another issue that should be addressed is individual-level patterns of migration and spawning. Clearly, the question of recruitment patterns is central to understanding *P. saltatrix* life history and more work is warranted, especially with regard to quantifying recruitment magnitude to different juvenile nursery habitats, comparing birthdate distributions among nursery habitats, and comparing these data with ichthyoplankton data.

When age–length relationships from global *P. saltatrix* populations are compared, three groupings are apparent (Fig. 3). The ‘fast’ growth group includes populations off north-eastern North America and north-western Africa. The ‘medium’ growth group includes populations in the Black Sea and off eastern South America. The ‘slow’ growth group includes the South African, Mediterranean and Australian populations. These growth patterns appear to be correlated with patterns in size at maturity, i.e. high-growth populations tend to have large sizes at maturity (430–

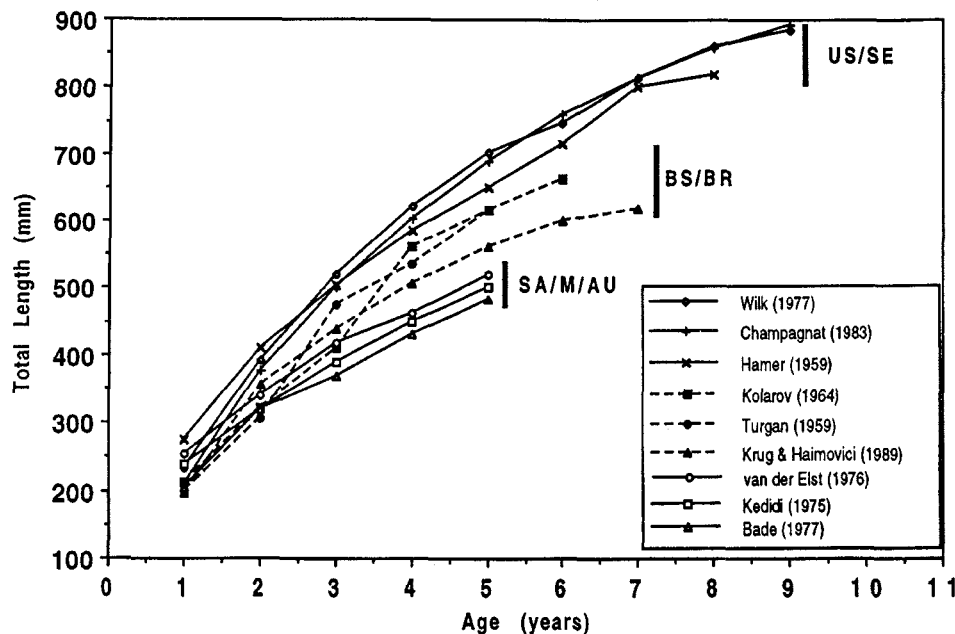


Fig. 3. Length-age relationships for global populations of *P. saltatrix* adults. Data are lumped by region and sources are provided in the legend: US, United States; SE, Senegal; BS, Black Sea; BR, Brazil; SA, South Africa; M, Mediterranean; AU, Australia. The order of the legend entries is the same as that of the plotted data sets.

450 mm), medium-growth populations have intermediate sizes at maturity (340–350 mm) and low-growth populations correspond to relatively small sizes at maturity (250–270 mm) (Table 1).

These patterns can be further quantified by comparing parameters of the von Bertalanffy growth equation (L_{∞} , von Bertalanffy asymptotic length; K , Brody growth coefficient) with length at maturity (L_m) for those populations for which data are available (Table 1). The ratio of L_{∞}/L_m is relatively constant, varying from 1.89 (Brazil) to 3.36 (South Africa), and there is a negative relationship between L_{∞} and K ($\log L_{\infty} = -0.423 \log K + 2.637$, $r^2 = 0.74$, $P < 0.001$, $n = 8$) as predicted by life history theory (see Charnov and Berrigan 1991; Roff 1991, 1992). Size at age 1 year also appears to vary regionally in approximately the same order, suggesting that large size at age 1 year is correlated with rapid growth, large size at maturity and large asymptotic sizes. In marine fishes, however, age-length relationships are quite variable (Erzini 1994; Bowker 1995), which in the case of *P. saltatrix* could be due to biased sampling (e.g. interannual differences in growth [see Fig. 4], or gear selectivity [see Ivanov and Beverton 1985; McBride *et al.* 1995]) and/or error due to incorporation of different cohorts with different age-length relationships (Fig. 5).

