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Ontogeny and intervals of development in five reef-associated species of blenny from the northern Gulf of Mexico (Teleostei: Blenniidae)

James G. Ditty
Louisiana State University and Agricultural and Mechanical College

ONTOGENY AND INTERVALS OF DEVELOPMENT IN FIVE REEF-ASSOCIATED SPECIES OF BLENNY FROM THE NORTHERN GULF OF MEXICO (*TELEOSTEI*: *BLENNIIDAE*)

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James Gregory Ditty
B.S., Marshall University, 1977
M.S., Louisiana State University, 1981
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DEDICATION

For my father, James C. Ditty, who modeled the virtues of honesty and hard work, and in memory of my mother, Genevieve Ditty (1924-1967). For my wife, Karen, who despite health problems made great personal sacrifices, allowing me to spend the long hours over many years to make this dream a reality. For my children, Ryan, Jordan, and Erinn, who unselfishly permitted me time out of their lives and late nights away from home during their formative years. For J. Robert and Catherine Ditty, who have always been pillars of strength and support throughout my life. To God, who provided the inner strength and through whom all things are possible.

PREFACE

Metamorphosis is much like higher education.

It's easy to know where to begin but difficult to know where to stop.

External influences often control the rate of progression.

Timing is critical and survival depends on unpredictable events,

and,

Successful completion requires flexibility, adaptability, and luck.

JGD

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ABSTRACT

I examined patterns and timing of ontogeny and relative growth in five species of blenny (*Teleostei*: *Blenniidae*) from the northern Gulf of Mexico by assigning a suite of discrete character state scores to ontogenetic events (10 external traits; 218 total specimens). This is the first study to evaluate developmental patterns in reef-associated fishes relative to the timing of metamorphosis and settlement by applying scaling techniques and statistical methods to quantify, differentiate, and select criteria for defining intervals of development across taxa.

Blennies settle at a common state of ontogeny and share a common pattern of body and fin/cirrus growth. Three 'natural' intervals of development (labeled 'larvae', 'metamorphs', and 'settlers') were consistently identified based on scoring and summing character states, and cluster analysis. Shape differences separate larvae from metamorphs, but not metamorphs from recent settlers. The common growth pattern consists of a general deepening of the head and abdomen, a narrowing of the interorbital region, and elongation of the pectoral and pelvic fins. These changes during metamorphosis produce the common shape and basic adult body form at settlement. Differences in shape show little relationship to phylogenetic distance.

Estuarine blennies settle at a smaller size but similar state of ontogeny as coastal/shelf species, which suggests the timing, rate, and state of ontogeny at important periods of ecological transition, may influence survival. The smaller size at settlement in estuarine blennies is consistent with natural selection emphasizing rapid ontogeny in species or areas where competition for available habitat or resources is great. Differences in fin and body pigmentation patterns and in the number of teeth between estuarine and coastal/shelf blennies suggest that development reflects adaptive convergence to similar ecological niches and habitats, rather than revealing any evolutionary relationship.

In blennies, ontogeny progresses gradually and continuously rather than in a stepwise fashion, as postulated by saltatory theory. Differential growth rates of individual body parts provide a similar conclusion. Variability in the timing and magnitude of ontogeny make recognizing proposed thresholds between 'steps' difficult, if not impossible. Blennies are not juveniles at settlement as commonly accepted for many other demersal and reef-associated species.

CHAPTER 1: OVERVIEW

Introduction

'Critical periods of development' and factors influencing fluctuations in stock size have long been the focus of fisheries research (May, 1974; reviewed in Hempel, 1979; Shepard and Cushing, 1980; McGurk, 1984). Fabre-Domergue and Bietrix (1897) introduced the idea of 'critical periods' of development by recognizing that high mortality occurs during yolk absorption. Hjort (1914) reinterpreted this critical period concept and suggested that survival depends on 'successful transition of yolk-sac larvae to exogenous feeding,' effectively linking early survival to adult stock size (Vladimirov, 1975). Hjort's 'critical period' hypothesis changed the direction of fisheries research and became an important ecological concept (May, 1974; Sissenwine, 1984; Bradford, 1992; Frank and Leggett, 1994). Other potentially 'critical periods' of development have since been proposed including: hatching (Vladimirov, 1975); 'swim-up' or first filling of the swim bladder (Blaxter, 1988); metamorphosis (Kuznetsov, 1972; reviewed in Youson, 1988; Thorisson, 1994); and early settlement (Gosselin and Qian, 1996), all of which are poorly understood.

Critical periods generally occur during developmental and ecological transitions when larvae are more vulnerable to external influences (Vladimirov, 1975). Because proper development of behavioral patterns, escape responses, and sensory and motor skills depends on adequate nutrition and sensory input during critical periods (Browman, 1989), delays in acquiring sensory and motor skills can reduce the ability of larvae to avoid predators and capture prey (Higgs and Fuiman, 1998). Environmental or other factors that slow or interfere with developmental processes hinder growth, prolong development time and stage duration, increase the window of vulnerability to predation, and can result in higher mortality (Chambers and Leggett, 1987; Houde, 1987; Browman, 1989; Pepin, 1991; Galis, 1993). The extent by

which survival through developmental critical periods determine stock size remains controversial, although elevated accumulative mortality is generally accepted as a forcing function (May, 1974; Houde, 1987; Blaxter, 1988; Bradford, 1992).

Hjort's critical period hypothesis was the basis for using ichthyoplankton surveys as a method of monitoring year-class strength in fishes. Estimates of abundance based on conventional ichthyoplankton surveys, however, correlate poorly with year-class strength for numerous reasons (Bradford, 1992), one of which is that most surveys under-sample 'pre-recruits' or developmental stages preparing for settlement. Accordingly, subsequent research has focused on monitoring stages nearing settlement (Anderson, 1988; Peterman et al., 1988; Fritz et al., 1990; Pepin and Myers, 1991). Although relationships between recruitment and year-class strength do not strengthen sufficiently until after settlement in reef and other demersal fishes, accurate estimation of the number of individuals approaching settlement may provide correlations of year-class strength nearly as strong (Bradford, 1992; Milicich et al., 1992; Thorrold, 1992; Meekan et al., 1993). Thus, the number of 'pre-recruits' can serve as a surrogate for the number of 'settlers' in examining the distribution and abundance patterns of reef and other demersal fishes (Schmitt and Holbrook, 1999).

Current theories on factors that affect survival primarily follow three general hypotheses: 1) bigger-is-better (size), 2) faster-is-better (growth), or 3) shorter-is-better (stage-duration) (Kingsford and Milicich, 1987; Hare and Cowen, 1997). The stage-duration hypothesis proposes that both the length of time spent in each developmental stage and the timing of settlement influence survival, and can affect distribution and abundance patterns. The high mortality rates experienced by fishes approaching or immediately after traversing

important ecological transitions demonstrate the sensitive nature of critical developmental periods like metamorphosis (Bryan and Madraisau, 1977; Neave, 1984; Keefe and Able, 1993).

Metamorphosis may be the result of a heterochronic shift in the actions of juvenile hormones that interrupted the ancestral growth trajectory (Truman and Riddiford, 1999). The fact that larviparous development has evolved independently at least eight times among extant animals suggests that metamorphosis is an adaptive and durable developmental strategy (Hadfield, 2000). Metamorphosis has been well studied in many organisms: insects (Locke, 1981; Truman and Riddiford, 1999); marine invertebrates (Hadfield and Strathmann, 1996; Pechenik et al., 1998); amphibians (Alberch, 1989; Werner, 1986); and lampreys (reviewed in Potter, 1982), but not bony fishes. Cartilaginous fishes, such as hagfishes (Myxiniformes), and sharks, skates, and rays (Chondrichthyes) do not undergo metamorphosis (Youson, 1988).

Understanding metamorphosis and other critical periods of transition requires knowledge of the timing and synchronization of ontogenetic change (Kawamura et al., 1984; Kawamura and Ishida, 1985; McCormick, 1993; Fuiman and Delbos, 1998; Higgs and Fuiman, 1998; Poling and Fuiman, 1998). 'Ontogeny' is the appearance of new traits (e.g., head or body spination, precocious characters), capabilities, or behaviors, or the reorganization/loss of existing traits, capabilities, or behaviors. 'Development' encompasses both growth and ontogeny. Anecdotal evidence suggests that the pelagic larval stages of demersal fishes metamorphose and settle within a temporal window of opportunity delimited by the ability to control the rate of development. Even though rates of growth and ontogeny interact, evidence suggests that the progression of ontogeny is linked more closely to body size than age within a given species. The fact that body size at settlement is less variable than age within a given species, but more variable among species (Gerking and Rausch, 1979; Chambers and Leggett,

1987; Fuiman, 1994), raises the possibility that habitat shifts occur at a common state of ontogeny (Fuiman, 1997), a hypothesis not yet examined in reef fishes.

The wide variety of definitions (Table 1.1) and criteria (Table 1.2) used to characterize metamorphosis, the common misuse of developmental terminology, and the myriad of descriptive names for depicting developmental intervals has created confusion in taxonomy and in our understanding of developmental processes. Various synonyms have been assigned to fishes approaching or undergoing metamorphosis, including: postlarva (Russell, 1976); metalarva (Synder, 1976; Labelle and Nursall, 1985); pelagic postlarva (Ninos, 1984); demersal larva (Breitburg, 1989); metamorphic larva (Gozlan et al., 1999); transition stage (Ahlstrom, 1968; Kaufman et al., 1992); transformation stage (Kendall et al., 1984); prejuvenile (Hubbs, 1958; Brothers and McFarland, 1981; Labelle and Nursall, 1985; McFarlane et al., 2000); and pelagic juvenile (Moser and Boehlert, 1991). Adding to this overall confusion, metamorphic stages of some fishes, such as the leptocephalus stage of eels, scutatus stage of frogfish, querimana stage of mullet, macristiella stage of bathysaurid lizardfish, and whitebait stage of Pacific tarpon (Johnson, 1974; de Sylva and Eschmeyer, 1977; Kendall et al., 1984; Tsukamoto and Okiyama, 1997), have been described as distinct species.

Separate schools of thought have emerged to describe subdivisions of fish ontogeny and the progression, rate, and timing of developmental sequences. Vasnetsov (1953) and Kryzhanovsky et al. (1953) first applied the concept of 'saltatory ontogeny' to fishes, a concept later redefined by Balon (1979), who incorporates saltation into his life history model (Balon, 1979; 1984; 1986). Saltatory development depicts ontogeny as a process that consists of a hierarchy of stabilized, distinguishable steps and periods separated by less stable thresholds that progress in a series of leaps rather than as a continuous sequence of events (Balon, 1979; 1986;

Table 1.1. Some definitions of metamorphosis in fishes.

Ahlstrom and Counts (1958)	The interval during which marked changes occur in body proportions and structures without any marked increase in length.
Doyle (1977)	Developmental changes in non-reproductive structures completed within a time period and during which a larva adapted to one mode of life transforms into a juvenile with a different mode of life.
Just et al. (1981)	A change in non-reproductive structures between embryonic life and sexual maturation when the larva occupies a ecological niche different from the embryo and adult. The morphological changes at the end of the larva phase triggered by an external and/or internal cue.
Youson (1988)	A second larval phase following the initial growth phase of larvae and marked by an abrupt transformation from the larval phenotype. The period of change between the initiating and terminating events that usually leads to settlement in demersal fishes.
Alberch (1989)	The transition period encompassing metamorphosis is one of rapid morphogenesis and differentiation characterized by progressive accumulation of developmental events within a narrow timeframe, punctuated at both ends by stages of growth.

Table 1.2. Survey of primary criteria used to determine when non-pleuronectiform, reef-associated fishes metamorphose and settle. N/A means information not available. All measurements in mm standard length.

Author	Family	Species	Metamorphosis	Settlement	Onset of scalation	Pigmentation	Behavior
	Order Perciformes						
Bryan and Madraisau (1977)	Siganidae	*Siganus lineatus*	~16.0-19.0			X	X
Fukuhara (1985)	Sparidae	*Pagrus major*	7.6-8.6	~10.5		X	X
Toyoda and Uematsu (1994)	Sparidae	*Pagrus major*		12.0-15.0		X	X
Fukuhara (1987)	Sparidae	*Acanthopagrus schlegeli*	9.0-11.0				
Kohno et al. (1993)	Serranidae	*Epinephelus fuscoguttatus*	~12.5-16.5			X	
Able and Fahay (1998)	Lutjanidae	*Lutjanus griseus*	10.0-15.0	10.0-15.0			
Clarke et al. (1997)		*Lutjanus analis*	10.2-14.6			X	
		Lutjanus synagris	>10.0			X	
		Lutjanus chrysurus	~10.0-13.9			X	
Able and Fahay (1998)	Sciaenidae	*Cynoscion regalis*		~8.0-10.0	14.0		
		Leiostomus xanthurus		~8.0-10.0	23.0-25.0		
		Micropogonias undulatus		~8.0-10.0	14.0-16.0		
Poling and Fuiman (1999)	Sciaenidae	*Sciaenops ocellatus*		~4.7	~20.0		
		Cynoscion nebulosus		~5.7	~20.0		
		Micropogonias undulatus		~10.2	~30.0		

(Table 1.2 continued)

Species	Squamation	All fin elements	Fin shape	Settlement	Gut Length	Swimming mode	Body shape	Ossification	Misc. internal	No data provided
Order Perciformes										
Siganus lineatus					X					
Pagrus major	X	X	X			X			X	
Pagrus major	X	X	X			X			X	
Acanthopagrus schlegeli	X	X	X			X			X	
Epinephelus fuscoguttatus		X								
Lutjanus griseus										X
Lutjanus analis	X	X		X						
Lutjanus synagris	X	X		X						
Lutjanus chrysurus	X	X		X						
Cynoscion regalis	X									
Leiostomus xanthurus	X									
Micropogonias undulatus	X									
Sciaenops ocellatus	X									
Cynoscion nebulosus	X									
Micropogonias undulatus	X									

(Table 1.2 continued)

Author	Family	Species	Metamorphosis	Settlement	Onset of scalation	Pigmentation	Behavior
	Order Gadiformes[1]						
Markle et al. (1992)	Gadidae	*Microstomus pacificus*					
Able and Fahay (1998)	Phycidae	*Urophycis chuss*	23-49	23-49			
		Urophycis regia	25-30	25-30			
		Urophycis tenuis	50-80	50-80			
	Order Scorpaeniformes[1]						
Moser (1972)	Scorpaenidae	*Sebastes macdonaldi*	16.0-22.0	>45.0		X	
Richardson and LaRoche (1979)	Scorpaenidae	*Sebastes crameri*	16.0-21.0	>46.0		X	
		Sebastes pinniger	12.8-18.4	NA		X	
		Sebastes helvomaculatus	12.0-18.6	NA		X	
LaRoche and Richardson (1981)	Scorpaenidae	*Sebastes entomelas*	~22.0-31.0	>42.0		X	
		Sebastes zacentrus	13.7-19.6	>35.0		X	
Matsumoto and Tanaka (1996)	Scorpaenidae	*Hexagrammos agrammus*	16.0-20.0 24.8-39.6				
Able and Fahay (1998)	Trigilidae	*Prionotus evolans*	7.0-12.0	7.0-12.0	>10.0		
		Prionotus carolinus	7.0-12.0	7.0-12.0	>10.0		

(Table 1.2 continued)

Species	Squamation	All fin elements	Fin shape	Settlement	Gut Length	Swimming mode	Body shape	Ossification	Misc. internal	No data provided
Order Gadiformes[1]										
Microstomus pacificus					X					
Urophycis chuss										X
Urophycis regia										X
Urophycis tenuis										X
Order Scorpaeniformes[1]										
Sebastes macdonaldi		X					X			
Sebastes crameri	X	X								
Sebastes pinniger	X	X								
Sebastes helvomaculatus	X	X								
Sebastes entomelas	X	X								
Sebastes zacentrus	X	X								
Hexagrammos agrammus		X						X		
Prionotus evolans	X									
Prionotus carolinus	X									

[1] Some gadiform and scorpaeniform fishes reportedly have both pelagic and benthic juvenile phases.

1999). 'Gradualists,' on the other hand, view ontogeny as a series of small progressive changes that occur continuously but not necessarily at a constant rate (Zweifel and Lasker, 1976; O'Connell, 1981; Markle et al., 1992; Fuiman and Higgs, 1997). Although laboratory observations have been interpreted as supporting saltatory ontogeny (McElman and Balon, 1979; 1980; Paine and Balon, 1984a; 1984b; Crawford and Balon, 1994; Gozlan et al., 1999; Solbakken et al., 1999), the theory has not been objectively examined.

Most reef fishes undergo dramatic changes in morphology, physiology, and behavior as they approach settlement (Victor, 1991) so that larvae are functionally prepared for their new environment (Sponaugle and Cowen, 1997; Higgs and Fuiman, 1998; Poling and Fuiman, 1998). Few studies, however, have examined and compared the timing of ontogeny and ecological transitions even though evidence suggests that closely related species from different habitats sometimes exhibit different patterns of ontogeny (Markle et al., 1992; Keefe and Able, 1993; Fuiman, 1997; Poling and Fuiman, 1998). Understanding processes that affect the timing of ontogenetic shifts in resource and habitat use (Juanes et al., 1994; Simonovic et al., 1999) and functional and ecological relationships (Fuiman and Magurran, 1994; Cowen and Sponaugle, 1997) will require a systematic examination of metamorphosis in a wide range of taxa (Chambers and Leggett, 1987; Fuiman and Higgs, 1997).

If habitat shifts occur at a common state of ontogeny, characterization of the timing and progression of ontogeny will facilitate evaluation and comparison of important ecological and early life history questions (Youson, 1988). The stage of development at which potential recruits arrive at nursery areas may determine their ability to avoid predation (Keefe and Able, 1993; Higgs and Fuiman, 1998; Poling and Fuiman, 1998). If mortality rates are stage-specific, critical periods of development will be defined as those suffering the highest cumulative

mortality (Pepin, 1991). Thus, categorization of intervals of development would permit evaluation of stage-specific mortality rates and provide a meaningful test of the concept of critical periods of development.

The taxonomically and ecologically diverse marine fishes known as blennies (*Teleostei*: *Blenniidae*) contain 21 described species in the western central North Atlantic, of which at least 11 occur in the northern Gulf of Mexico (Gulf; Table 1.3). Blennies are demersal or semi-demersal and generally reside in reef, oyster bed, or biofouling communities. Several females may deposit eggs in the same nest and each nest may contain multiple cohorts of eggs at different states of development. Males guard the nest until eggs hatch and young become pelagic (Labelle and Nursall, 1992). This research includes new information on the developmental patterns of five species of blenny found in the Gulf.

The site-specific nature, wide geographic distribution, abundance, and relative ease of collection make blennies ideal for examining interspecies developmental and ecological questions regarding differences/similarities in ontogeny and the timing of settlement. My overall hypothesis is that ontogenetic characters can be used to delineate 'natural' intervals of development and that ontogeny is a better predictor of the timing of settlement than either age or body size. The overall study objectives are to: 1) compare the timing and progression of ontogeny among multiple species; 2) examine the timing of changes in shape relative to that of metamorphosis and settlement, and, 3) place study findings in the context of the two primary theories of development in fishes, saltatory and gradual ontogeny.

Table 1.3. Meristic and distribution data for western-central North Atlantic blennies. GOMEX means Gulf of Mexico; N/A means information not available.