These potential biases notwithstanding, the data suggest distinct growth groups that may reflect either the ecological conditions in each of these areas or the phylogenetic relationships among the populations considered. Goodbred and Graves (1996) present a hypothesis for the phylogenetic

relationships among six of the populations considered here. The patterns in adult growth are not consistent with the proposed phylogeny. For example, the Brazilian population forms a phylogenetic sister group to all other populations examined, but its growth is intermediate between the North American/north-western African group and the South African/Mediterranean/Australian group. Thus, it seems likely that these growth patterns are a result of the specific ecological conditions of each area. The incorporation of data pertaining to other adult life history traits (e.g. age at maturity) and early life history traits (e.g. larval growth, age and size at the larval-juvenile transition) from a variety of populations will allow further evaluation of these hypotheses.

There are also differences in the types of habitats that are used by juveniles. These varied nursery areas include surf zones (McDermott 1983; Bennett 1989b; Ayvazian and Hyndes 1995), permanently and seasonally open estuaries (Grant 1962; Blaber and Blaber 1980; Friedland *et al.* 1988; Bennett 1989c; McBride and Conover 1991; McBride *et al.* 1993; Juanes *et al.* 1993, 1994), coastal lagoons and shore zones (Oven 1957; de Sylva *et al.* 1962; Porumb 1971; Haimovici and Krug 1992), more exposed coastal zones (Smale 1984) and shallow reefs (Bennett 1989b). Future work should involve sampling in different habitats in each region to quantify the importance of various habitats to juvenile *P. saltatrix*.

P. saltatrix occurs within a range of physical systems, yet there seems to be a component of along-shore advective

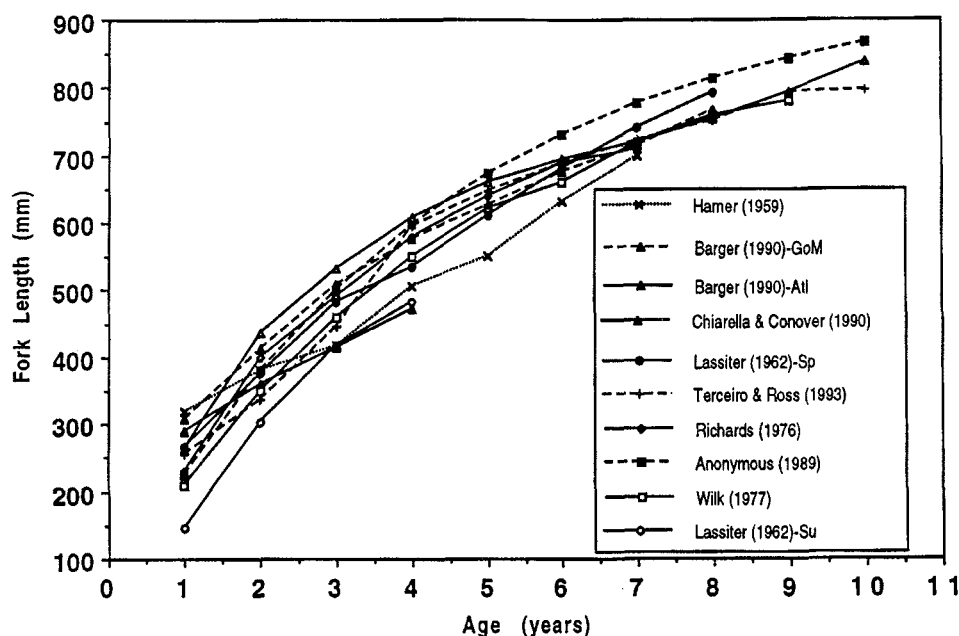


Fig. 4. Length-age relationships for US populations of *P. saltatrix* adults. Data sources are provided in the legend. The order of the legend entries is the same as that of the plotted data sets. GoM, Gulf of Mexico; Atl, Atlantic; Sp, spring-spawned cohort; Su, summer-spawned cohort.

transport of larvae from spawning grounds to nursery habitats in most systems. Even this component is variable in the sense that larval transport occurs either poleward (e.g. SAB, eastern Australia, eastern South America, south-eastern Africa) or towards the equator (e.g. Black Sea, north-western Mediterranean, MAB, north-western Africa, western Australia). Poleward transport typically involves the influence of a strong boundary current (e.g. Gulf Stream, Brazil Current, East Australian Current), whereas transport towards the equator is linked with variable shelf currents. In

the latter case, reversals in flow due to wind or upwelling may be an important component of larval transport but remain largely unstudied.