Taxa	Spinous dorsal	Total dorsal elements (Mode)	Total anal elements (Mode)	Total vertebrae	Pelvic rays	Pectoral rays	Caudal ray count (Mode)	Epurals
Chasmodes								
bosquianus	X-XI (XI)+16-19 (18)	28-30 (29)	18-22 (20)	34-35	I, 3	11-13 (12)	4+11-12+3-4=19	1
saburrae	X-XII (XI)+16-20 (18)	27-31 (28-30)	19-21 (20)	34-36 (34)	I, 3	11-13 (12)	4+11-12+3-4=19	1
Entomacrodus								
nigricans	XII-XIII+13-16 (14-15)	(27-28)	16-19 (18)	33-35 (34)	I, 4	13-14	N/A	1
vomerinus	XII-XIV (XIII)+15-17 (16)	28-30 (29)	17-20 (19)	34-36 (35)	I, 4	12-15 (14)	N/A	1
Hypleurochilus								
bermudensis	XI-XII (XII)+12-13 (13)	25	16-17 (17)	30-31 (31)	I, 4	13-14 (14)		1
caudovittatus	XII+14-15 (14)	26-27 (26)	17-19 (18)	33	I, 3	14	5-6+13+4-5=23	1
geminatus	XII+14-16 (15)	26-28 (27)	16-20 (18-19)	32-33 (33)	I, 3-4 (3)	13-15 (14)	5-6+13+4-5=23	1
multifilis [1]	XII+13-16 (15)	26-27 (27)	17-20 (18-19)	32-33	I, 3	14	5-6+13+4-5=23-24	1
pseudoaequipinnus	XI-XII (XII)+11-15 (13-14)	(25-26)	16-18 (17-18)	31-32 (32)	I, 3-4 (4)	13-15 (14)	4-6+13+4-5=22-24	1
springeri	XI-XIII (XII)+12-13 (13)	25	16-18 (16-17)	32	I, 4	13-15 (14)	N/A	1
Hypsoblennius								
exstochilus	XI-XII (XII)+13-15 (14)	25-26 (26)	17-18 (18)	32-33	I, 3	13-15 (14)	6-7+13+5-6=25	1
hentz	XI-XIII (XII)+13-16 (14-15)	25-28 (26-27)	16-19 (18)	31-34 (32)	I, 3	13-15 (14)	5-6+13+5-6=23-24	1
invemar [1]	XI-XII (XII)+11-12 (12)	23-24 (24)	15-16 (16)	30-32 (31)	I, 4	13-15 (14)	6-7+13+6-7=26	1
ionthas [1]	XI-XIII (XII)+13-15 (14)	25-27 (26-27)	16-19 (17-18)	30-33 (31-32)	I, 3	13-15 (14)	5-6+13+4-6=23	1
Lupinoblennius								
dispar = vinctus	XII+13-14	25-26	17-18	31-32	I, 4	12-14 (13)	5+11-13+4-5=21-23	1
nicholsi	XII-XIII (XII)+13-15 (15)	26-27	18-19	32-35 (33)[1]	I, 3	13-14 (13)	5+11-13+4-5=21-23	1
Omobranchus								
punctatus	XI-XIII (XII)+19-22 (21)	31-34 (32)	23-26 (25-26)	38-40 (39)	I, 2	12-14 (13)	6-8+13+6-8=25-29	1
Ophioblennius								
atlanticus atlanticus	XII+20-23	33-35 (33-34)	24-25	36	I, 4	14-16	N/A	2
atlanticus macclurei	XII+20-21	31-32	22-23	N/A	I, 4	14-16 (15)	7-8+13+7-8=28	2
Parablennius								
marmoreus [1]	XI-XII (XII)+17-18 (18)	30	21-22	36	I, 3	14	6+13+6=25	1
Scartella								
cristata [1]	XI-XII (XII)+14-15	26-27	17-19 (18)	33	I, 3	14[2]	6-7+13+5-6=25	2

(Table 1.3 continued)

Taxa	Hypural minimal	Gill opening	Canines		Median supra-temporal pore	Last anal ray free	Dentary pores	Distribution	Literature
			Upper	Lower					
Chasmodes		Greatly							
bosquianus	1-0 (fuses)	restricted	No	No	No	Yes	4	U. S. Atlantic through northern GOMEX	Springer (1959)
saburrae	1-0 (fuses)		No	No	No	Yes	>6	East and west coasts of Florida	Bath (1977)
Entomacrodus		Unrestricted							
nigricans	1		No	Yes	Yes	No	N/A	Florida, Bermuda, Caribbean	Springer (1967)
vomerinus	1		No	Yes	Yes	No	N/A	Brazil	
Hypleurochilus		Slightly							
bermudensis	1	restricted	Yes	Yes	Yes	No	4 (3)	Bermuda	Bath (1994)
caudovittatus	1		Yes	Yes	Yes	No	5	Eastern GOMEX off Florida	Randall (1966)
geminatus	1		Yes	Yes	Yes	No	5	U. S. Atlantic coast only	
multifilis [1]	1		Yes	Yes	Yes	No	5	northern GOMEX	
pseudoaequipinnus	1		Yes	Yes	Yes	No	5	East coast of Florida southward	
springeri	1		Yes	Yes	Yes	No	5	West Indies	
Hypsoblennius		Restricted							
exstochilus	0		No	No	Yes	No	3	Bahamas and Virgin Islands	Smith-Vaniz (1980)
hentz	0		No	No	Yes	No	4	U. S. Atlantic and GOMEX but not Mexico	
invemar [1]	0		No	No	Yes	No	3	GOMEX, Caribbean, Colombia, Venezuela	
ionthas [1]	0		No	No	Yes	No	3	U. S. Atlantic and GOMEX	
Lupinoblennius		Slightly							Dawson (1970)
dispar = vinctus	0	restricted	Male	Both	Yes	No	3	Mexico, Central America and Caribbean	Tavolga (1954)
nicholsi	0		Male	Both	Yes	No	3	Florida	Bath (1996)
Omobranchus		Greatly							
punctatus	0	restricted	Yes	Yes	Yes	No	N/A	Caribbean	Springer & Gomon (1975)
Ophioblennius		Unrestricted							
atlanticus atlanticus	1		No	Yes	N/A	Yes	N/A	Africa and east coast of Brazil	Springer (1962)
atlanticus macclurei	1		No	Yes	N/A	Yes	2	U. S. Atlantic, GOMEX and Caribbean	Re and Almeida (1981)
Parablennius		Unrestricted						U. S. Atlantic and GOMEX coasts through	
marmoreus [1]	1		Yes	Yes	Yes	No	2	Central America and Caribbean	Bath (1977; 1990)
Scartella		Unrestricted							
cristata [1]	0		No	Yes	No	No	6-16	Florida, GOMEX through Central America	Bath (1970; 1977)

[1] Indicates one of the five primary species studied; the early-life stages of several other taxa were used for comparison

[2] Lower pectoral fin rays thickened

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CHAPTER 2: TIMING AND PROGRESSION OF ONTOGENY IN FIVE REEF-ASSOCIATED SPECIES OF BLENNY

Introduction

The complex life cycle of many marine fishes consists of different intervals of development, each interconnected but with different growth and survival requirements and population dynamics (Hempel, 1965; Frank and Leggett, 1994). Approximately 80% of all marine organisms have a complex life cycle that includes both a physical metamorphosis and a spatial habitat shift (Bhaud and Duchene, 1996). Despite the extensive invertebrate literature on metamorphosis (Pechenik, 1990; Bhaud and Duchene, 1996; Hadfield and Strathmann, 1996; Gebauer et al., 1999), our understanding of metamorphosis in marine fishes remains poor.

Individual, geographical, and seasonal variability in planktonic duration and timing of metamorphosis and settlement has become the subject of increased scrutiny because of the inverse relationship between planktonic duration and survival (Cowen, 1991; McCormick, 1994; Bell et al., 1995). Interspecific differences in the timing and duration of ontogenetic events have important implications for survival and year-class strength because fluctuating environmental conditions can modify the duration of developmental intervals (Smith-Gill and Berven, 1979; McCormick and Molony, 1992; 1995; Fuiman and Higgs, 1997), the state of sensory and morphological development, and an organism's ability to avoid predators and capture prey (Chambers and Leggett, 1987; Houde, 1987; Pepin, 1991; Higgs and Fuiman, 1998). Thus, metamorphosis can be a critical transition period when density-dependent mortality may be most intense (Frank and Leggett, 1994; Schmitt and Holbrook, 1999).

Various scientific disciplines have subdivided and labeled intervals of development differently, creating overlapping and confusing terminologies. In fact, what appear to be similar descriptors often refer to very different stages of development (see Kingsford, 1988) and even multiple stages (Gorodilov, 1996). Understanding metamorphosis and settlement requires the consistent use of clearly defined intervals because factors that influence survival may be interval-

specific (Richards and Lindeman, 1987; Kingsford, 1988; Noakes and Godin, 1988). Attempts to characterize natural intervals of development in bony fishes, however, have been disappointing because of poorly defined characters resulting from the lack of precise information on the position and timing of a trait in a developmental sequence (Ahlstrom, 1968; Youson, 1988; Fuiman and Higgs, 1997).

Metamorphosis and settlement at a fixed length or age expresses a belief in the relative balance between rates of growth and differentiation. The fact that age and length at metamorphosis have been positively correlated, negatively correlated, and uncorrelated with growth rate suggests that the environmental conditions that trigger or govern the timing of metamorphosis are complex (Werner, 1986; Youson, 1988; Pfennig et al., 1991; Fuiman, 1994). While standard length (SL) is an adequate index for intraspecific comparisons, size is not as effective in direct interspecific comparisons because genetic and environmental factors can induce differences in size and age at a comparable state of ontogeny (Fuiman and Higgs, 1997; Fuiman et al., 1998). Interspecific comparisons of the timing and progression of ontogeny require a dimensionless metric that accounts for non-linear rates of ontogeny and differences in size among taxa (Fuiman, 1994; Fuiman and Higgs, 1997). The ontogenetic index (O_L) of Fuiman (1994) expresses the state of a larva at any point in time in its ontogeny as a percentage of a logarithmic developmental period, as $O_L = \log L / \log L_{juv} \times 100$, where L = SL, and L_{juv} = SL at the beginning of the juvenile period in a given species. The resultant index represents the percentage of development that has taken place before a given size. Using L_{juv} to calculate O_L corrects for interspecific size differences, while the logarithmic transformation reflects the multiplicative nature of ontogeny (Fuiman and Higgs, 1997).

Two schools of thought have emerged to describe the progression of ontogeny in fishes. The theory of saltatory development views ontogeny as a series of distinguishable, stabilized

intervals (steps and periods) separated by less stable thresholds, with most changes in form, ability, and behavior occurring at thresholds (Balon, 1999). Intervals of saltatory development are sequential, hierarchical, and progressively larger units of ontogeny. Balon (1999) considers 'stage' an instantaneous state and not an interval of development. The theory of gradual development, on the other hand, views ontogeny as a series of small, progressive, continuous, and cumulative changes in form and structure that may result in a modified ecological role (Kovac and Copp, 1999). Gradualism views ontogeny as a dynamic process that varies in rate over the course of development (Alberch, 1985), progressing more rapidly early than later in life (Gorbman et al., 1982; Markle et al., 1992; Fuiman and Higgs, 1997; Kovac and Copp, 1999).

Four central questions frame this research: 1) Are there discrete, recognizable intervals of development in blennies, and is there a common suite of interspecific traits that identify them? 2) Does settlement occur at a common state of ontogeny, as proposed by Fuiman (1997)? 3) When does the juvenile period begin and end in blennies? 4) Does ontogeny progress gradually and continuously, or in a saltatory fashion?

Materials and Methods

This chapter will quantitatively examine the timing of ontogeny in five species of blenny from the northern Gulf, with the purpose of understanding general features of their morphological and behavioral development. The five primary species studied include: tessellated blenny (*Hypsoblennius invemar*); freckled blenny (*H. ionthas*); *Hypleurochilus multifilis* (no common name); seaweed blenny (*Parablennius marmoreus*); and molly miller (*Scartella cristata*), all in the tribe Parablenniini, according to Bock and Zander (1986). I also examined a few specimens of other members of the Parablenniini for comparison, including: Florida blenny, *Chasmodes saburrae*; striped blenny, *C. bosquianaus*; feather blenny,

Hypsoblennius hentz; and redlip blenny, *Ophioblennius atlanticus*, in the tribe Salariini. Observations of young *Lupinoblennius vinctus* were taken from Dawson (1970). Generally, *C. saburrae*, *C. bosquianaus*, *L. vinctus*, and *L. nicholsi* are shallow brackish/estuarine species (Springer, 1959; Dawson, 1970), whereas *H. hentz* and *H. ionthas* are estuarine/coastal species (Smith-Vaniz and Acero, 1980). *Scartella cristata* and *H. multifilis* are inner shelf species often associated with pilings, jetties, and petroleum platforms (Randall, 1966; Hastings, 1972), whereas *H. invemar* and *P. marmoreus* are mid-shelf, relatively clear water species (Smith-Vaniz and Acero, 1980). *Ophioblennius atlanticus* is primarily a Caribbean, natural reef-associate who's young are frequently collected in deeper waters (Labelle and Nursall, 1985).

Understanding developmental processes involves the following terms:

Development - progressive and concurrent changes in growth and ontogeny**.**

Ontogeny - appearance of new traits (head spination, precocious characters, etc), capabilities, or behaviors, or the reorganization/loss of existing traits, capabilities, or behaviors.

Scaling - the effect of changes or differences in size when making interspecific comparisons of individual traits.

Larvae - young not having begun to metamorphose (Note: 'metamorphs' are considered 'larvae' as normally defined).

Metamorphosis - the transition period of rapid ontogeny, characterized by the progressive accumulation of developmental events within a narrow timeframe; often associated with the larva-to-juvenile transition.

Late metamorphs - those individuals with high total character state scores that remain planktonic but exhibit some characteristics of early settlers.

Recent settlers -those individuals that may retain some larval but have mostly juvenile characteristics.

Settlement – Process by which a larva or juvenile leaves the pelagic environment and adopts a demersal life-style; not applicable to species that are pelagic as adults; sometimes associated with the larva-to-juvenile transition.

Presettlers of the five primary species of blenny were collected during light trap sampling of oil and gas platforms off Louisiana over a 3-yr period (1995-1997). Recent settlers were hand-netted over oyster shell reefs and along rock jetties; with slurp guns along the legs of oil and gas platforms; and following explosive removal of platforms (Appendix). Specimens were fixed in 10% formalin and transferred to 70% ETOH after 24 h. Sample sizes differed among species depending on abundance and the range of sizes available for study, although each data set contained a nearly continuous size series of specimens with minor gaps in length. Supplementary material included: *Chasmodes bosquianus* (2 specimens, 7.4 mm); *C. saburrae* (1, 9.5 mm); *Hypsoblennius hentz* (2, 5.0 mm and 11.0 mm); and *Ophioblennius atlanticus* (3, 36.0-46.0 mm), although poor specimen condition limited observations in some of this material (Table 2.1). Lengths are reported as standard length (SL) throughout.

Overall, I examined 55 *H. invemar*, 42 *H. ionthas*, 41 *H. multifilis*, 50 *P. marmoreus*, and 30 *S. cristata*. Each specimen was scored for a suite of 'individual character states' with each state representing an ontogenetic event (Table 2.2). Specimens dipped in a solution of Cyanine Blue 5R stain, also known as Acid Blue 113 (Saruwatari et al., 1997), improved the contrast of anatomical structures such as sensory pores, fin rays, and cirri. I cleared and stained a developmental series of each species following the methods outlined by Potthoff (1984), to reveal skeletal characters and observe general patterns of ossification. I also assigned character state scores to patterns of ossification (Table 2.3). Uptake of Alizarin Red stain differentiated ossifying bone from Alcian Blue-stained cartilaginous structures. The process of calcification may begin before developing skeletal structures absorb Alizarin Red, but for practical purposes

Table 2.1. Observations of supplemental material from the northern Gulf of Mexico not included in the primary study but used in comparisons.

Species	***C. bosquianus***	***Chasmodes saburrae***	***Hypsoblennius hentz***	***Lupinoblennius vinctus***	***Ophioblennius atlanticus***
Size (mm SL)	7.4; 7.4	9.5	5.0;[1] 11.0	10.0; 14.0 [2]	36.0, 38.0, 46.0
Meristics					
Dorsal/Anal rays	XI, 17; II, 18	XI, 18/II, 18	XII, 14/II, 16	XII, 13; II,15	XII, 20-21; II, 20
Caudal rays	4-6+5-4	4-6+5-4	5-7+6-5	5-6+5-5	7-7+6-7
Teeth					
Maxillary/Dentary	6/6	18/14-16	12/12	16/16; 18/19	>150/>150
Canines	No	No	No	No	Yes
Preopercle					
Spine	Nub/No	No	Yes	No	No
Pores	5	5	4	3	2
Cirrus					
Orbital/Nasal	Nub/No	Yes/No	Yes/No	No data	Yes/Yes
Late metamorph/Settler	Metamorph	Settler	Metamorph	Settler	Metamorph
Pigmentation	Multiple trunk bands	Multiple trunk bands	Poor condition		38.0 mm specimen with light pectoral fin pigment nuchal cirrus

[1] Illustrated only

[2] Observations taken from Dawson (1970)

Table 2.2. Character state codes used to score young of five species of blenny from the northern Gulf of Mexico. Each character state represents a separate ontogenetic event.

Score	Dorsal fin rays
0	Finfold, fin base thickening, or anlag only
1	Initial segmentation of any fin ray
2	Terminal ray of dorsal and anal fins initially segmented
3	Pigment along shaft of at least one ray
4	Pigment along shaft of all ray
5	Consolidation of pigment into a pattern of stripes, bars or bands
	Caudal fin elements
0	Preflexion, hypural plate differentiating
1	Initial segmentation of any primary caudal ray
2	All primary caudal rays segmented, secondary rays forming
3	All primary and secondary rays formed, may have pigment on lower-most rays
4	Roughly 50% of primary caudal rays pigmented at least along shaft
5	Pigment along entire shaft of all primary rays but no pattern of vertical bands
6	First primary caudal ray initially bifurcating
	External body pigment
0	Original pigment pattern characteristic of blenny larvae
1	Head pigment increasing
2	First band of pigment forming in nape area
3	Two or more bands of pigment present along trunk
	Pectoral fin rays
0	Finfold or incipient rays only
1	Initial segmentation of any pectoral ray
2	All rays initially segmented
3	New pigment present externally on pectoral axil, rays, or fin membrane
4	Reduction in original pigment pattern of larvae[1], external pigment increasing
5	All original fin pigment characteristic of blenny larvae gone[1]
	Pelvic fin pigment
0	Absent
1	One or two large melanophores midway along shaft of any pelvic fin ray
2	Any pelvic ray with pigment scattered lightly over base

(Table 2.2 continued)

Score	
	Orbital cirrus
0	Not present or thickening nub, without free distal margin
1	Distal margin free but unpigmented; may be furcate
2	Cirrus at least initially pigmented, may be multiply furcate
	Nasal cirrus
0	Not present or thickening nub, without free distal margin
1	Distal margin free but unpigmented; may be furcate
2	Cirrus at least initially pigmented, may be multiply furcate
	Number of teeth
0	6 or fewer teeth
1	8-10 teeth
2	12-14 teeth
3	16-18 teeth
4	20-22 teeth
5	24 or more teeth
	Bony ossicles of upper lateral line
0	Ossicles do not extend past 3rd dorsal spine
1	Ossicles end between 3rd and 6th dorsal spines
2	Ossicles end between 6th and 9th dorsal spines
3	Ossicles extend beyond 9th dorsal spine
	Longest preopercular spine as a % of orbit diameter
0	Spine(s) increasing in length
1	Spine(s) regressing, some secondary spines may be reduced to nubs
2	Longest spine less than 50% of maximum length
3	Longest spine reduced to nub or entirely resorbed
	Type of teeth[2]
0	Villiform teeth only
1	Mixed villiform and incisiform teeth
2	Incisiform, except posterior-most, minor changes in tooth shape hereafter
	Dorsal spines[2]
0	Finfold or anlag
1	Some but not all partially formed
2	All spines structurally distinct

[1] Reverse definitions for character states 4 and 5 because *Parablennius marmoreus* larvae lacl pectoral fin pigment; fin becomes pigmented in late metamorphs just before settlemen

[2] Characters included in total character state score but not further analyzed

Table 2.3. Character state scores for following the progression of ossification in five species of blenny from the northern Gulf of Mexico. Each character state represents a separate ontogenetic event.

Assigned Score	Pectoral radials[1]; Hypural[1] and Epural[1] bones
0	Differentiating and chondrifying, some elements may have slight pink tinge
1	Clearly ossifying but still differentiating
2	All but tip or outer rim ossified, tip or rim remains cartilaginous
3	Structurally distinct and ossified, no cartilage indicated
	Vertebral column
0	Centra differentiating, some vertebrae may have pink tinge
1	All centra ossifying, most neural and haemal spines differentiating, some ossifying
2	Centra ossified, neural arches developing, neural and haemal spines nearly ossified
3	Neural canal closed on each vertebra; vertebral elements structurally distinct
	Pterygiophores of dorsal and anal fins
0	Differentiating, chondrifying, few may have pink tinge
1	Proximal pterygiophores developed, interdigitation pattern with neural or haemal spines evident; fewer than 50% ossifying
2	All proximals ossifying, most distal elements cartilaginous
3	All elements structurally distinct and ossified
	Spines; Rays
0	Differentiating, mostly anlage, some elements may have slight pink tinge
1	Most ossifying, terminal element of dorsal and anal fins differentiating
2	All elements structurally distinctly and ossified
	Suborbitals 4 and 5
0	Differentiating, chondrifying
1	Chondrifying, may have pink tinge; suborbitals do not abutt
2	Suborbitals ossified, bones abutt; infraorbital canal continuous
	Dentary
0	Differentiating, chondrifying
1	Roughly 50% ossifying
2	Dentary structurally distinct; all sensory pores encased in bone
	Pleural ribs
0	Differentiating, primarily cartilaginous, some ribs may have slight pink tinge
1	Roughly 50% ossifying
2	All structurally distinct and ossified

[1] Each trait scored separately

uptake of stain was used to represent the onset of calcification (Dunn, 1983). I considered skeletal elements formed when the entire structure absorbed Alizarin Red (no blue remained), but do not imply that the process of calcification is complete. Pectoral rays were numbered in a dorsal to ventral sequence to describe fin pigmentation patterns. Summing scores for individual character states (Table 2.2) produced a 'total character state' score for each individual. The minimum score was 1 and the maximum score was 41; except in *S. cristata*, which had a total character state score of 42 because only they have nuchal cirri.

Confidently assigning individuals to intervals of development requires methods for reducing ambiguity. To help identify natural intervals of development within species, a cluster analysis was performed on total character state score using complete linkage and Manhattan distance rules, to organize and map group structure (James and McCulloch, 1990). A minimum linkage distance of 20% separated major clusters within species. Cluster techniques attempt to find the best solution to classify cases into groups even when data lack clear group structure (DePatta Pillar, 1999); therefore, cluster stability requires a method of testing partition strength (James and McCulloch, 1990). To test cluster stability, I used the bootstrap resampling method of DePatta Pillar (1999) with 1000 iterations, to determine the probability distribution and the nonparametric estimates of standard error. When clusters are stable, random variability between clusters should exceed variability within clusters. Thus, failure to reject the null hypothesis of stable group structure for the proposed number of clusters is consistent with group stability at the suggested $\alpha = 0.10$ (DePatta Pillar, 1999). I assigned resultant clusters descriptive 'labels' but do not imply any particular hierarchical terminology. To develop a criteria to classify specimens into one of the clusters (developmental intervals), I ran a Discriminant Function Analysis (DFA) on the states for 10 characters, which permitted development of a more exact character index for assigning individuals to clusters.

Traditionally, SL at complete formation of all median fin rays, at initial squamation, or SL at settlement has defined the beginning of the juvenile period, L_{juv} (Leis and Rennis, 1983; Fuiman, 1994), although Fuiman (1997) has suggested more recently that squamation should be complete. This criterion, however, cannot be applied to scaleless fishes, such as blennies. If settlement were used as the criterion, detecting differences in the state of ontogeny at settlement would be impossible; therefore, I designated the SL at initial bifurcation of any primary caudal ray as L_{juv} because only the primary caudal rays bifurcate in blennies (Randall, 1966). No *P. marmoreus* had bifurcate caudal rays over the size range examined, so I estimated L_{juv} in this species as the natural log of mean SL at settlement (x 100), divided this quantity by the overall mean O_L at settlement for the other four species (86.1), and took the anti-log of the result, which estimated L_{juv} as 31.2 mm.

Regression of total character state score (the sum of ontogenetic events) against O_L illustrates the overall rate of change in ontogeny, or the species' ontogenetic profile. A piecewise linear regression using the distance-weighted least squares method and the quasi-Newtonian iteration, estimated coefficients and located the 'breakpoint,' or location where the rate of ontogeny changed most rapidly (StatSoft, 1999). Regressing character state scores for individual traits against O_L assessed the concurrence in timing of ontogeny over physiological time.

Results

Morphological Development

Despite the widespread distribution and potential ecological significance of blennies, adequate descriptions of their larvae are available for only two of the eleven Gulf species. The following comparative descriptions of characters, pigmentation, and intervals of development represent new information on blenny larvae (Figs. 2.1-2.6). Two general pigment patterns were evident in the blennies studied. *Hypsoblennius invemar*, *H. ionthas*, *H. multifilis*, and *S. cristata*,

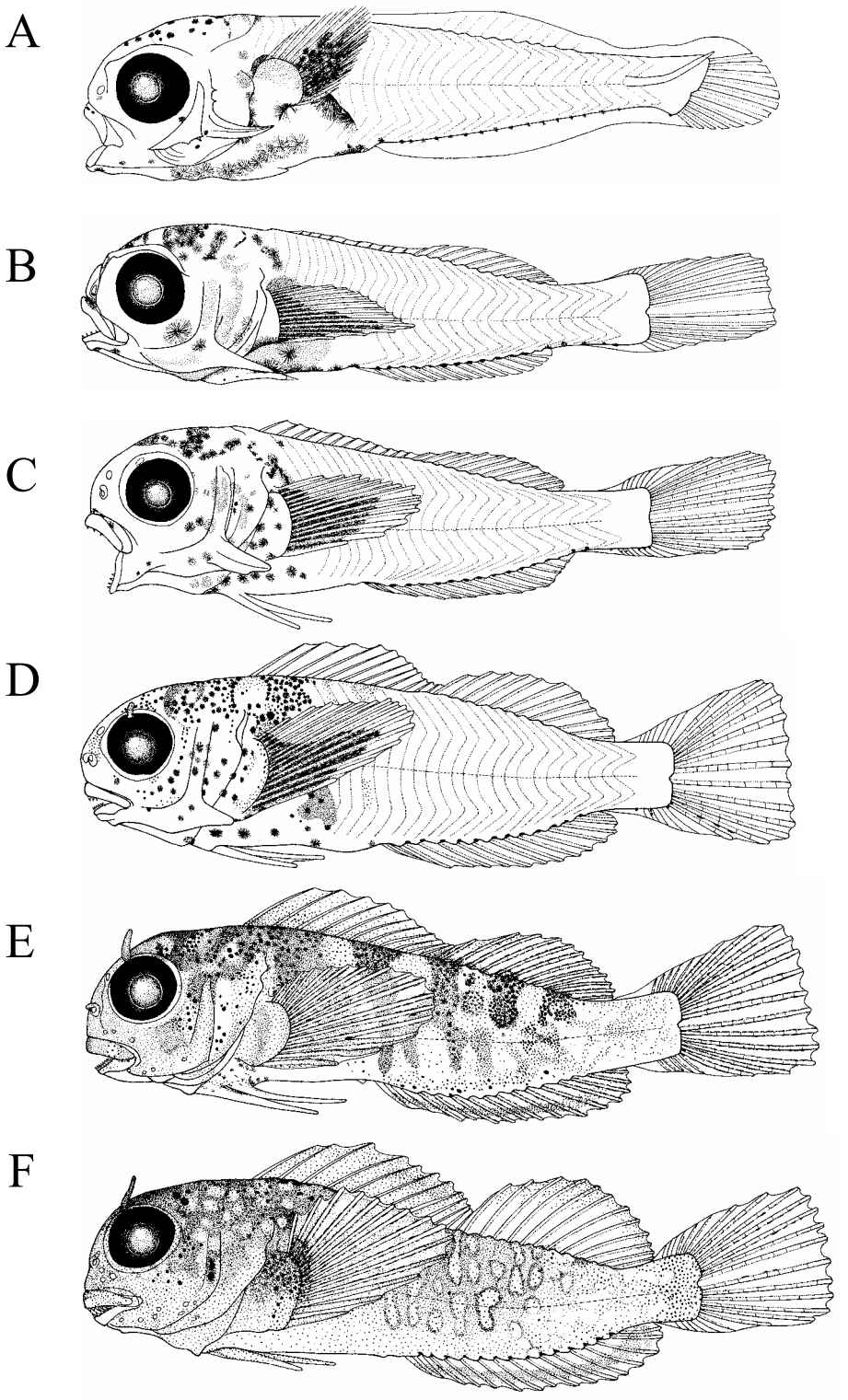


Figure 2.1. Early life stages of *Hypsoblennius invemar* from the northern Gulf of Mexico. A. 5.1 mm; B. 7.0 mm; C. 10.4 mm; D. 12.7 mm; E. 13.0 mm; F. 14.0 mm (in mm standard length). Larvae (A and B), metamorphs (C and D), and settlers (E and F). Note remnant of preopercular spine in 13.0 mm specimen (E).

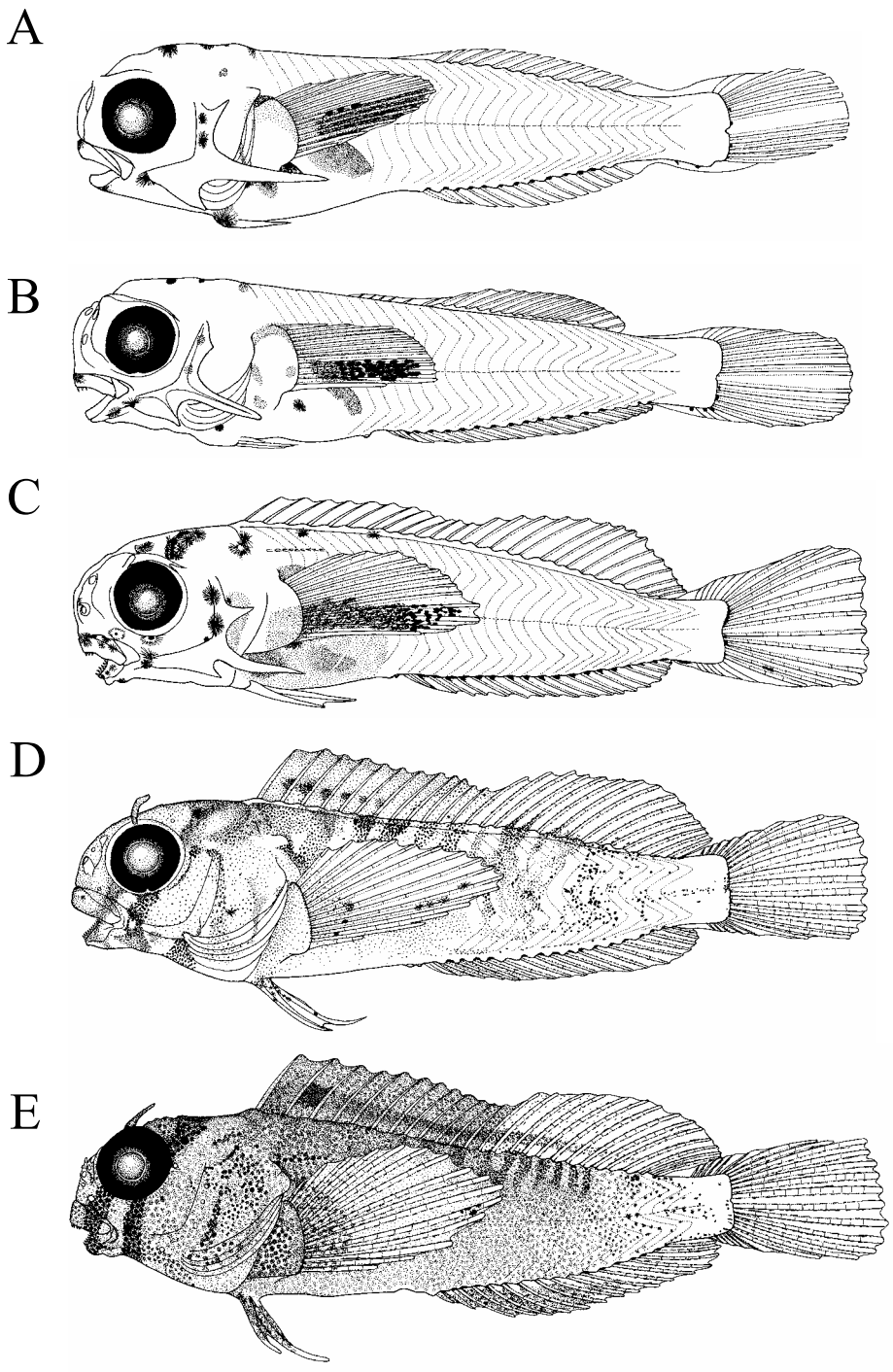


Figure 2.2. Early life stages of *Hypsoblennius ionthas* from the northern Gulf of Mexico. A. 5.4 mm; B. 7.5 mm; C. 10.2 mm; D. 11.8 mm; E. 12.7 mm (in mm standard length). Larvae (A and B), metamorph (C), and settlers (D and E).

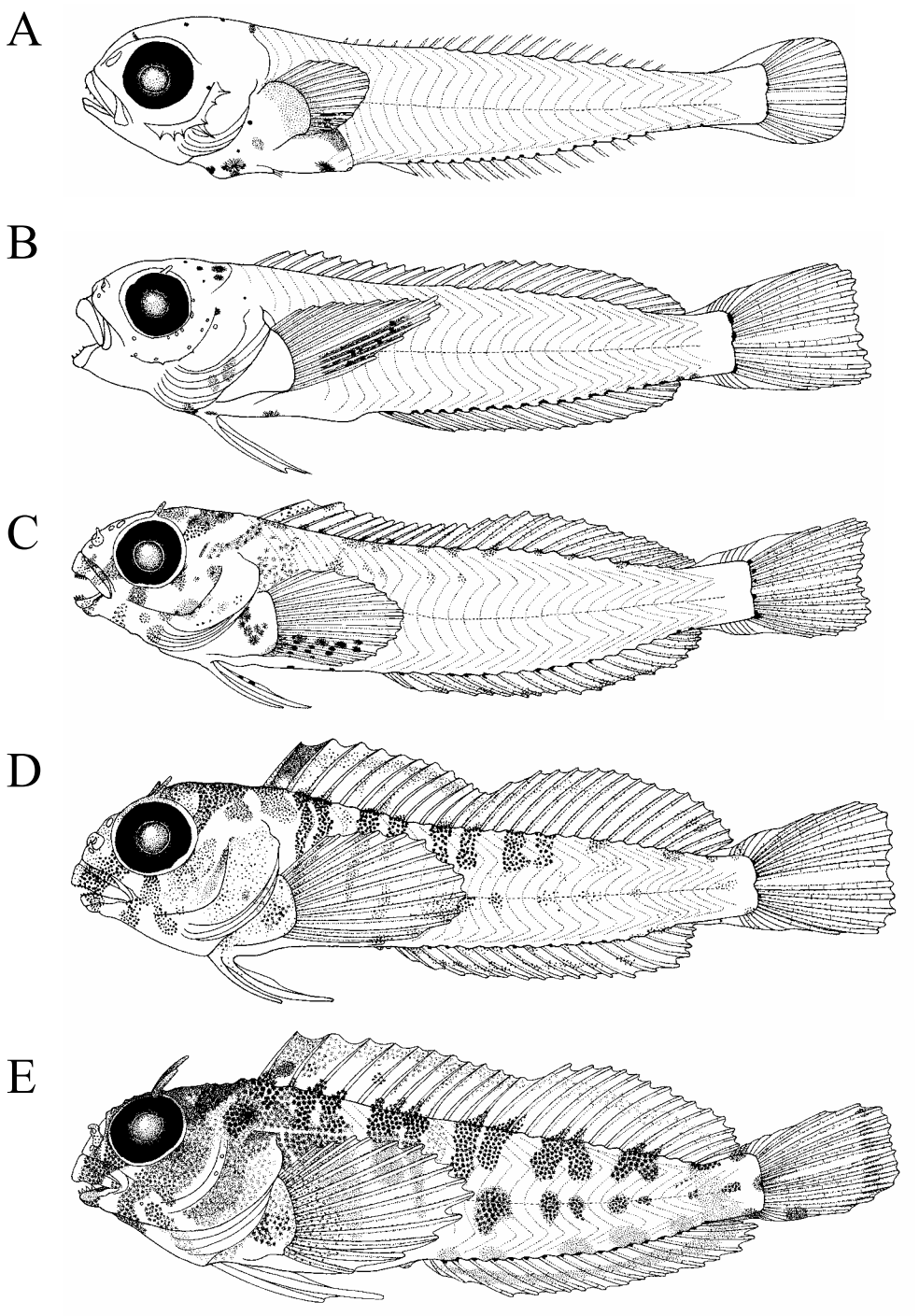


Figure 2.3. Early life stages of *Hypleurochilus multifilis* from the northern Gulf of Mexico. A. 6.4 mm; B. 10.7 mm; C. 11.8 mm; D. 12.3 mm; E. 14.5 mm (in mm standard length). Larvae (A and B), late metamorph (C), and settlers (D and E).

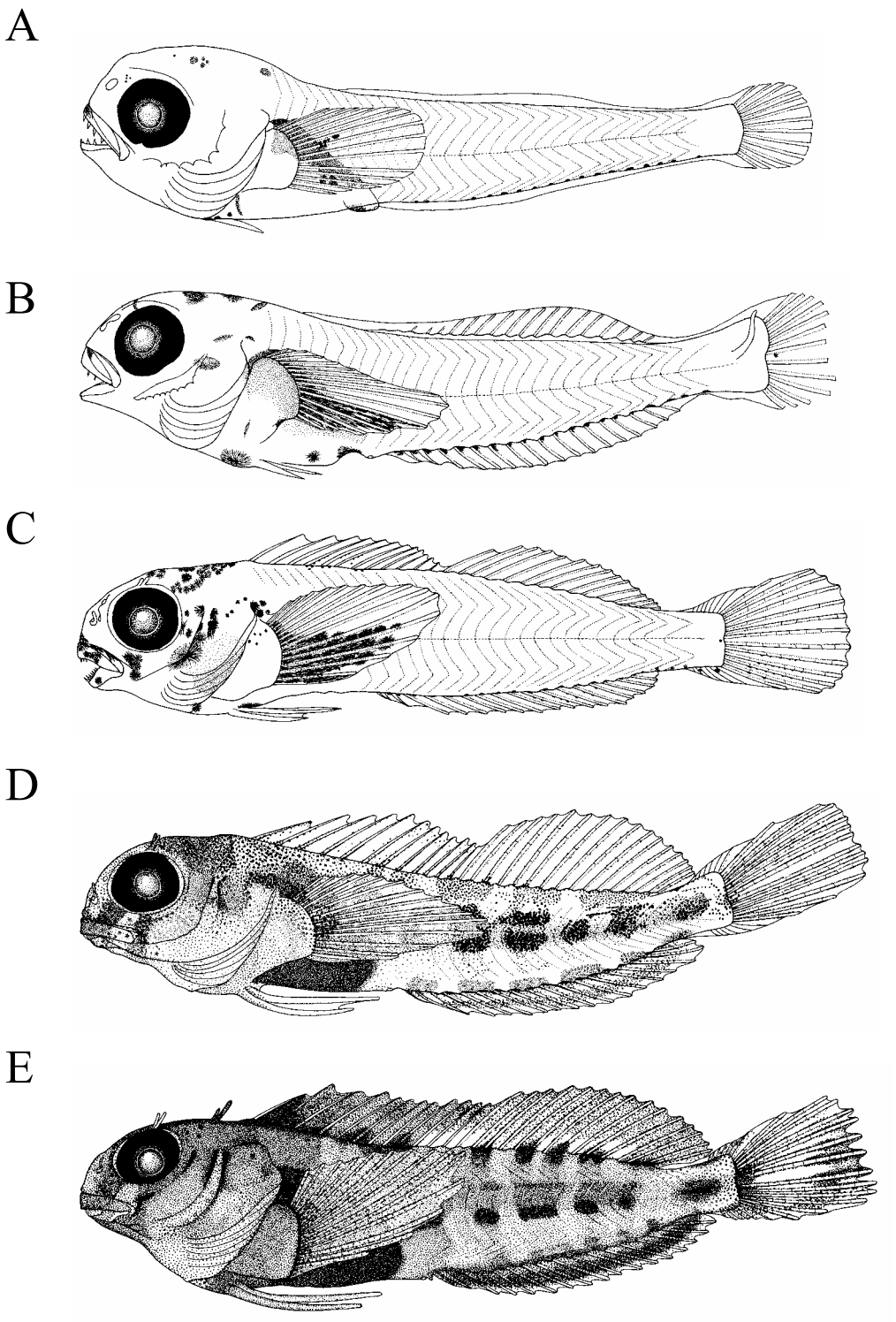


Figure 2.4. Early life stages of *Scartella cristata* from the northern Gulf of Mexico. A. 5.3 mm; B. 7.3 mm; C. 10.2 mm; D. 12.0 mm; E. 14.5 mm (in mm standard length). Larvae (A and B), metamorph (C), and settlers (D and E).

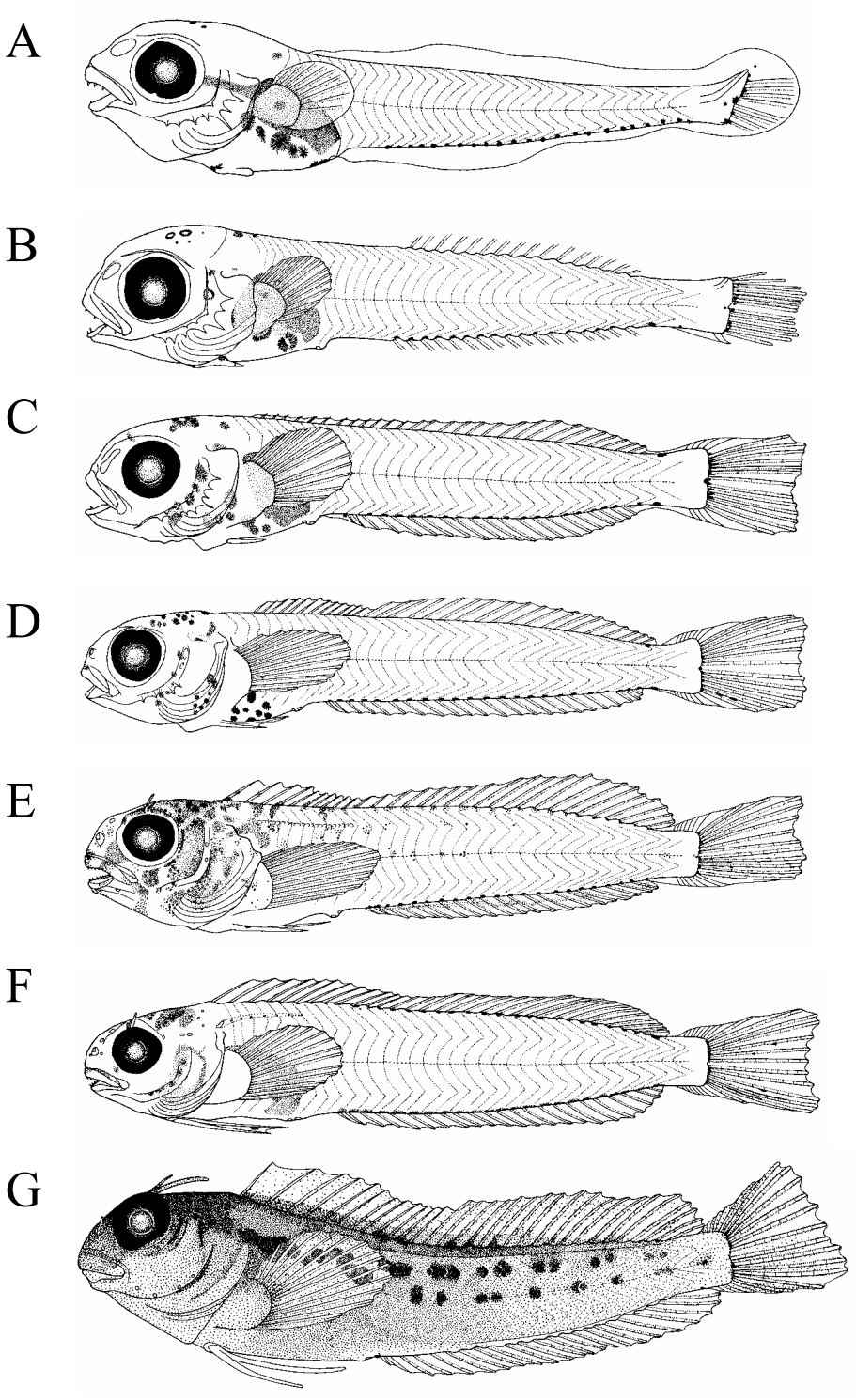


Figure 2.5. Early life stages of *Parablennius marmoreus* from the northern Gulf of Mexico. A. 5.8 mm; B. 7.5 mm; C. 9.6 mm; D. 13.7 mm; E. 17.3 mm; F. 20.9 mm; G. 23.0 mm (in mm standard length). Larvae (A through C), early metamorph (D), late metamorphs (E and F), and settler (G). Note differences in size and state of development between metamorphs E and F.