Juanes *et al.* (1994) and Juanes and Conover (1995) have hypothesized that a common pattern in spawning, along-shore advection and coastal recruitment has evolved so as to accelerate the onset of piscivory, which in turn maximizes growth and survival of juvenile *P. saltatrix*. Similar patterns of spawning, advection and consistent recruitment to coastal areas where conditions are conducive to optimal survival of juveniles have been hypothesized for walleye pollock (*Theragra chalcogramma*) populations in the Shelikof Strait (Gulf of Alaska) and Funka Bay (Hokkaido, Japan) (Kendall and Nakatani 1992; Carlson 1995), menhaden (*Brevoortia tyrannus*) populations in the south-eastern US (Warlen 1994), and the Japanese squid winter subpopulation off the coast of Japan (Okutani 1983; Jefferts 1986). These hypotheses mirror the triangle of fish migration presented by Harden Jones (1968) (see also Baker 1978). As ideas regarding *P. saltatrix* populations from around the world are refined, this hypothesis can be considered in greater detail.

Another, non-exclusive hypothesis pertaining to *P. saltatrix* life history is that spawning place and time are not 'perfectly' adapted to the present-day physical regime of the western North Atlantic, in that larvae may be produced (i.e. in the southern MAB in the late spring and early summer; in the SAB in the autumn) when larval survival to estuarine recruitment is predictably low (Hare and Cowen

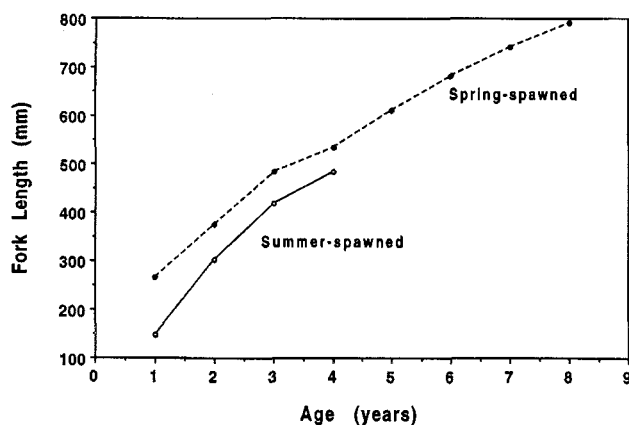


Fig. 5. Length-age relationships for spring- and summer-spawned cohorts of US *P. saltatrix*. Data are from Lassiter (1962).

1993). There are many explanations for this possibility, but one explored by Hare and Cowen (1993) is that the oceanography of the western North Atlantic has changed significantly in response to glacial cycles. A prediction based on this hypothesis is that in systems that have changed relatively little in response to glacial cycles over the past million years, *P. saltatrix* reproductive patterns should be more closely linked to patterns in larval survival and nearshore recruitment by juveniles.

A third hypothesis that develops from the body of work reviewed here is that reproduction is constrained by water temperature and by a seasonal component (perhaps light). The seasonal component is implied by the fact that spawning typically does not occur in the winter even though water temperatures may be in the appropriate range (see Ditty and Shaw 1995; Lenanton *et al.* 1996; Table 1). In addition, there are regional constraints in the distribution of *P. saltatrix*; populations do not occur in the Kuroshio Current system or in the eastern Pacific (Briggs 1960). These systems are analogous to other systems in which *P. saltatrix* does occur and thus it is not clear why these areas do not support populations of *P. saltatrix*. It is possible that these areas do not contain certain requirements of the life history (e.g. appropriate juvenile nursery habitats) or that there are barriers to adult or larval dispersal. Future evaluation of these issues should lead to greater understanding of the distributional constraints imposed upon globally distributed species.

In conclusion, it is clear that the early life history of *P. saltatrix* is broadly similar across geographically separated populations. There are, however, differences. Future efforts should work towards understanding the nature of spawning, larval survival, larval transport, coastal recruitment dynamics and juvenile survival in each of the regions where *P. saltatrix* occurs, thus 'filling in the gaps' visible in Table 1. Such studies would allow testing of the hypotheses presented above, thereby elucidating the degree to which local populations of a global species are adapted to their local environment.

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