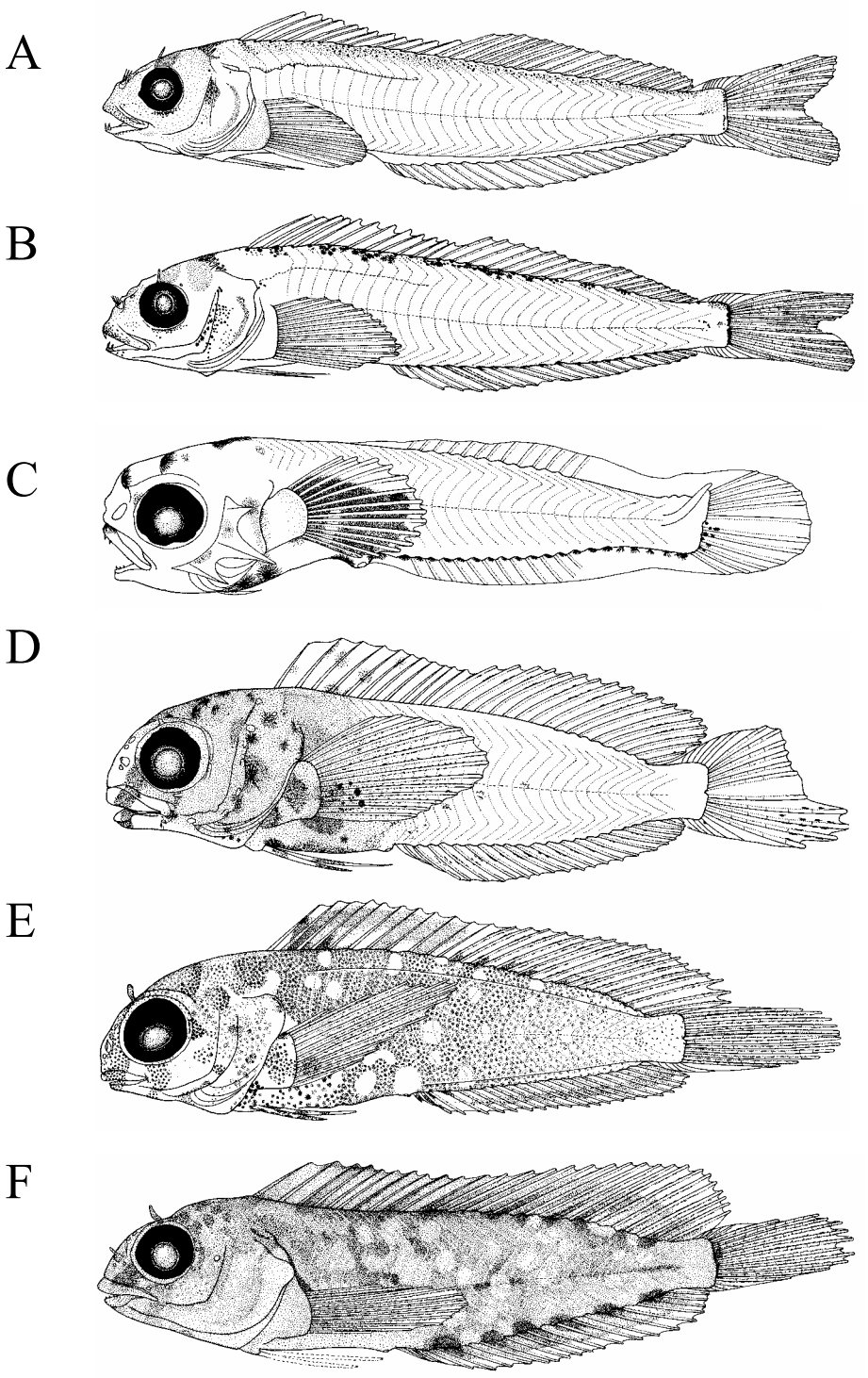


Figure 2.6. Pelagic metamorphs of *Ophioblennius atlanticus* from the Caribbean Ocean. A. 38.0 mm; B. 46.0 mm (in mm standard length). Larva of *Hypsoblennius hentz* (C) and three settlers of *Chasmodes saburrae* (D through F) from the northern Gulf of Mexico. C. 5.0 mm; D. 8.5 mm; E. 11.0 mm; F. 18.0 mm (in mm standard length).

had pigment pattern #1, while *P. marmoreus* and *O. atlanticus*, had pigment pattern #2. Pattern #1 consisted of a series of punctuate melanophores along the ventral midline of the tail that were closely associated with each anal pterygiophore, moderately to heavily pigmented pectoral fins, pigment on the visceral mass, and a melanophore internally over the forebrain and nape. Most species sharing pattern #1 also had a small melanophore externally on the inner shelf of the preopercle behind the eye. Pigmentation increased over the head and operculum of late larvae of *H. invemar*, but generally not until metamorphosis had begun in the other three species with pattern #1. Consolidation of pigment into bands, first near the nape and then progressively along the trunk signaled approaching settlement. Although bands of pigment formed dorso-laterally along the trunk earlier in metamorphs of *H. invemar* than in *H. ionthas*, *H. multifilis*, and *S. cristata*, pigment seldom extended past mid-body before metamorphs disappeared from light traps collections (Figs. 2.1-2.4; Table 2.4). The other estuarine blennies examined, *H. hentz* (Fig. 2.6c), *C. saburrae* (Fig. 2.6d-f), and *C. bosquianaus*, had pigment pattern #1.

Parablennius marmoreus had a slightly different pigmentation pattern (#2) than the other primary species studied and the body remained poorly pigmented until late metamorphosis (Fig. 2.5). Ventrally, pigmentation along the tail resembled that of pattern #1, except that no pigment was present anterior to the first anal spine. Early larvae had a patch of pigment behind the axil of the pectoral fin, which disappeared before metamorphosis began. The pectoral fin rays of *P. marmoreus* remained unpigmented of until just before settlement. *Parablennius marmoreus* larvae had relatively little body pigment either dorsally or laterally, except for a melanophore internally on the nape and a series of melanophores that tracked the inner shelf of the preopercle. A single melanophore was present dorsally on the caudal peduncle behind the base of the last pterygiophore of late larvae, with a series of melanophores along the dorsal midline of the body between the soft dorsal fin origin and its termination in early metamorphs.

Table 2.4. Comparison of the timing of ontogeny in five species of blenny from the northern Gulf of Mexico. Larval ontogeny index (O_L) = log SL/log Ljuv x 100, where Ljuv = SL is standard length at the start of the juvenile period. The range of values is the lowest O_L value with the character and the highest value without the given character. If represented by a single value, all subsequent specimens have the character.

Taxon	Orbital cirrus with free distal margin	Nasal cirrus with free distal margin	Terminal ray of median fins initially segmented	Longest preopercle spine resorbed	Body pigment (2 or more trunk bands)	Settled	Suborbitals 4 and 5 abutt	Dentary teeth 16-18
Hypsoblennius invemar	77.7-80.5	>83.1	83.1-86.1	87.6-90.2	85.6-88.9	85.6-90.2	86.1-89.9	86.1-88.4
Hypsoblennius ionthas	77.9-82.3	85.3-85.6	82.0-83.7	87.1-89.7	86.8-90.0	86.2-86.8	90.0-92.4	86.8-90.0
Hypleurochilus multifilis	>82.5	86.6-87.2	84.0-86.9	84.0-87.4	87.2-90.3	84.9-90.3	>87.4	84.9-89.0
Parablennius marmoreus	81.8-84.7	85.0-88.0	81.8-85.0	82.6-85.0	82.6-88.5	85.0-88.5	86.0-87.2	82.6-87.5
Scartella cristata	77.9-80.3	80.3-82.3	80.3-82.3	77.9-80.3	83.0-86.0	>83.0	>84.5	80.3-82.3

The presence of melanophores along the dorsal midline, proliferation of pigment over the head, formation of pigment bands along the trunk, and appearance of pigment on the rays of the pectoral fin characterized *P. marmoreus* preparing to settle. Pelagic metamorphs of *O. atlanticus* also followed pigment pattern #2 (Fig. 2.6a-b).

The similarity of pigmentation patterns made *H. multifilis* and *S. cristata* difficult to separate, especially when small. Early larvae of *S. cristata* had a diffuse patch of pigment above the upper lip at 6.5 mm, whereas *H. multifilis* lacked upper lip pigment until just before settling (ca. 12 mm; Figs. 2.3-2.4). The number of epural bones and the width of gill openings relative to the insertion of the pelvic fins also differed between species (Table 1.3). *Scartella cristata* had wide gill openings that narrowly attached to the throat by a delicate frenum, so that a probe inserted under the outer edge of the operculum passed nearly unobstructed along the throat. In *H. multifilis*, a probe inserted under the outer edge of the operculum generally does not go beyond the insertion of the pelvic fins. The frenum connecting the operculum to the throat in larvae of *S. cristata*, and the membrane connecting the operculum to the body in larvae of *H. multifilis*, however, is delicate and easily torn. Until these membranes thicken sufficiently in early metamorphs to obstruct the probe, these characters have little value for separating species.

The presence or absence of pelvic and pectoral fin pigment in blennies was species-specific and helped to separate taxa. Late larvae of *H. multifilis* had a single melanophore on the longest pelvic fin ray, as did early metamorphs of *P. marmoreus*, and late metamorphs of *S. cristata*. Neither *H. invemar* nor *H. ionthas* had pelvic fin pigment until after settlement (Figs. 2.1-2.5). The pectoral fin pigment in the two species of *Hypsoblennius* was not resorbed until after settlement, whereas little pectoral fin pigment remained in *H. multifilis* and *S. cristata* at settlement. *Parablennius marmoreus* lacked pigment on the pectoral fins until shortly before settlement. Pigment extended outward from the base of the 6th pectoral ray outward to the tip of

the 14th ray in *H. ionthas*; outward from the base of the 5th ray out to the tip of 8th ray in *H. invemar*; and outward from the base of the 9th or 10th pectoral ray to the tip of the 14th ray in *H. multifilis*. Pigment also covered nearly 50% of the back of the pectoral axil in *H. multifilis*. Pigment extended outward from the base of the 6th pectoral ray to the tip of the 15th ray in *S. cristata* (Figs. 2.1-2.5).

Formation and pigmentation of the orbital cirrus preceded that of the nasal cirrus in all species (Table 2.4). The orbital cirrus usually formed as a nub in late larvae or early metamorphs of each species and was lightly pigmented in late metamorphs. The nasal cirrus formed about mid-way through metamorphosis in *H. invemar*, *H. multifilis*, and *S. cristata*, and was lightly pigmented before settlement. In *H. ionthas* and *P. marmoreus*, the nasal cirrus formed just before settlement and remained unpigmented until after settlement. The appearance of pigment on the orbital cirrus in late metamorphs, and formation of the nasal cirrus, signaled impending settlement in all species (Figs. 2.1-2.5). Only *S. cristata* had nuchal cirri (Fig. 2.4e). The smallest *S. cristata* with the nuchal cirrus was a settled, 13.5-mm male ($O_L = 90$). Two other settlers with O_L values of 92.5 and 94.8 (14.5 mm and 15.5 mm, respectively) had two nuchal cirri each, and a 22.0-mm female had six nuchal cirri.

Length of the longest preopercular spine was species-specific in blennies and timing of complete resorption depended on spine length. The two species of *Hypsoblennius* had the longest preopercular spines of the species examined, whereas *H. multifilis*, *P. marmoreus*, and *S. cristata* had a series of short spines along the edge of the preopercle, and a generally similar placement pattern (Figs. 2.1-2.5). The preopercular spines were resorbed in early metamorphs of the three species with short spines. *Hypsoblennius invemar* had one elongate spine along the preopercle, whereas *H. ionthas* had three elongate spines, a character that easily separated presettlers and recent settlers of *H. invemar* from *H. ionthas* (Figs. 2.1-2.2). The preopercular

spines began to regress in late larvae of both species of *Hypsoblennius*, but the angle spine was not completely resorbed until after settlement, and earlier in *H. invemar* than in *H. ionthas*. The largest *H. hentz* examined (11.0 mm but in poor condition) had orbital cirri but no nasal cirri, and the spines along the preopercle were already resorbed. Separation of the larvae of *H. hentz* and *H. ionthas* will remain problematic in areas of overlap and will require a thorough description of a developmental series of *H. hentz*. Illustrations of a 5.0-mm larva of *H. hentz* (Fig. 2.6c), and settlers of the strictly estuarine species *C. saburrae* (Fig. 2.6d-f), permit limited comparison with the primary species studied. The two specimens of *C. bosquianus* examined were in poor condition and were not illustrated.

The timing and sequence of cephalic and lateral line pore formation was similar in all species. Pore openings were usually concealed by epidermis and nearly invisible in larvae. The pore openings were exposed as the cephalic canals ossified in early metamorphs, permitting Cyanine Blue stain to penetrate and highlight the canal system. Cephalic pores were first evident along the lower jaw and operculum, followed by those along the otic, supratemporal, and circumorbital regions. Lateral line pores were first present behind the head, with bony ossicles developing in late larvae and early metamorphs. Bony ossicles extended along the lateral line to about the 6th dorsal spine in late metamorphs, and covered the entire upper portion of the lateral line at settlement.

All five species had similar numbers of teeth at comparable intervals of development (Table 2.5). Villiform teeth initially formed near the front corners of the upper and lower jaws before notochord flexion, whereas incisiform teeth erupted after completion of notochord flexion. Incisiform teeth nearly replaced villiform teeth in early metamorphs, but the switch was gradual and transited a phase of mixed dentition. Subsequent changes in dentition were restricted mainly to addition of teeth and modifications in tooth shape. Early metamorphs of all five species of

Table 2.5. Dentition in blennies from the northern Gulf of Mexico at different intervals of development. Larval ontogeny index (O_L) = log SL/log L_{juv} x 100, where L_{juv} = SL is standard length at the start of the juvenile period. Total character state scores is the sum of individual states for the 10 characters listed in Table 2.2.

Taxa	Life stage	Lower/ upper teeth	N	Mean SL	Mean Score		Mean number of teeth	Teeth		
					Total character state	O_L		C. I. (+/- 95%)	Range	SD
Chasmodes bosquianus	Adult	Not Available								
C. saburrae	Adult	Not Available								
Hypleurochilus caudovittatus	Adult	21-27/18-26								
H. geminatus	Adult	20-28/20-28								
H. multifilis [1]	Larvae		6	8.9	7.5	75.1	6.8	5.4-8.2	5-9	1.3
	Metamorphs		21	12.5	20.5	86.9	14.2	13.5-15.0	12-17	1.6
	Settler		12	14.1	37.8	90.8	19.8	18.2-21.3	17-25	2.5
	Adult									
H. pseudoaequipinnus	Adult	19-30/20-30								
Hypsoblennius hentz	Adult	20-49/18-43								
H. invemar [1]	Larvae		10	9.5	8.7	77.8	9.5	8.3-10.7	8-14	1.7
	Metamorphs		19	12.3	19.7	86.9	14.1	13.4-14.7	12-18	1.4
	Settler		18	13.8	36.9	90.7	21.1	19.7-22.5	17-27	2.9
	Adult	24-42/21-36								

(Table 2.5 continued)

Taxa	Life stage	Lower/ upper teeth	N	Mean SL	Mean Score		Mean number of teeth	Teeth		
					Total character state	O_L		C. I. (+/- 95%)	Range	SD
H. ionthas [1]	Larvae		7	8.2	7.1	74.0	8.7	8.3-9.2	8-9	0.5
	Metamorphs		18	10.7	14.9	83.5	12.8	12.2-13.5	10-14	1.3
	Settler		8	14.2	36.3	93.2	18.8	16.0-21.5	16-25	3.2
	Adult	18-34/17-30								
Lupinoblennius nicholsi	Adult	16-20/20-25								
L. vinctus	Adult	16-24/16-30								
Ophioblennius atlanticus	Adult	>175/>175								
Parablennius marmoreus [1]	Larvae		14	14.2	9.7	76.4	9.1	8.4-9.9	8-12	1.2
	Metamorphs		19	19.5	20.8	85.6	15.6	14.8-16.7	12-20	2.0
	Settler		8	20.3	36.4	86.8	20.5	19.9-20.6	20-22	0.8
	Adult									
Scartella cristata [1]	Larvae		5	7.9	7.0	71.3	7.6	4.5-10.7	6-12	2.5
	Metamorphs		6	10.6	21.0	81.7	15.5	14.6-16.4	14-16	0.8
	Settler		17	13.5	37.0	89.6	20.8	19.5-22.2	16-27	2.6
	Adult	20-34/22-38								

[1] One of the five primary species studied, others are comparative species

blenny often transitioned through a spade-shaped incisor before the teeth achieved the typical incisiform shape just before settlement.

Overall, larvae averaged 8-10 teeth; metamorphs averaged 14-16 teeth; and late metamorphs and recent settlers usually had 18 or more teeth. *Hypsoblennius ionthas* generally had two fewer teeth than the other primary species studied during comparable intervals of development (Table 2.5). Differences in the number of teeth at settlement between *H. invemar* and *H. ionthas* suggest an ecological rather than evolutionary relationship between species. If so, the 11.0-mm *H. hentz* captured near Port Aransas, Texas, with 12 incisiform teeth in the lower jaw could be an early metamorph, although higher character state scores for other traits imply a more advanced state of ontogeny. Two other primarily estuarine genera, *Chasmodes* and *Lupinoblennius*, also had fewer dentary teeth at comparable intervals of development than the primary coastal/shelf species studied (Table 2.5).

Only two of the primary species studied had canines as adults, *H. multifilis* and *P. marmoreus*. 'Pre-canines' were sometimes visible behind the posterior-most incisors of each jaw in early metamorphs of *P. marmoreus* ($O_L \geq 76.4$; 14.1 mm SL), but these teeth typically did not exceed the height of surrounding teeth until after settlement. True canines appeared at O_L values from 82.6 to 88.5 in *P. marmoreus*, and at 95.4 in *H. multifilis*, with the lower canines usually present before the upper canines.

Fin Development and Skeletal Ossification

All species followed a similar sequence of fin development (pectoral-caudal-soft dorsal and soft anal-pelvic fins) but the timing of fin completion differed somewhat among species. Incipient rays of the pectoral and caudal fins formed before notochord flexion, with initial ray segmentation coinciding with notochord flexion in both fins. Dorsal and anal fin anlagen appeared shortly after notochord flexion, followed by the pelvic fin buds and dorsal spines.

Rays of the median fins formed progressively outward from the mid-fin base with the terminal ray of the dorsal and anal fins the last elements to form and segment. All rays of the dorsal and anal fins were initially segmented in late metamorphs of each species (Table 2.4). The posterior-most dorsal and anal fin rays continued to elongate as development progressed, with the posterior rays extending beyond the anterior-most secondary caudal rays in recent settlers of each species. The appearance of pigment along the shaft of each dorsal and anal ray in late metamorphs signaled approaching settlement. Shortly after settlement, blennies developed a longitudinal stripe of iridescent bluish chromatophores along the outer margin of both the dorsal and anal fins. In addition, a large ocellus formed between the first and usually fourth dorsal spines of most species, with the exact location species-dependent.

Timing of caudal fin ray bifurcation was species-specific and independent of settlement. Mean sizes and O_L values at settlement in four of the five species ranged from 11.3 mm (O_L= 84.0) in *S. cristata* to 12.1 mm (O_L= 87.9) in *H. ionthas*. *Parablennius marmoreus* settled at a mean size of 19.3 mm (O_L= 86.0). Initial bifurcation of the primary caudal fin rays (L_{juv}, O_L= 100) generally occurred between 17.0 mm and 18.0 mm, except in *P. marmoreus*, where L_{juv} was estimated to occur at 31.2 mm (Table 2.6). The upper O_L value of 88.5 for *P. marmoreus* was the result of not having collected juveniles of this species.

Generally, these blennies had similar patterns of skeletal differentiation and ossification. Skeletal structures required for swimming, feeding, and respiration, developed and ossified first. The upper and lower jaws, branchiostegal rays, vertebral centra, and the primary hypural elements of the caudal complex began to develop and chondrify before notochord flexion, and to ossify during late notochord flexion. The branchiostegal rays, pleural ribs, and vertebral centra were well developed shortly after metamorphosis began. The pectoral radials, neural and haemal spines, and dorsal and anal pterygiophores differentiated and chondrified during notochord

Table 2.6. Summary information for five species of blenny from the northern Gulf of Mexico. Ontogenetic categories (larvae, metamorphs, settlers) were determined by cluster analysis of 10 characters. Ontogenetic index (O_L) = log SL/log L_{juv} x 100, where SL is standard length of an individual and L_{juv} is SL at the start of the juvenile period. Total character state score is the sum of individual character states as defined in Table 2.2.

Category	*Hypsoblennius invemar*	*Hypsoblennius ionthas*	*Hypleurochilus multifilis*	*Parablennius marmoreus*	*Scartella cristata*
Specimen summary data					
Number	55	41	42	50	30
Size range (mm SL)	5.4-18.3	5.0-17.5	5.3-18.3	5.8-21.5	5.8-18.0
Ontogenetic index (O_L)	58.5-100.7	56.8-101.0	57.4-100.0	50.7-88.5 [1]	60.6-100.0
Range of total character state scores	1-41	1-41	1-41	1-37 [1]	1-42 [2]
Larvae (mean and range)					
Number	9	8	6	14	5
Size (mm SL)	9.7 (8.2-11.0)	8.0 (7.0-9.1)	8.9 (8.0-11.0)	14.2 (12.2-16.0)	7.9 (6.8-9.5)
Ontogenetic index	78.4 (72.9-81.2)	73.3 (68.7-77.9)	75.1 (71.5-82.5)	76.4 (72.2-80.0)	71.3 (66.3-77.9)
Total character state scores	9.2 (6.0-13.0)	6.8 (4.0-9.0)	7.7 (6.0-12.0)	9.7 (7.0-11.0)	7.0 (6.0-9.0)
Metamorphs (mean and range)					
Number	19	18	19	19	6
Size (SL)	12.3 (11.0-13.5)	10.7 (9.7-11.5)	12.5 (11.5-13.8)	19.5 (17.0-21.5)	10.6 (10.2-11.0)
Ontogenetic index	86.9 (83.1-90.2)	83.5 (80.2-86.2)	86.9 (84.0-90.3)	85.6 (81.8-88.5)	81.7 (80.3-83.0)
Total character state scores	19.7 (16-27)	14.9 (12-18)	19.5 (15.0-24.0)	20.8 (15-30)	21.0 (16-25)
Size range (mm SL) [3]	12.7 (12.0-13.5)	11.3 (11.0-11.5)	12.9 (12.2-13.8)	20.9 (20.5-21.5)	10.6 (10.2-11.0)
Ontogenetic index [3]	88.1 (86.1-90.2)	85.6 (84.6-86.2)	87.8 (86.1-90.3)	87.7 (85.7-88.5)	81.5 (80.3-83.0)
Total character state scores [3]	23.2 (22-27)	17.2 (16-18)	26.4 (23-31)	21.8 (19-24)	22.0 (19-25)

(Table 2.6 continued)

Category	*Hypsoblennius invemar*	*Hypsoblennius ionthas*	*Hypleurochilus multifilis*	*Parablennius marmoreus*	*Scartella cristata*
Settlers (mean and range)					
Number	18	8	14	9	17
Size (mm SL) [4]	12.2 (11.8-12.8)	12.1 (11.7-12.7)	12.1 (11.8-12.3)	19.3 (19.0-19.5)	11.3 (11.0-11.5)
Ontogenetic index [4]	86.7 (85.6-88.4)	87.9 (86.8-89.7)	85.8 (84.9-86.3)	86.0 (85.5-86.5)	84.0 (83.0-84.5)
Total character state scores [4]	27.3 (25-32)	32.7 (30-38)	34.0 (31-36)	37.0 (37-37)	29.3 (27-33)
SL at juvenile (L_{juv}) [5] in mm	17.9	17.0	18.3	31.2 [6]	18.0
Number sexually dimorphic	11	4	11	0	9
Number measured	27	25	27	29	14
Number cleared and stained	19	14	12	16	7

[1] Low O_L and total character state score is the result of not having collected specimens with bifurcate caudal fin rays (i.e., juveniles)

[2] Only *Scartella cristata* have nuchal cirri

[3] Three largest (mm SL) metamorphs

[4] Three smallest (mm SL) settlers

[5] SL at initial bifurcation of the any primary caudal rays

[6] Estimated standard length at initial bifurcation of any primary caudal ray

flexion, began to ossify in late larvae/early metamorphs, but did not ossify completely until after settlement. Epurals, the hypural minimal (hypural 5, when present), dentary bone, and fourth and fifth suborbital were the last elements examined to begin ossifying (in late metamorphs) and did not complete ossification shortly after settlement.

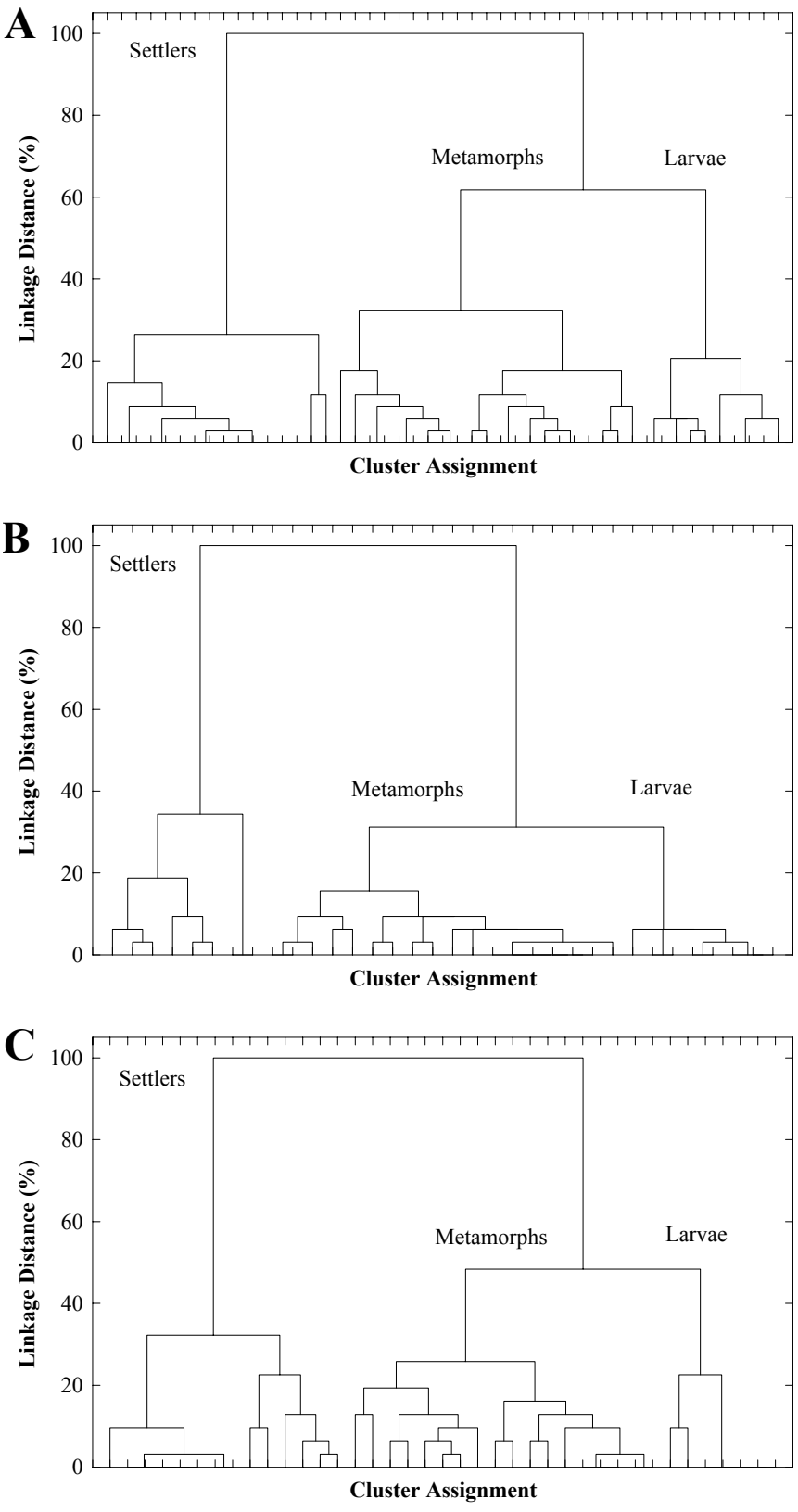
Sexual Dimorphism

Sexually dimorphic differences became increasingly evident in each species after settlement. Female *H. ionthas* developed a pigmentation pattern resembling 'freckles' over the operculum shortly after settlement, whereas the orbital cirrus began to lengthen in probable males. Generally, differences in sexual dimorphism in most parablenniins were evident by 14-15 mm, consistently so by 17-18 mm. The smallest blenny captured with the external signs normally associated with being in spawning condition was a 20-mm male and a 21-mm female of *H. multifilis*. Since L_{juv} was at 18.3 mm in *H. multifilis*, and assuming the 20-mm male was sexually mature or nearly so, the onset of sexual maturity in *H. multifilis* would be at O_L= 103.1. If I am correct about the timing of sexual maturity in blennies, initial bifurcation of the primary caudal ray was not the completion of metamorphosis but approximates the start of the adult period.

Intervals of Development

Overall, I followed the progression of ontogeny for 10 external characters in each of five species of blenny (N= 218 total specimens). Cluster analysis of total character state scores for each species revealed three primary clusters, each representing an interval of development (Figs. 2.7a-e). Bootstrap resampling of data at the three-cluster level failed to reject the null hypothesis of group stability ($p > 0.15$) for each species; consequently, I assigned each cluster a descriptive name. One cluster, termed 'larvae,' contained individuals with total character state scores ≤ 13 and O_L values less than 80. A second cluster (termed 'metamorphs') contained

Figure 2.7. Intervals of development (clusters) in five species of blenny from the northern Gulf of Mexico. Intervals were determined by clustering total character state scores (the sum of states for 10 characters; see Table 2.2). Minimum linkage distances of 20% separate major intervals. A. *Hypsoblennius invemar* (47 cases); B. *Hypsoblennius ionthas* (34); C. *Hypleurochilus multifilis* (39); D. *Parablennius marmoreus* (41); and E. *Scartella cristata* (28).



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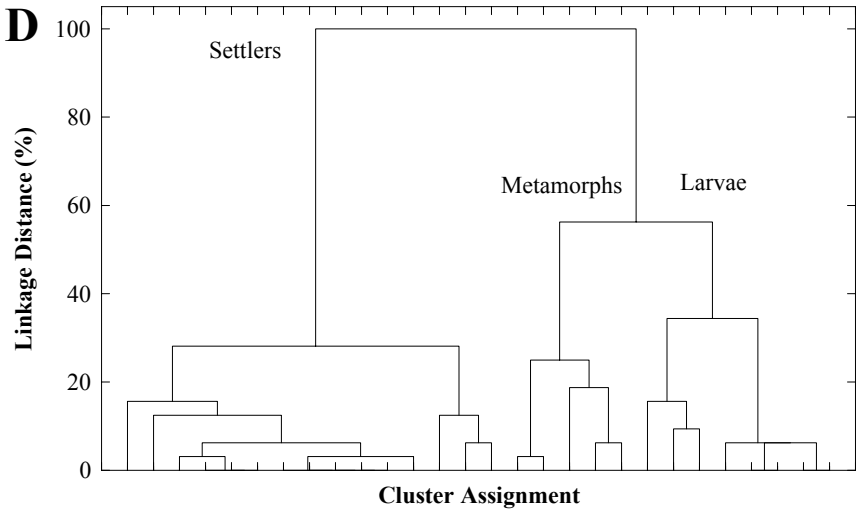
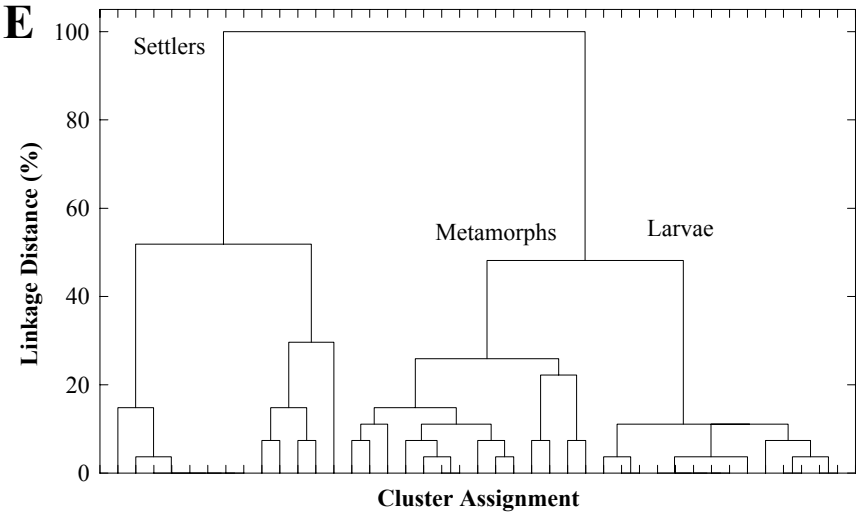




(Figure 2.7 continued)

specimens with total character state scores generally from 15 to 25. Metamorphs had O_L values >80. The third cluster, labeled 'settlers,' included individuals with total character state scores ≥25 (Table 2.6) that were collected from a demersal habitat. Recent settlers had O_L values of 85 to 90 (Table 2.6). The 'larval period' as commonly defined includes both my 'larvae' and 'metamorphs' categories, which were simply artificial labels assigned to these categories for clarity.

Assigning multiple discrete states to individual ontogenetic events helped to define natural intervals of development, permitted examination of the timing, rate, and progression of ontogeny, and characterized the minimum state of ontogeny required for settlement. A Discriminant Function Analysis (DFA) performed on the states for 10 characters (Table 2.2) in each of the five species developed intraspecific criteria to classify each species' into one of the three developmental intervals (Table 2.7; Fig. 2.8a-f). A second DFA performed on the species-pooled data set provided the interspecific criteria that characterized intervals of development (Table 2.7). Two canonical roots extracted all within-group variability in each species and interval of development ($p < 0.0001$; Table 2.8). Root 1 discriminated settlers from metamorphs and larvae, and root 2 provided some separation between metamorphs and the other two intervals of development in both discriminant analyses (Table 2.9; Fig. 2.8f).

Characters that made the greatest contribution to interval discrimination varied by species, although two or three characters generally explained most of the differences between intervals (Table 2.10). For *H. invemar*, state of nasal cirrus development was most important for separating settlers from presettlers (root 1) and the same character together with pectoral fin score separated metamorphs from larvae (root 2). Settlers of *H. invemar* had higher nasal cirrus, lateral line, median fin, and preopercular spine scores (representing resorption of the spine) than metamorphs, whereas metamorphs had a higher nasal cirrus and pectoral fin scores than larvae

Table 2.7. Coefficients and constants derived from Discriminant Function Analysis of 10 characters used to distinguish intraspecific and interspecific intervals of development in five species of blenny from the northern Gulf of Mexico. Each root is a different interval.

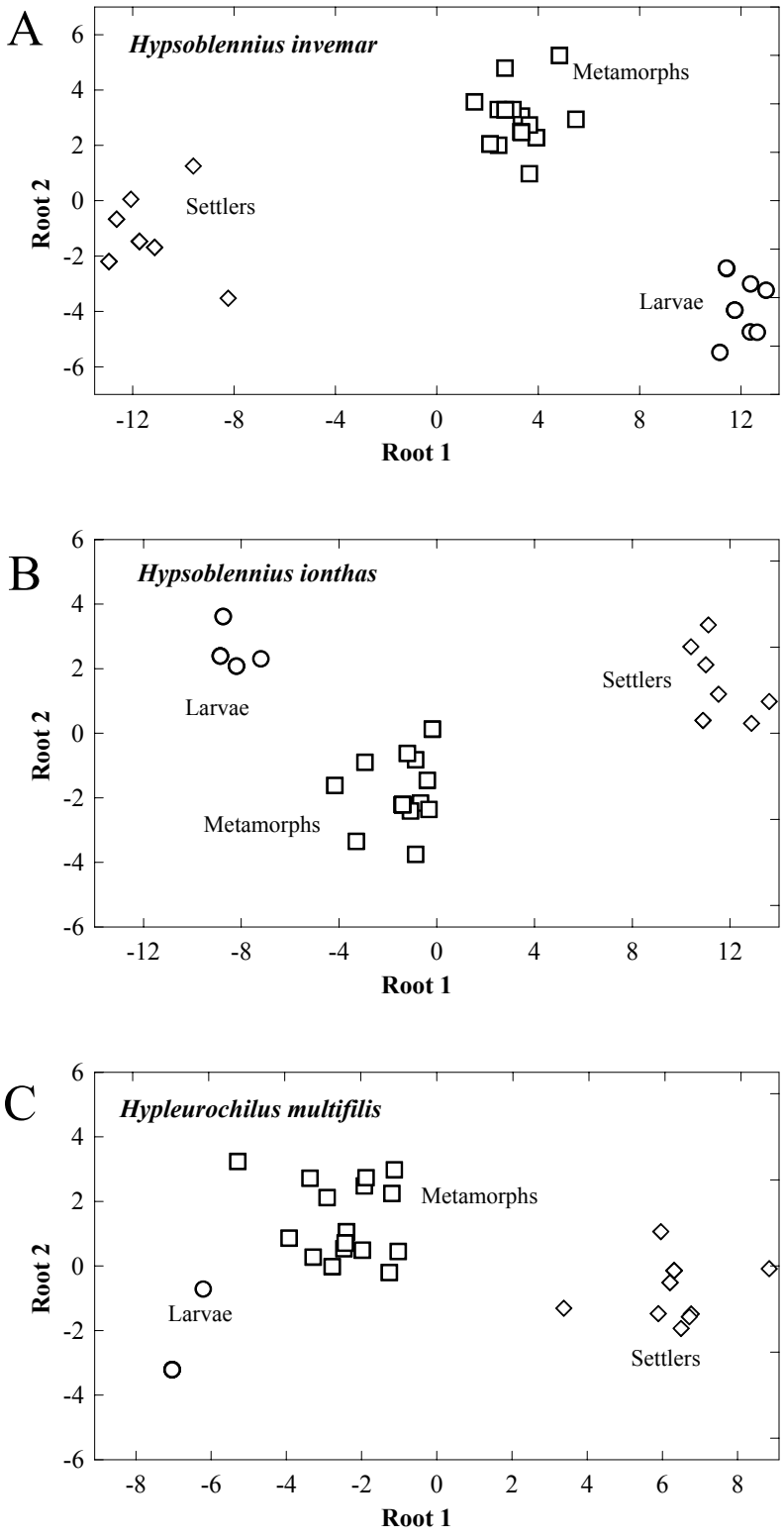
Variable	Intraspecific coefficients and constants								
	Hypsoblennius invemar			***Hypsoblennius ionthas***			***Hypleurochilus multifilis***		
	Root 1	**Root 2**	**Root 3**	**Root 1**	**Root 2**	**Root 3**	**Root 1**	**Root 2**	**Root 3**
Preopercular spine	13.257	30.700	44.194	2.647	5.874	9.547	17.494	29.180	30.084
Orbital cirrus	4.450	15.928	8.321	2.667	19.369	35.034	5.218	12.628	20.126
Nasal cirrus	13.845	124.634	195.394	-6.247	-16.209	-6.287	-6.187	-7.755	-7.370
Number of teeth	-4.480	-11.285	-19.283	-25.629	-27.751	-39.206	-3.888	-6.914	-8.330
Dorsal/anal rays	7.241	10.352	45.952	20.239	42.486	76.255	-3.945	-2.908	4.053
Pectoral fin	-5.900	-29.629	-33.696	4.078	-0.519	4.945	-0.734	-1.340	-1.588
Pelvic pigment	2.460	5.580	37.608	-66.244	-92.875	-131.483	-3.769	-1.766	-1.548
Caudal fin	19.904	39.921	57.776	83.406	113.537	149.319	40.333	54.857	78.290
Body pigmentation	-4.767	-3.531	2.246	-2.006	-7.603	0.070	-6.637	-12.670	-7.541
Lateral line	-7.584	-13.262	-34.267	3.044	13.708	15.756	-2.073	3.055	-2.058
Constant	-21.243	-117.669	-397.341	-83.631	-200.710	-466.228	-46.148	-105.576	-230.233

(Table 2.7 continued)

Variable	Intraspecific coefficients and constants						Interspecific coefficients and constants		
	Parablennius marmoreus			*Scartella cristata*					
	Root 1	**Root 2**	**Root 3**	**Root 1**	**Root 2**	**Root 3**	**Root 1**	**Root 2**	**Root 3**
Preopercular spine	4.596	2.922	-19.229	63.330	108.174	99.330	0.742	0.621	0.153
Orbital cirrus	6.508	34.484	125.361	[1]	[1]	[1]	2.489	10.333	15.573
Nasal cirrus	-22.025	-30.691	-60.523	-2.127	-1.388	-3.462	-1.607	-0.636	-0.064
Number of teeth	-1.723	0.079	-18.269	7.699	18.274	15.188	1.719	4.999	3.432
Dorsal/anal rays	15.328	23.167	73.208	-0.098	-1.820	2.581	2.002	4.475	15.508
Pectoral fin	1.869	-0.387	-3.841	-3.174	-3.177	-1.761	-1.420	-1.682	-1.802
Pelvic pigment	-11.139	-15.127	-35.240	-0.534	-3.918	-2.746	-3.518	-4.990	-5.439
Caudal fin	15.067	19.594	35.525	4.824	4.463	3.371	9.174	11.835	14.763
Body pigmentation	7.141	19.677	61.017	-1.154	6.257	14.201	-0.125	-1.931	0.744
Lateral line	-5.021	0.633	1.789	-6.461	-10.573	4.029	0.113	4.520	8.287
Constant	-31.239	-71.440	-323.254	-63.888	-184.669	-209.856	-12.950	-35.510	-100.134

[1] Orbital cirrus score disciminates clusters in *Scartella cristata*

Figure 2.8. Intervals of development (clusters) based on ontogeny for five species of blenny from the northern Gulf of Mexico. A Discriminant Function Analysis of states for 10 characters (see Table 2.2 for explanation of codes) determined the discriminatory power and identified the characters that distinguished intraspecific and interspecific intervals of development. A. *Hypsoblennius invemar*; B. *Hypsoblennius ionthas*; C. *Hypleurochilus multifilis*; D. *Parablennius marmoreus*; E. *Scartella cristata*; and F. species combined.



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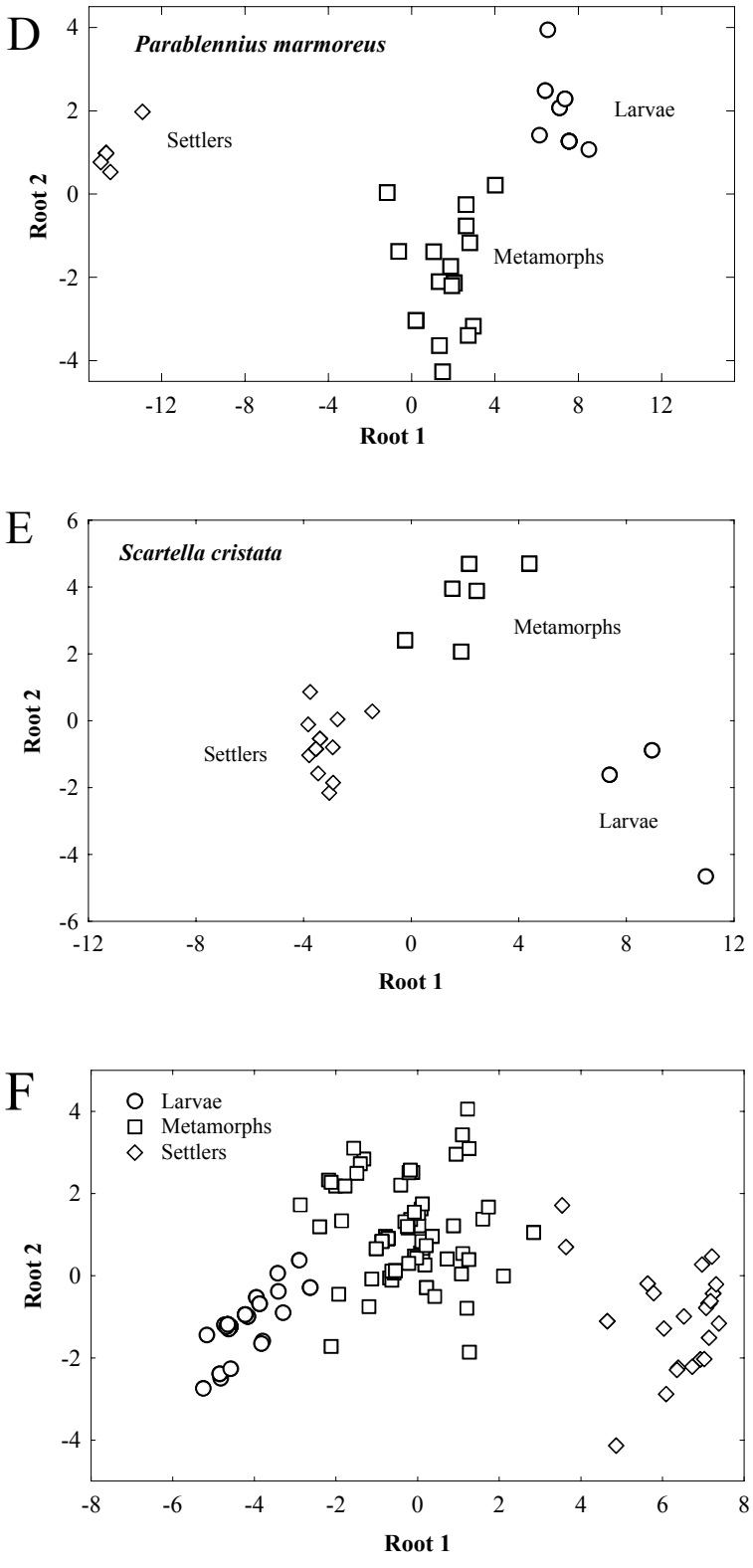


(Figure 2.8 continued)

Table 2.8. Significance of canonical roots in discriminating intraspecific and interspecific intervals of development in five species of blenny from the northern Gulf of Mexico. Two roots accounted for all variability.

Taxa	Canonical root	Eigenvalue	Variability explained (%)	Canonical correlation	Chi-square	ρ
Intraspecific						
Hypsoblennius invemar	1	83.9	91.7	0.994	253.9	<0.0001
	2	7.6	100.0	0.943	82.9	<0.0001
Hypsoblennius ionthas	1	53.9	92.8	0.991	149.7	<0.0001
	2	4.2	100.0	0.898	43.5	<0.0001
Hypleurochilus multifilis	1	26.5	91.8	0.982	142.6	<0.0001
	2	2.4	100.0	0.839	38.3	<0.0001
Parablennius marmoreus	1	70.0	95.4	0.993	192.5	<0.0001
	2	3.4	100.0	0.879	49.7	<0.0001
Scartella cristata	1	23.5	84.7	0.979	102.0	<0.0001
	2	4.2	100.0	0.900	34.8	<0.0001
Interspecific	1	13.8	92.5	0.966	515.2	<0.0001
	2	1.1	100.0	0.727	112.3	<0.0001

Table 2.9. Canonical root means used to discriminate intervals of development for five species of blenny from the northern Gulf of Mexico. Distance between means is a measure of how clearly discriminant functions separate developmental intervals. Compare sign of each root with traits in Table 2.10 to determine which intraspecific and interspecific characters are associated with each interval of development. The interval most clearly separated by a given root is in bold.

Taxa	Interval of development	Number of specimens	Size range (mm SL)	Root 1	Root 2
Intraspecific					
Hypsoblennius invemar	Larvae	9	8.0-11.0	12.115	-3.991
	Metamorphs	21	11.0-13.5	3.418	**2.721**
	Settlers	16	11.8-18.3	**-11.301**	-1.326
Hypsoblennius ionthas	Larvae	8	7.0-9.1	-8.454	2.612
	Metamorphs	18	9.7-11.5	-1.371	**-1.798**
	Settlers	8	11.7-17.5	**11.539**	1.433
Hypleurochilus multifilis	Larvae	6	8.0-11.0	-6.900	-2.788
	Metamorphs	19	11.5-13.8	-2.453	**1.328**
	Settlers	14	11.8-18.3	**6.286**	-0.608
Parablennius marmoreus	Larvae	14	12.2-16.0	7.202	1.890
	Metamorphs	18	17.0-21.5	1.636	**-1.978**
	Settlers	9	19.0-20.5	**-14.475**	1.016
Scartella cristata	Larvae	5	6.8-9.5	8.719	-1.923
	Metamorphs	6	10.2-11.0	2.024	**3.626**
	Settlers	17	11.0-18.0	**-3.279**	-0.714
Interspecific	Larvae	42	6.8-16.0	-4.283	-1.154
	Metamorphs	82	9.7-21.5	-0.206	**1.013**
	Settlers	64	11.0-20.5	**6.410**	-0.978

Table 2.10. Discriminant Function Analysis of states for 10 characters to identify traits that distinguish intervals of development within (intraspecific) and among (interspecific) taxa for five species of blenny from the northern Gulf of Mexico. Standardized function coefficients represent the magnitude of each variable's contribution to that root. Compare sign of each character with roots on Table 2.9 to determine which characters are associated with each interval. Primary discriminating characters are in bold.

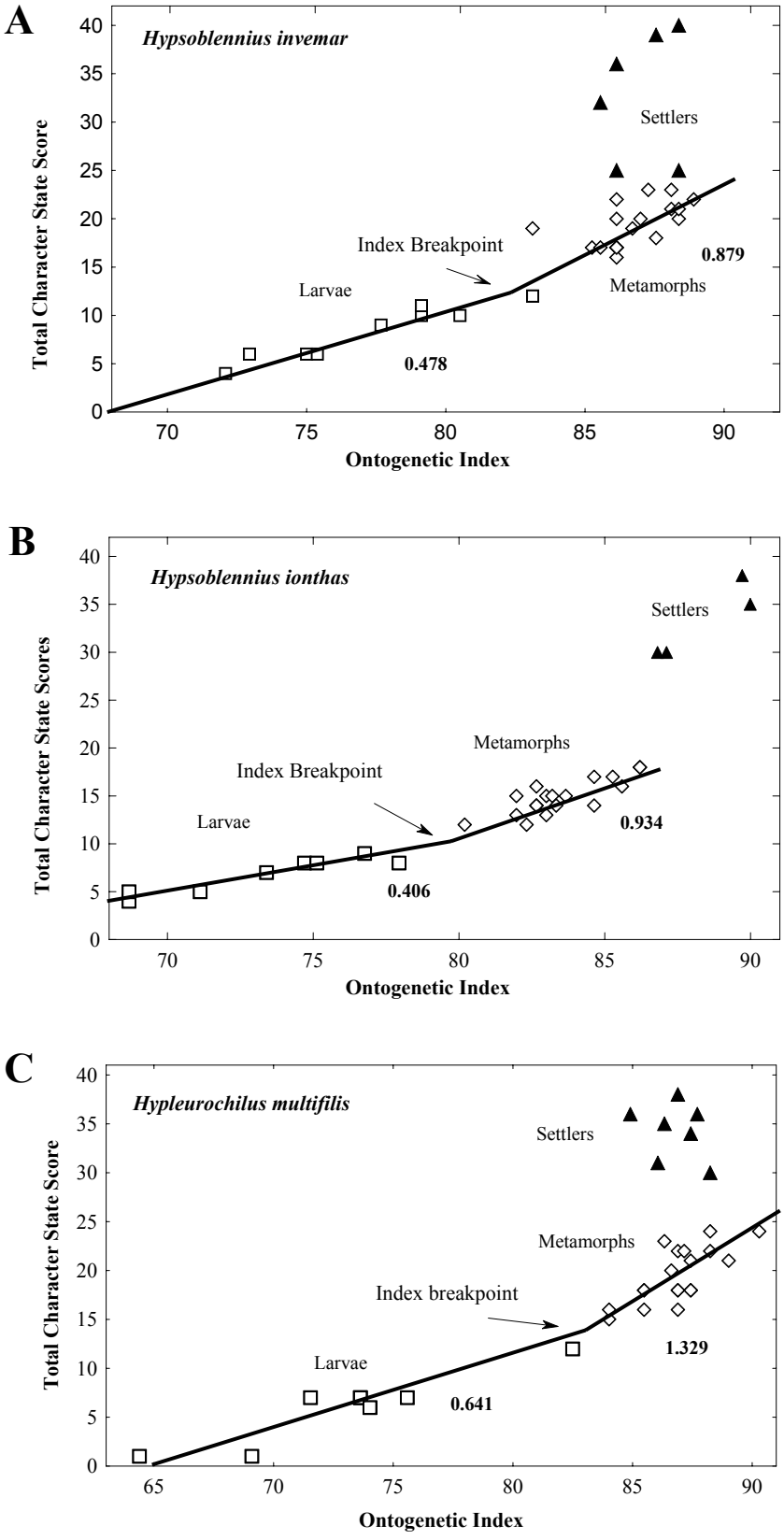
Character	Intraspecific coefficients										Interspecific coefficients	
	Hypsoblennius invemar		***Hypsoblennius ionthas***		***Hypleurochilus multifilis***		***Parablennius marmoreus***		***Scartella cristata***			
	Root 1	**Root 2**	**Root 1**	**Root 2**	**Root 1**	**Root 2**	**Root 1**	**Root 2**	**Root 1**	**Root 2**	**Root 1**	**Root 2**
Preopercular spine	-0.571	0.495	0.144	-0.085	0.264	**0.981**	0.476	-0.506	**-0.445**	**0.909**	-0.047	0.042
Orbital cirrus	-0.012	0.698	0.373	-0.318	0.350	0.243	**-1.192**	0.151	[1]	[1]	**0.399**	**0.451**
Nasal cirrus	**-1.006**	**1.104**	0.041	**0.708**	-0.013	-0.143	0.581	-0.109	0.089	0.190	0.058	0.075
Number of teeth	0.341	-0.128	-0.313	-0.293	-0.128	-0.220	0.333	**-0.665**	-0.279	**0.745**	0.067	**0.601**
Dorsal/anal rays	-0.594	-0.678	**0.899**	-0.196	0.296	-0.211	**-1.077**	**0.755**	-0.200	-0.455	**0.580**	**-0.576**
Pectoral fin	0.574	**-1.405**	0.077	**0.822**	-0.036	-0.070	0.120	0.102	-0.130	-0.157	-0.025	-0.040
Pelvic pigment	-0.491	-0.500	**-1.413**	0.388	0.037	0.129	0.445	-0.237	0.117	-0.369	-0.099	-0.201
Caudal fin	-0.637	0.454	**1.148**	-0.610	**0.800**	0.146	-0.457	0.096	0.099	0.070	0.256	0.125
Body pigmentation	-0.145	-0.108	0.078	0.629	0.115	**-0.921**	**-0.936**	0.134	**-0.447**	-0.081	0.057	**-0.594**
Lateral line	0.673	0.380	0.235	-0.666	-0.119	**0.721**	-0.120	-0.474	-0.355	-0.672	0.361	0.294

[1] Distinct orbital cirrus scores disciminated all three intervals of development in *Scartella cristata*

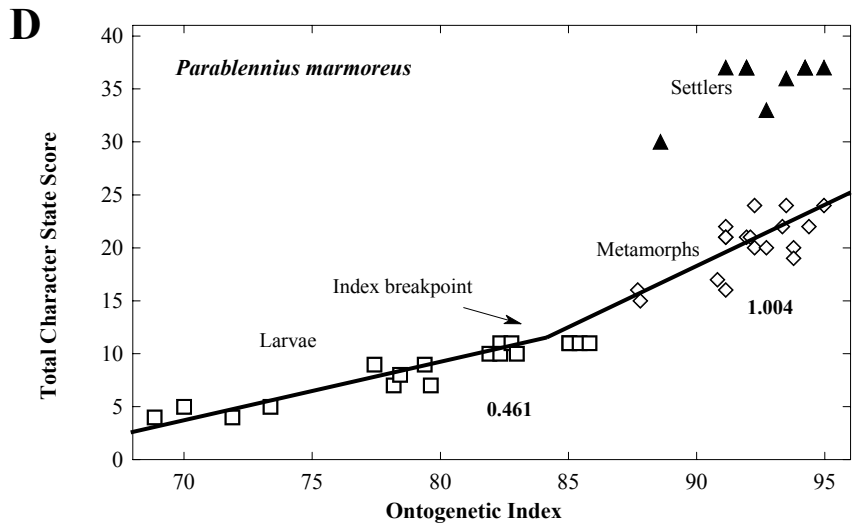
(Table 2.10; Fig. 2.1). In *H. ionthas*, settlers had pigmented pelvic fins and higher caudal and dorsal/anal fin scores than metamorphs and larvae (root 1). Metamorphs of *H. ionthas* had higher pectoral, lateral line, nasal cirrus, and trunk pigmentation scores than larvae (root 2; Table 2.10; Fig. 2.2). Settlers of *H. multifilis* had a higher caudal fin score than metamorphs (root 1), who had higher preopercular spine, lateral line, and trunk pigmentation scores than larvae (root 2; Table 2.10; Fig. 2.3). Distinct orbital cirrus scores discriminated all three clusters of *S. cristata*. Settlers also had higher body pigmentation and preopercular spine scores than metamorphs and larvae. Metamorphs had higher dentition and preopercular spine scores than larvae (Table 2.10; Fig. 2.4). High orbital cirrus, dorsal fin, and trunk pigmentation scores (root 1) defined *P. marmoreus* settlers. Metamorphs of *P. marmoreus* had higher dentition and dorsal fin scores (root 2) than larvae (Table 2.10; Fig. 2.5). Ontogenetic characters also discriminated intervals across multiple taxa. Settlers (root 1) had higher dorsal/anal fin and orbital cirrus scores than metamorphs, and metamorphs (root 2) had higher trunk pigmentation, dorsal/anal fin, orbital cirrus, and tooth scores than larvae (Table 2.9).

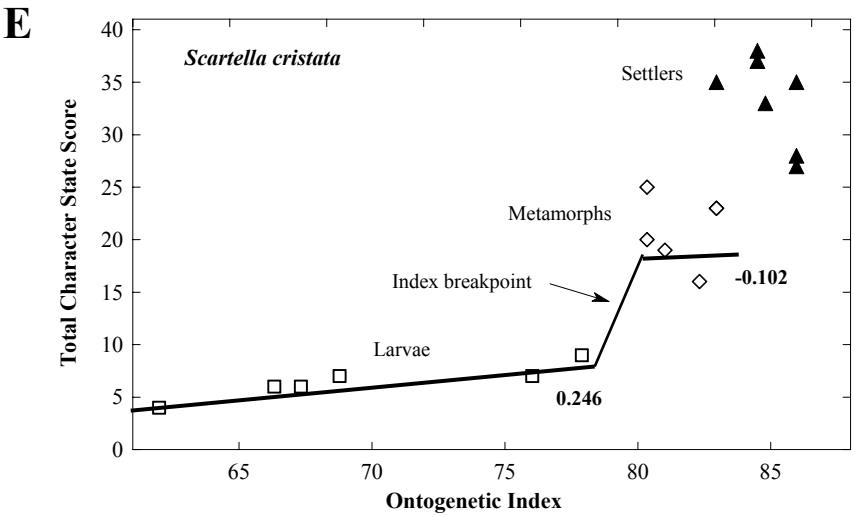
Rates of ontogeny were species-specific (Fig. 2.9a-e; plots were truncated for graphic presentation). Although each species contained a nearly continuous size series of specimens with only minor gaps in SL, no *H. ionthas* captured had a total character state score between 18 and 30 (Table 2.6). This gap in scores between the most advanced pelagic specimen and the earliest settler corresponded to a 0.2 mm increase in SL, and an increase of only 0.6 along the ontogenetic index. Such a finding, and the fact that the most advanced metamorphs (total character scores of 17 or 18) of *H. ionthas* had characteristics found in recent settlers, suggests rapid ontogeny with little or no increase in SL, despite the lower than expected rate of ontogeny in metamorphs compared to the other species (Fig. 2.9a-e). This lower apparent rate of ontogeny

Figure 2.9. Change in total character state score during ontogeny for five species of blenny from the northern Gulf of Mexico. Decimal numbers are coefficients (slopes) for each line segment. A. *Hypsoblennius invemar*; B. *Hypsoblennius ionthas*; C. *Hypleurochilus multifilis*; D. *Parablennius marmoreus*; and E. *Scartella cristata*. Settlers were omitted from calculations. Plots were truncated for graphic presentation. Note that the O_L scales differ among species.



(Figure 2.9 continued)





(Figure 2.9 continued)

in metamorphs of *H. ionthas* may be due to the narrow range of total scores and O_L values during metamorphosis.

Rates of ontogeny were also interval specific and nearly doubled during metamorphosis in most species (Fig. 2.9a-e). The rate of change in total character state scores as ontogeny progresses, however, does not support a saltatory pattern for ontogeny (Fig. 2.10) before metamorphosis. Differences in the timing and rate of ontogeny for individual characters provide a similar conclusion, although the timing of ontogeny for most characters overlaps in late metamorphs, which suggests metamorphosis is a major threshold (Fig. 2.11a-e).

Despite the fact that the timing of character development was species-specific in these blennies, late metamorphs had a common suite of characteristics. The minimum suite of characters shared by late metamorphs of each species, included: all fin rays segmented; generally 16-18 dentary teeth; all primary cephalic pores developed; bony ossicles along the entire upper portion of the lateral line; lightly pigmented orbital and nasal cirri; and bands or saddles of pigment along the trunk. Most species lose pectoral fin pigment during metamorphosis, except *P. marmoreus*, which had unpigmented pectoral fins until just before settlement.

Discussion

Are There Discrete, Recognizable Intervals of Development in Blennies, and Is There a Common Suite of Interspecific Traits That Identify Them?

Three 'natural' intervals of development, each comprised of individuals of similar ontogenetic state, were consistently identified in the blennies studied (Figs. 2.7-2.8). Larvae had total character state scores ≤13 and an O_L <80; metamorphs had total character state scores from 15 to 25 and an O_L from 80 to 90; and settlers had total character state scores >25 and an O_L >85 (Table 2.6). Common sets of interspecific characters also discriminated intervals. Settlers had higher dorsal/anal fin and orbital cirrus scores than metamorphs, and metamorphs had higher

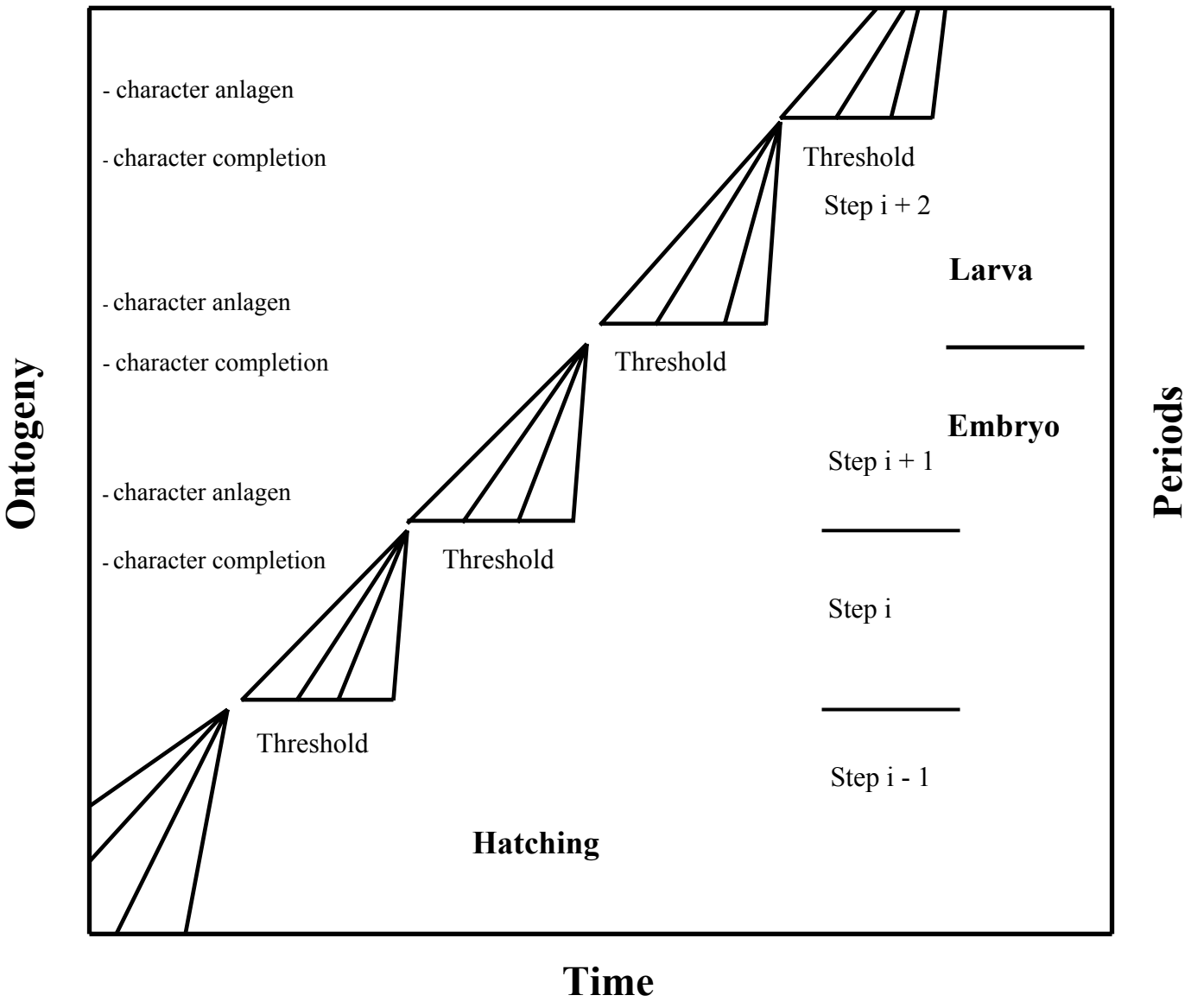
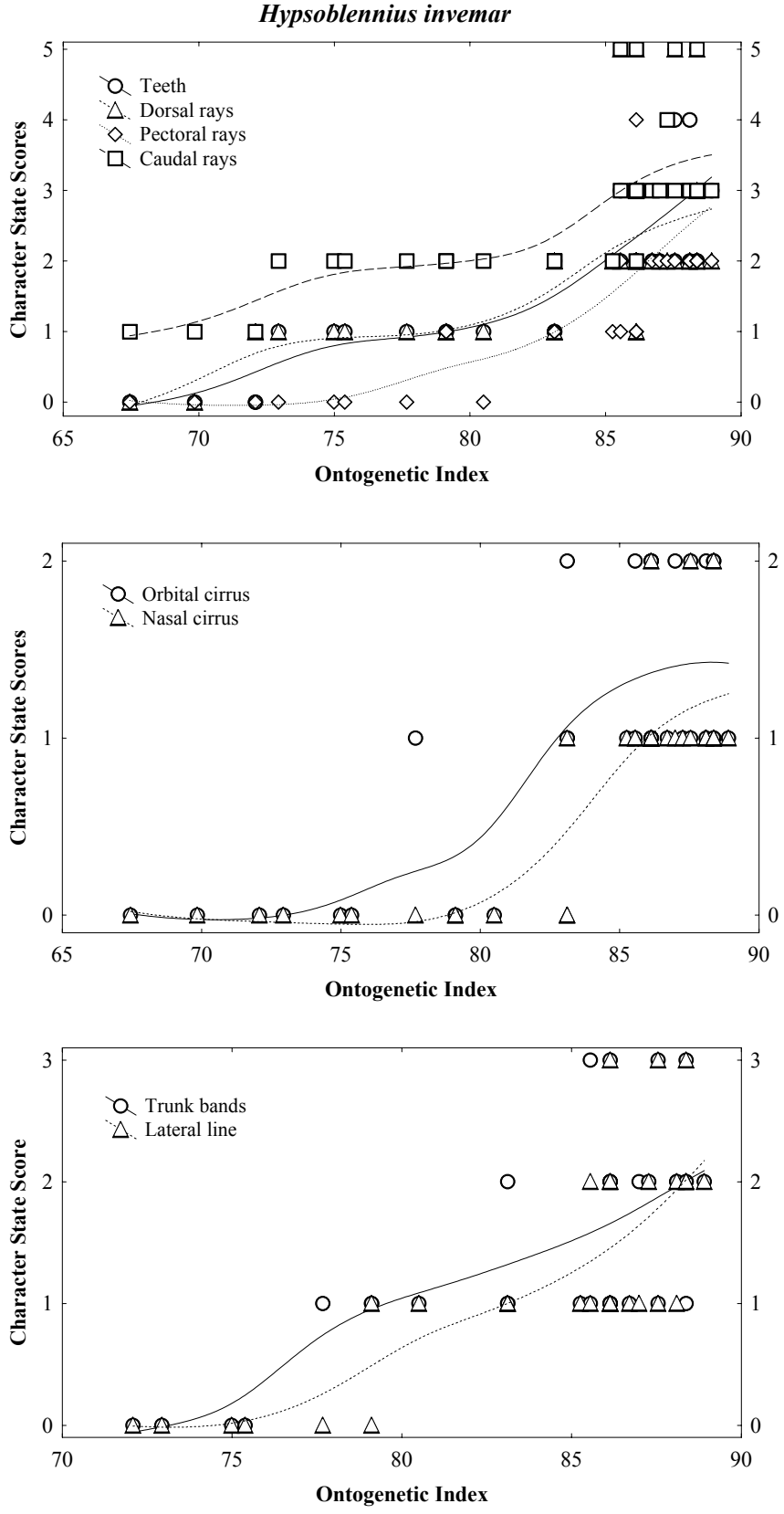


Figure 2.10. Progression of ontogeny as depicted by saltatory theory. Modified from Balon (1984). Each of the four converging lines represents an ontogenetic character; structures have completed development at the convergence.

Figure 2.11. Timing and progression of ontogeny for individual traits in five species of blenny from the northern Gulf of Mexico. A. *Hypsoblennius invemar*; B. *Hypsoblennius ionthas*; C. *Hypleurochilus multifilis*; D. *Parablennius marmoreus*; and E. *Scartella cristata*. Lines fitted by distance-weighted least squares method. A character state score of zero represents anlagen and the highest score represents element completion.



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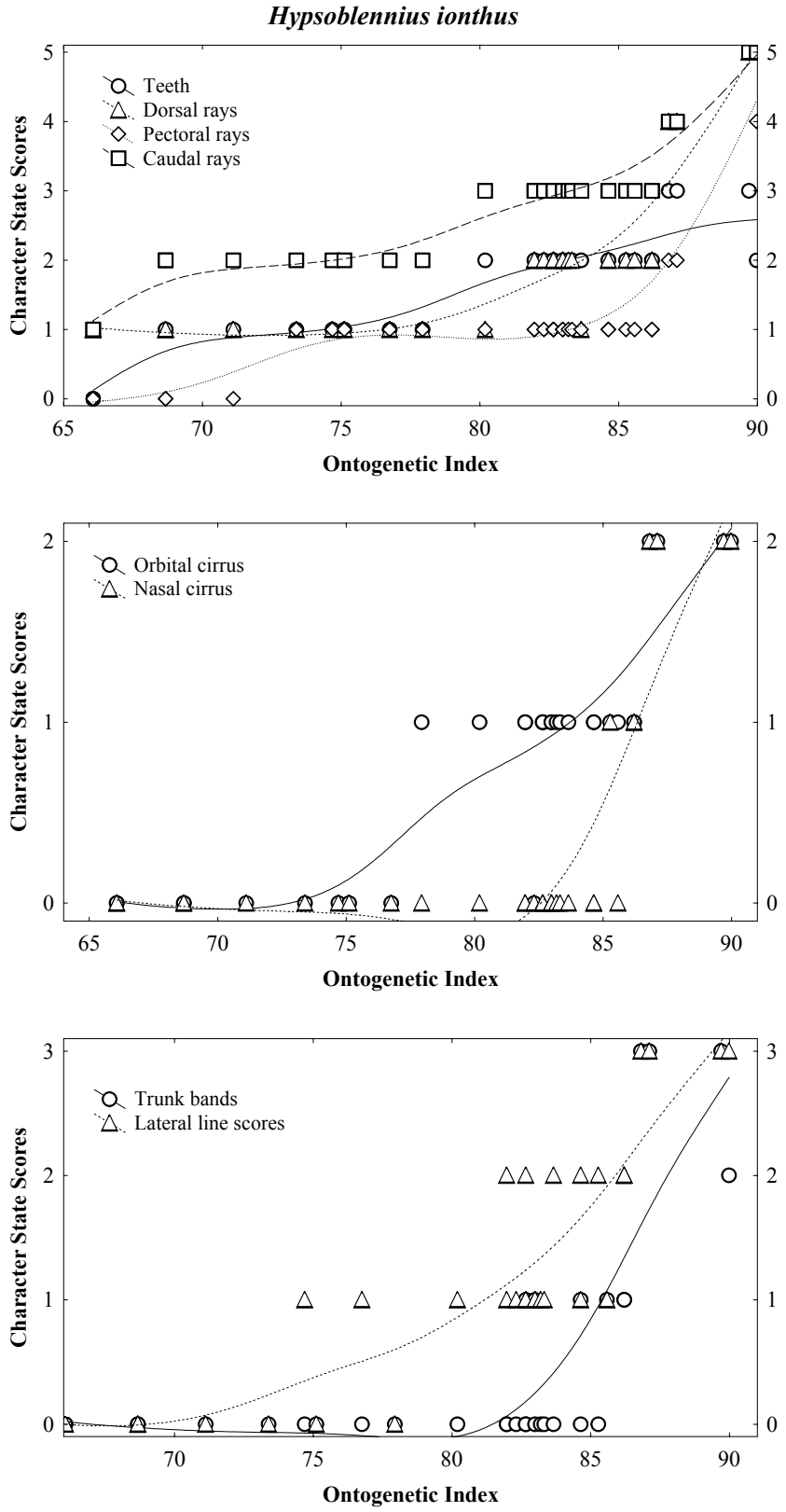

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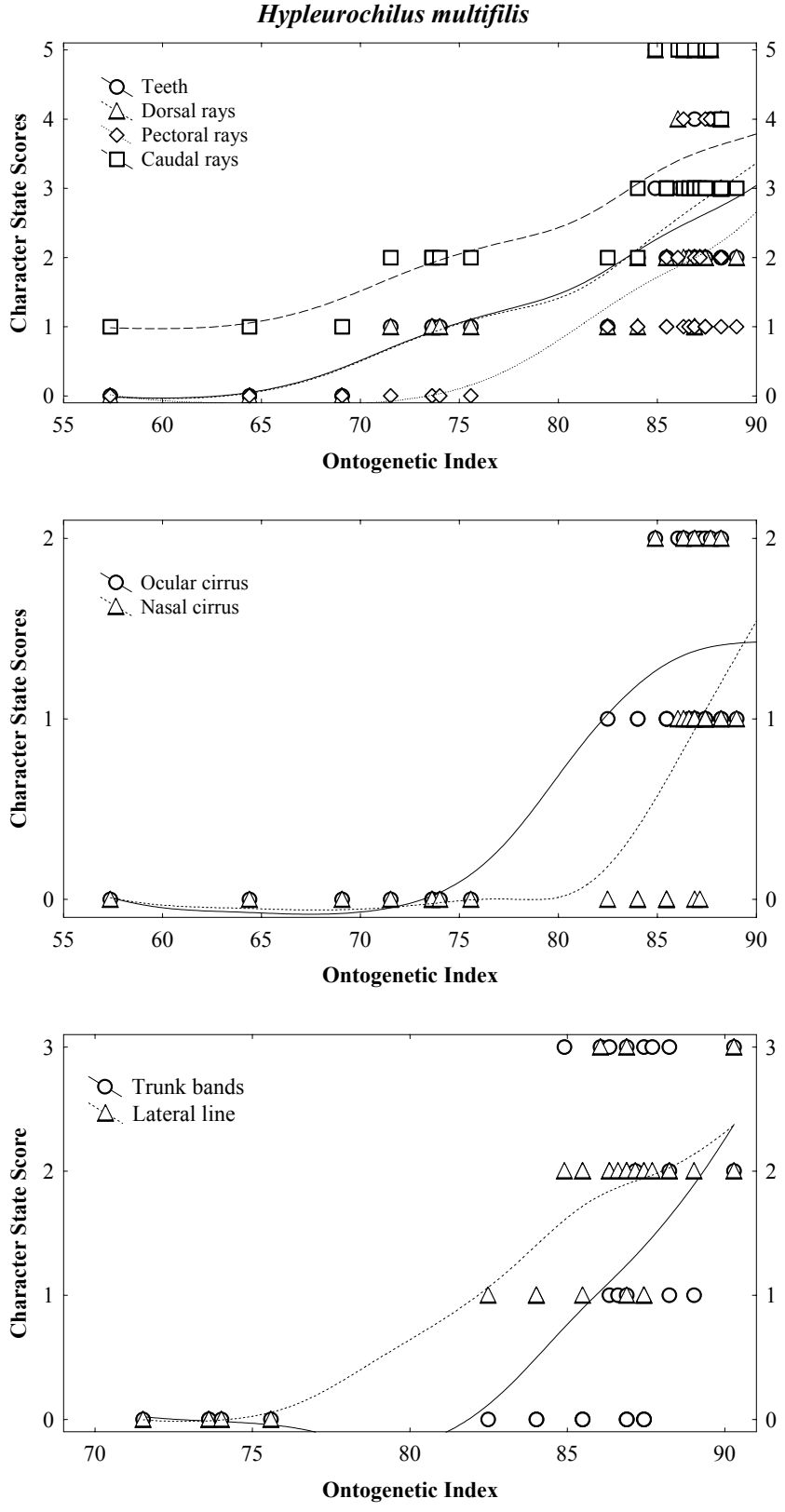

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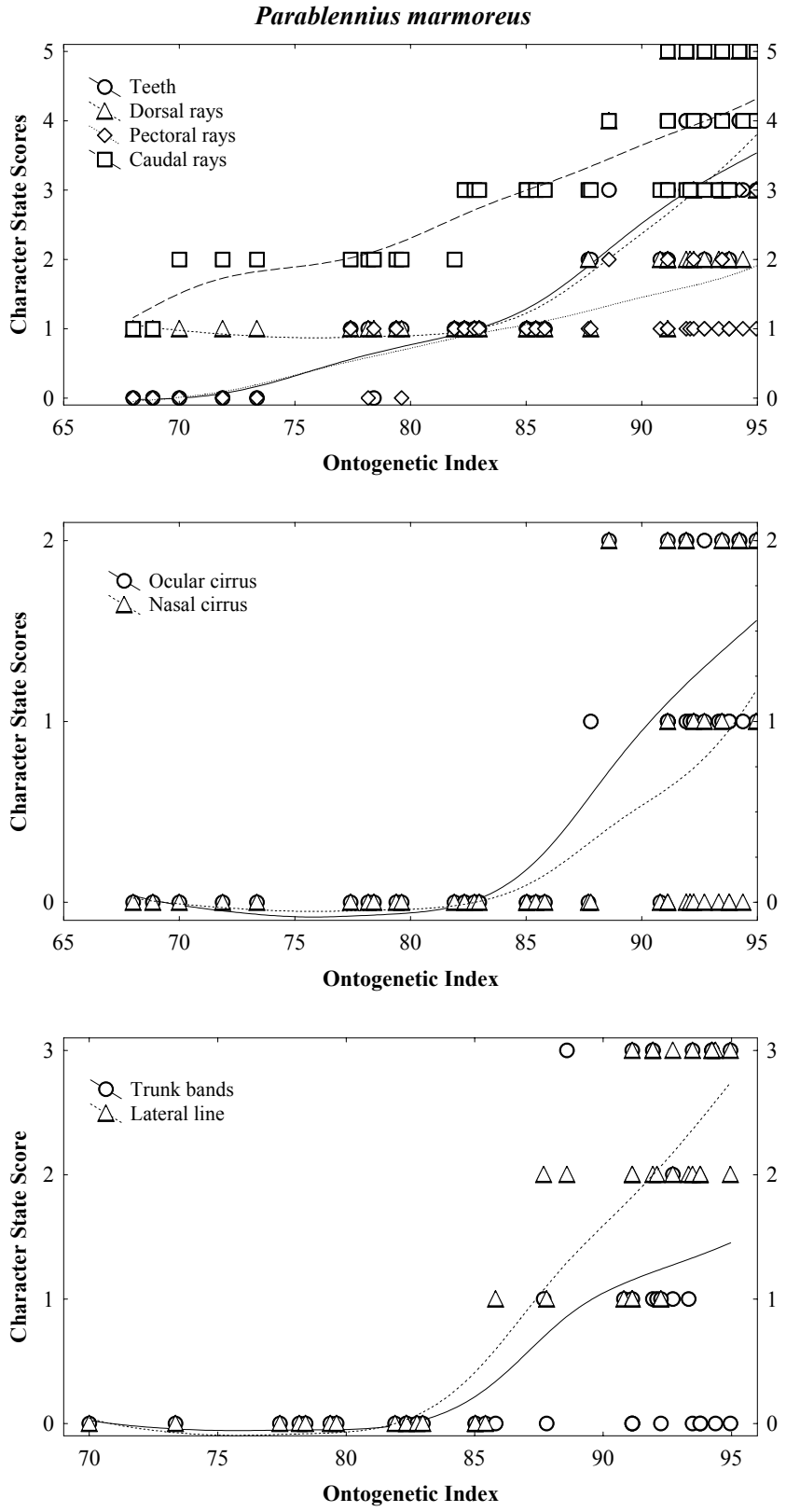

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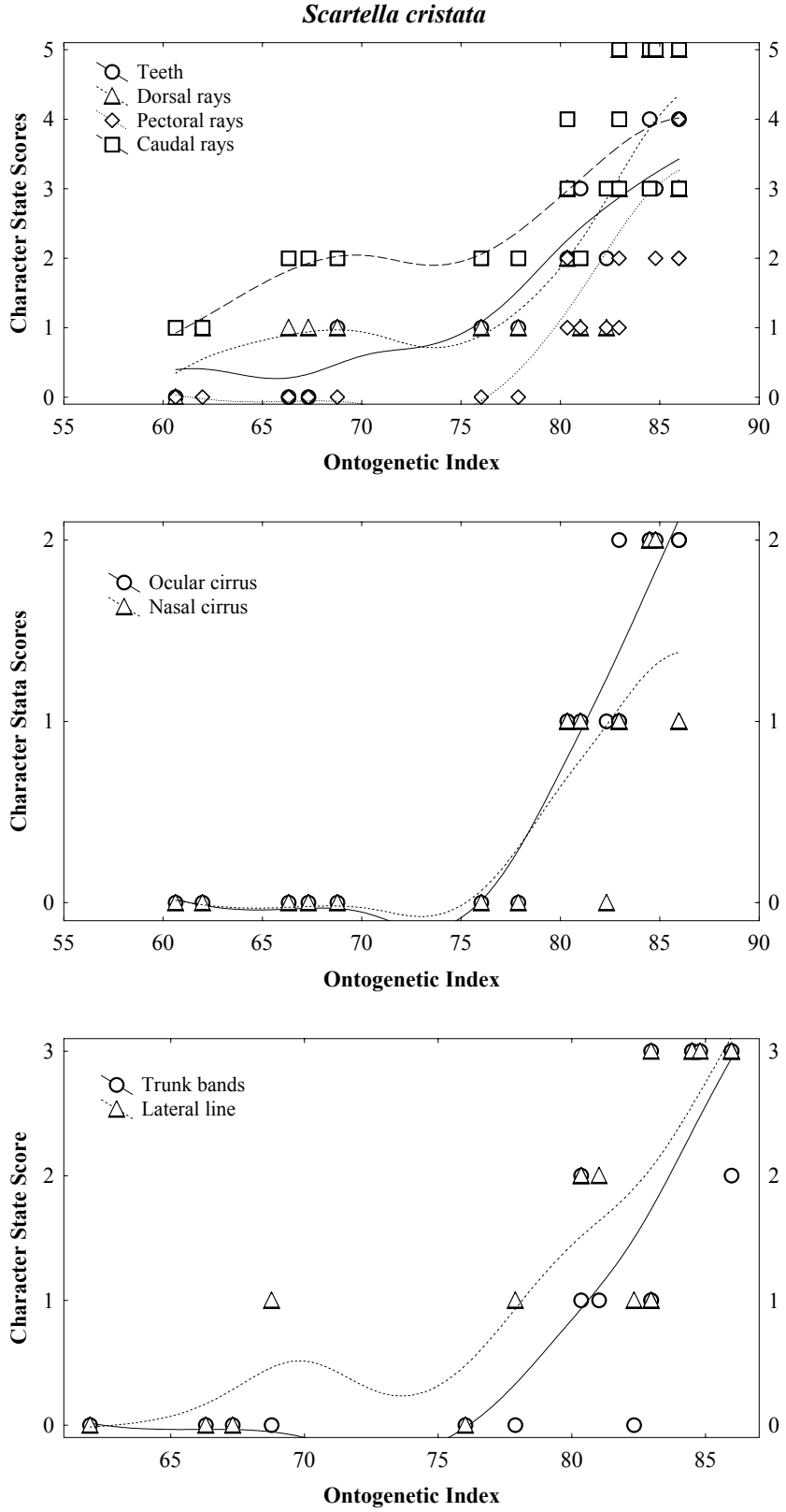

(Figure 2.11 continued)

trunk pigmentation, dorsal/anal fin, orbital cirrus, and tooth scores than larvae (Table 2.10). Late metamorphs/recent settlers have the following pigmentation characteristics: lightly pigmented orbital and nasal cirri, and multiple bands or saddles of pigment along the trunk. Length and timing of resorption of preopercular spines, presence or absence of pectoral fin pigment, and timing of nasal cirrus development are species-specific traits that must be eliminated from the sets of interspecific traits used to delineate intervals, if the objective is to compare different taxa. Some traits, particularly those related to pigmentation, are subject to individual variation and inter-population differences (Stevens and Moser, 1982; Watson, 1996) and should be used in combination with other traits to provide better resolution.

Does Settlement Occur at a Common State of Ontogeny?

Although size at settlement is species-specific (Table 2.11), study findings and those for some other taxa (blennies, Watson, 1983; some epinepheline serranids, Leis, 1987) provide several lines of evidence consistent with settlement taking place at a common state of ontogeny. In blennies, this evidence includes settlement over a narrow range of total character state scores, at a comparable state of structural development, and within a narrow range of O_L (Table 2.4). In fact, the timing and variation of settlement as measured by the ontogenetic index was over an order of magnitude more precise than SL for characterizing the timing of settlement in interspecific comparisons (Table 2.12). Patterns of skeletal ossification have also been used as a criterion for determining intervals of development in both pelagic and demersal fishes (Tanaka et al., 1996; Tsukamoto and Okiyama, 1997; Kinoshita et al., 1999) based on the idea that individual bones ossify at different times and the sequence is unlikely to vary (Alberch, 1985). Youson (1988) questioned the value of structural ossification as an ontogenetic character, believing instead that progressive changes beginning in the embryo are not developmental events. The fact that some skeletal structures complete ossification just before, or just after settlement

Table 2.11. Literature survey of size at settlement in blenniids or the smallest blenniid settler collected on reefs.

Blenniid tribe	Taxa	Sizes (mm SL)	Location	Reference
Parablenniini	*Chasmodes saburrae* [1]	6.4 (reared)	Tampa Bay, Florida	Peters (1981)
		8.7 (reared)	Banana River, Florida	Ferry (1989)
Omobranchini	*Enchelyurus brunneolus*	~11.5	Hawaii	Watson (1987)
Salariini	*Entomacrodus nigricans*	15.5	Location unknown	Springer (1967)
Parablenniini	*Hypleurochilus aequipinnis*	19.1	Florida Keys	Springer (1966)
Parablenniini	*H. springeri*	12.6	Antigua	Springer (1966)
Parablenniini	*H. springeri* [3]	10.8; 11.5	Grand Cayman	Springer (1966)
Parablenniini	*H. pseudoaequipinnis*	16.7	Panama	Bath (1994)
Parablenniini	*H. caudovittatus*	19.3	Location unknown	Bath (1994)
Parablenniini	*Hypsoblennius ionthas* [2]	14.5; 15.0	Bahamas; Dauphin Island, AL	Smith-Vaniz & Acero (1980); Clarke (1979)
Parablenniini	*H. invemar* [2]	15.7	Location unknown	Smith-Vaniz & Acero (1980)
Parablenniini	*H. hentz* [1]	17.0	Cape May, New Jersey	Smith-Vaniz & Acero (1980)
Parablenniini	*H. gentilis*	12.0-14.0	Eastern North Pacific	Watson (1996)
Parablenniini	*H. gilberti*	18.0-21.0	Eastern North Pacific	Watson (1996)
Parablenniini	*H. jenkinsi*	12.0-14.0	Eastern North Pacific	Watson (1996)
Parablenniini	*Lupinoblennius nicholsi* [1]	8.0 (reared)	Tampa Bay, Florida	Peters (1985)
Parablenniini	*L. dispar= vinctus*	9.6-10.6	Guatemala	Dawson (1970)
Salariini	*Ophioblennius atlanticus* [1]	32.0-58.0	Caribbean	Springer (1962)
Salariini	*O. steindachneri*	33.0-66.0	Eastern North Pacific	Watson (1996)

(Table 2.11 continued)

Blennid tribe	Taxa	Sizes (mm SL)	Location	Reference
Omobranchini	*Omobranchus punctatus*[3]	17.2; 18.1	Panama	Springer and Gomon (1975)
Omobranchini	*O. elongatus*[3]	13.0; 13.2	Panama	Springer and Gomon (1975)
Omobranchini	*O. germaini*[3]	16.2; 17.0	Panama	Springer and Gomon (1975)
Omobranchini	*O. anolis*	12.7-17.2	Indo-Pacific	Neira et al. (1998)
Parablenniini	*Parablennius tasmanianus*[4]	17.7	Indo-Pacific	Neira et al. (1998)
Parablenniini	*P. postoculomaculatus*[4]	13.2	Indo-Pacific	Neira et al. (1998)
Parablenniini	*P. intermedius*	14.0-17.0	Indo-Pacific	Neira et al. (1998)
Salariini	*Petroscirtes lupus*	13.0-17.0	Indo-Pacific	Neira et al. (1998)
Salariini	*Salarias pavo*	~8.0	Mediterranean	Brandstatter and Pantzner (1989)
Parablenniini	*Scartella emarginata*[5]	<16.0	Eastern North Atlantic	Eyberg (1984)

[1] A species used for some comparisons

[2] One of the five primary species studie

[3] Smallest settler; largest non-settle

[4] Largest non-settle

[5] Smallest settle

Table 2.12. Timing and variation of settlement as measured by three scaling metrics applied to five species of blenny from the northern Gulf of Mexico. Each species consists of the three largest metamorphs and three smallest settlers based on standard length. Mean (coefficient of variation).

Comparison	Standard length (mm) Mean (CV)	Total character state score Mean (CV)	Ontogenetic Index Mean (CV)
Pooled by species (N= 6 specimens)			
Hypsoblennius invemar	12.5 (6.0%)	25.3 (17.2%)	87.4 (2.4%)
Hypsoblennius ionthas	11.7 (5.1%)	25.0 (32.0%)	86.8 (2.0%)
Hypleurochilus multifilis	12.5 (4.6%)	30.2 (16.6%)	86.8 (1.8%)
Parablennius marmoreus	20.1 (7.1%)	29.4 (18.6%)	86.6 (0.5%)
Scartella cristata	11.0 (6.2%)	25.7 (14.3%)	82.8 (2.6%)
Pooled by interval of development (N= 15)			
Metamorphs	12.7 (26.4%)	22.1 (15.2%)	86.1 (2.0%)
Settlers	13.4 (23.5%)	32.1 (10.0%)	86.0 (1.2%)
Taxa combined (N= 30)			
	13.1 (24.1%)	27.1 (20.4%)	86.1 (1.6%)

(epurals, hypural minimal, lower jaw, fourth and fifth suborbital bones), suggests that the timing of ossification is non-random and driven by natural selection, at least in these blennies. If settlement is adaptive, and evolutionary forces give priority to development of essential components that optimize survival (Osse and van den Boogart, 1995; Gisbert, 1999), the nearly parallel relationship between timing of structural ossification and other changes in morphology, physiology, and behavior should be expected (Fuiman, 1997).

When Does the Juvenile Period Begin and End in Blennies?

While sexual maturity easily delineates the juvenile and adult period, defining other important developmental thresholds remains largely subjective because most studies cover only the larvae (Copp and Kovac, 1996). Determining the end of the larval period and the beginning of the juvenile period in blennies requires knowledge of the events that initiate and terminate metamorphosis. The fact that some blennies settle before losing all pectoral fin pigment (Figs. 2.2d and 2.3c) and that some species have not completely resorbed the longest preopercle spine (Figs. 2.1d-e and 2.2d) at settlement, suggests that metamorphosis has not been completed. If resorption of all larval characters and acquisition of the juvenile pattern of pigmentation adequately characterize termination of the larva period, these blennies settle as larvae. Although many blenniids settle by 13 mm (Table 2.11), as do chaenopsiids (Hastings, 1991), neither group exhibits pronounced sexual dimorphism until about 15 mm SL or larger.

No information exists on the relationship between timing of caudal ray bifurcation and sexual maturity in blennies. I suggest that the onset of sexual maturity nearly coincides with bifurcation of all primary caudal fin rays, at least in the species studied, as demonstrated by a 20-mm male of *H. multifilis* (O_L = 103.1), which had the external signs normally associated with being in spawning condition. Becoming sexually mature relatively soon after settling is

supported by findings that the ecologically similar gobies, and some serranids, also reach sexual maturity not long after settlement (Lachner and Karnella, 1980; Shapiro, 1981).

If initial caudal ray bifurcation is an adequate marker of the onset of sexual maturity in blennies, and given some of the parameters in Table 2.6, SL can be estimated at other important early life events for a species. For example, most *O. atlanticus* settle by 37 mm SL or by about 45 mm total length (Springer, 1962; Labelle and Nursall, 1992). The natural log of SL at settlement (37 mm), multiplied by 100, divided by the overall mean O_L at settlement for four of the species studied (86.1; excludes *P. marmoreus* because settlement size and O_L were estimated for this species), and taking the anti-log of the result predicted L_{juv} at 43.0 mm SL in *O. atlanticus*. The estimated onset of sexual maturity, therefore, would be 48.3 mm SL, which is consistent with sexually mature, wild-caught *O. atlanticus* of 48 mm and 52 mm SL (Labelle and Nursall, 1985).

Determination of the characters that adequately define completion of metamorphosis is difficult, and magnified for blennies and other fishes that have little head spination, body ornamentation, and few other obvious external traits by which to characterize intervals. In addition, relying strictly on characters such as initial or complete squamation to determine the start of the juvenile period, as has been proposed, creates problems in scaleless fishes, such as blennies, and in fishes (swordfish, squirrelfish, tilefish, and anthiinae serranids) that complete scale development while still considered larvae (Kendall, 1979; Potthoff and Kelley, 1982; Leis and Carson-Ewart, 2000). Adaptive mechanisms can also induce development of juvenile structures before metamorphosis (Hadfield, 2000), while other juveniles retain larval characters in the caudal fin after metamorphosis (Copp and Penaz, 1988). Such diverse life-history patterns suggest that defining settlement, as the start of the juvenile period for all fishes, requires further justification.

Does Ontogeny Progress Gradually and Continuously, or in a Saltatory Fashion?

Objective examination of ontogenetic development without an ideological predisposition as to its progression is critical. Much of the existing literature that supports saltatory theory, nevertheless, has been purposely described from a saltation perspective (McElman and Balon, 1979; 1980; Paine and Balon, 1984a; 1984b), with little consideration of alternatives. Results of this study of ontogeny in blennies supports a continuous rather than stepwise progression of ontogeny, as do patterns of skeletal ossification (Alberch, 1985), character ontogeny (Gisbert, 1999), changes in foraging behavior (Dowling et al., 2000), and additional evidence (Gorbman et al., 1982; Markle et al., 1992) for other fishes. In the blennies examined, changes in dentition occur continuously rather than instantaneously, in both number and type of teeth. In fact, incisiform teeth protrude through foramina along the upper and lower jaws while the primary dentition pattern in larvae remains villiform. Early metamorphs have both the villiform teeth of larvae and the incisiform teeth of adults before incisors replace all villiform teeth along the jaw. Fin ray development also supports the gradual and continuous progression of ontogeny.

Saltatory ontogeny asserts that a suite of characters should complete simultaneously and incrementally along the age or time axis before the next developmental step initiates, which they do not (Figs. 2.10 and 2.11). The ordered progression of development can sometimes structure patterns that appear saltatory depending on the magnitude, rate, duration, and timing of ontogenetic events (Nelson, 1978; Alberch, 1985; Balon, 1985; Klingenberg and Zimmermann, 1992). Character selection can also affect how patterns are interpreted (Hartnoll, 1978; Crowley, 2000). Although the number of characters can influence the likelihood that intervals coincide with any natural process or important function, Gorodilov's (1996) suggestion that a large number of characters can make ontogeny appear continuous rather than saltatory is unfounded. Having a large number of characters has no effect on the progression of ontogeny because events

should converge and fall within one of the steps or progressively larger intervals of ontogeny defined by saltatory theory. On the other hand, examination of too few characters can make ontogeny appear saltatory when it is not.

If visible external changes reflect internal preparation (Tanaka et al., 1996), examination of external traits, as was done in this study, will provide evidence equivalent to that obtained by internal characters. Genetics largely control the timing of ontogeny and its variability during development (Atchley, 1984), and should regulate the timing and placement of steps and thresholds, if saltatory development is real. The likelihood of recognizing the minor thresholds between steps as proposed by saltatory theory, however, depends on the magnitude and concurrence of ontogenetic events. Recognition of developmental thresholds becomes more subjective as morphological complexity and individual variation increase, as revealed by the study of the diamond killifish, *Adinia xenica* (Cunningham and Balon, 1986). Although Cunningham and Balon (1986) describe ontogeny in this species according to saltatory theory, the high variability in the timing of ontogeny among individuals could also be interpreted as continuous ontogeny with one pronounced threshold.

The poor resolution of the internal saltatory thresholds that separate proposed 'steps' is compounded by the fact that little of an internal event remains in preserved specimens (Balon, 1985), which makes the presence and timing of steps based on internal traits and processes nearly impossible to verify and validate. Accordingly, developmental thresholds that separate larger intervals of development would be easier to recognize, a finding supported in this study by the convergence of ontogenetic events during metamorphosis, and existing behavioral, physiological, and morphological evidence (Noakes and Godin, 1988; Karjalainen et al., 1996; Masuda and Tsukamoto, 1999). In conclusion, saltatory steps would be nearly impossible to identify in larvae if the timing of each new ontogenetic event is highly variable and

developmental thresholds are vague. Study findings do not support such small incremental steps in ontogeny for blennies.

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CHAPTER 3: PATTERNS OF RELATIVE GROWTH AND TIMING OF SETTLEMENT IN FIVE REEF-ASSOCIATED SPECIES OF BLENNY

Introduction

Fish life histories consist of multiple intervals that occupy separate ecological niches and habitats (Stoner and Livingston, 1984; McCormick, 1998). Organisms filter the environment physiologically (Morey and Reznick, 2000) and how they respond to fluctuating environmental conditions often depends on their state of development. To better understand the relationship between morphology and ecology requires examination of developmental processes because patterns of relative growth can differ in closely related species (Osse, 1989; Klingenberg and Froese, 1991; Klingenberg et al., 1996; Fuiman et al., 1998). Quantification of shape change may assist in identifying intervals of development and reveal the timing of ecological transitions (Copp and Kovac, 1996; Muller and Videler, 1996; van Snik et al., 1997).

Differential rates of cell, tissue, or organ growth during early development can result in morphological remodeling in organisms with complex life cycles, such as reef and other demersal fishes (Alberch et al., 1979; Shea, 1985; Blackstone, 1987). Shape, a fundamental facet of an organism's overall design, is the result of differential growth of body parts (Strauss, 1993). If growth rates of individual structures reflect the priorities of development, structures important for making ecological transitions, such as settlement, should grow relatively faster during than after metamorphosis (van Snik et al., 1997). Previous studies that have examined shape change have revealed both similarities and differences between species (Fuiman, 1983; Shea, 1985), eco-morphological variants (Meyer, 1990), and the early life stages of fish (Strauss and Fuiman, 1985). The relationship between the timing of shape change and settlement has not been examined in reef fishes. Examination of developmental processes is important to better understand factors that affect survival, which may be interval-specific (Richards and Lindeman, 1987; Kingsford, 1988; Noakes and Godin, 1988).

Separate schools of thought have emerged to describe the timing and progression of ontogeny. 'Saltationists' promote development as a process consisting of a hierarchy of stabilized steps and periods separated by distinct but less stable thresholds (Balon, 1975; Youson, 1988; Balon, 1999). 'Gradualists', on the other hand, view development as a series of small progressive changes that occur continuously but not necessarily at a constant rate over time (Ahlstrom and Counts, 1958; Zweifel and Lasker, 1976; Markle et al., 1992; Fuiman and Higgs, 1997). Although laboratory observations have been interpreted as supporting saltatory ontogeny, this theory has not been objectively examined. Whether shape change is the accumulative result of a series of smaller, identifiable, stabilized steps separated by thresholds is uncertain. If changes in shape occur in a saltatory fashion, metamorphosis should transit a series of stabilized steps, rather than change continuously and differentially in various parts of the body.

The possibility that changes in shape are interval-specific and that these changes proceed in a saltatory fashion prompted the following questions: 1) Do blennies share a common growth pattern? 2) Are differences in shape interval-specific? 3) Do body and fin growth patterns reflect the timing of ecological and habitat changes? 4) Do patterns of relative growth contribute to our understanding of developmental theory?

Materials and Methods

This chapter will examine shape change relative to the timing of metamorphosis and settlement in the following five species of blenny from the northern Gulf of Mexico: tessellated blenny (*Hypsoblennius invemar*), freckled blenny (*Hypsoblennius ionthas*), *Hypleurochilus multifilis*, seaweed blenny (*Parablennius marmoreus*), and molly miller (*Scartella cristata*). Specimens were obtained during light trap sampling of oil and gas platforms off Louisiana over a 3-yr period (1995-1997). Recent settlers were hand-netted over oyster shell reefs and along rock

jetties, with slurp guns along the legs of oil and gas platforms, and after explosive removal of oil and gas platforms (Appendix). Specimens were fixed in 10% formalin and transferred to 70% ETOH after about 12 h. Sample size depended on taxon abundance and the size range of specimens available. Overall, 114 specimens were measured: 23 *H. invemar* (5.4-12.8 mm SL), 24 *H. ionthas* (5.0-12.8 mm), 24 *H. multifilis* (6.5-13.3 mm), 29 *P. marmoreus* (5.8-21.0 mm), and 14 *S. cristata* (5.8-12.0 mm). An additional 36 specimens were eliminated from morphometric analyses due to expressed sexual dimorphism (see below for statistical method of elimination). All measurements were made with a stereo-zoom microscope and Optimus Imaging Software (Optimus, 1996) calibrated with a stage micrometer. A cradle molded from tooth wax supported and positioned the specimen in nearly the same plane as the scale to help reduce optical distortion and parallax.

Statistical Analyses

The original 28-measurement data set consisted of 18 body truss measurements (plus standard length, upper jaw length, and interorbital width) and 7 linear fin and cirrus measurements (Table 3.1). I examined the fin and cirrus data set separately from the truss data set to explore the timing of changes in growth of fin elements and cirri relative to body shape. Residuals and multivariate outliers (±2.5 standard deviations, SD) were removed from each raw data set before natural log-transformation to reduce non-linearity and heterogeneity of variances. To help minimize the confounding effects of sexual dimorphism, I ran a Principal Component Analysis (PCA) on a species-specific subset of characters considered dimorphic for that species, using the covariance matrix of natural log-transformed data (Hastings, 1991). Each character was evaluated separately by regressing its natural log-transformed value against PC1 (a multivariate measure of overall body size) and plotting residuals about the regression line

Table 3.1. Original set of body truss (1-19), and linear fin and cirrus (20-28) measurements for five species of blenny from the northern Gulf of Mexico. Measurements analyzed are in boldface type. All distances were measured from the base or insertion of an element or structure.

	Truss or linear distance
1	Tip of the snout to base of caudal fin rays (standard length)
2	**Anterior tip of nasal bone to first dorsal spine**
3	First dorsal spine to first dorsal soft ray
4	**First soft dorsal ray to second anal spine**
5	Second anal spine to pelvic fin insertion
6	**Pelvic fin insertion to symphysis of premaxillary**
7	**First dorsal spine to pelvic fin insertion**
8	**First dorsal spine to second anal spine**
9	First soft dorsal ray to pelvic fin insertion
10	First to last soft dorsal fin ray
11	Last dorsal element to last anal fin ray
12	Last anal fin ray to second anal spine
13	First soft dorsal fin ray to last anal fin ray
14	Last dorsal fin ray to second anal spine
15	Last dorsal fin ray to base of uppermost primary caudal fin ray
16	**Uppermost to lowermost primary caudal fin ray**
17	Lowermost primary caudal ray to last anal fin ray
18	Last dorsal ray to lower primary caudal fin ray
19	Uppermost primary caudal ray to last anal fin ray
20	**Upper jaw length**
21	**Interorbital width at insertion of orbital cirri**
22	**Length of longest orbital cirrus**
23	**Length of longest nasal cirrus**
24	**Length of first dorsal spine**
25	**Length of last dorsal spine**
26	**Length of last soft dorsal fin ray**
27	**Length of longest pectoral fin ray**
28	**Length of longest pelvic fin ray**

(Hastings, 1991). All individuals with standardized residuals outside ±2.0 SD of the mean for any two sexually dimorphic characters for a given species were eliminated from morphometric analyses (Table 3.2).

Some species and intervals of development contained relatively few specimens. Thus, I performed a Discriminant Function Analyses (DFA; StatSoft, 1999) on the original 21 body measurements to help reduce the large number of highly correlated variables to a smaller data set. Only body measurements with $\rho \leq 0.05$ were included in subsequent analyses. This resulted in a final suite of eight body measurements (plus SL) that accounted for most of the variability in the data set (first 8 characters in boldface type in Table 3.1; Fig. 3.1). Eigenvalues from the DFA of the reduced data set were compared to those from the full data set to confirm the goodness-of-fit of the two models. All seven fin and cirrus measurements were used in subsequent analyses (last seven characters in boldface type in Table 3.1; Fig. 3.1).

Multivariate methods for studying morphological change have yielded techniques to help isolate the size component that can mask subtle and biologically interesting differences in shape not discernable from the original data (Shea, 1985; Strauss, 1985; Rohlf and Bookstein, 1987). While most descriptive tools simplify or summarize data, few specify the model or test hypotheses. One commonly used multivariate method for evaluating differences in shape is PCA, which summarizes changes in size and shape into separate variables and removes 'most' of the size component (Bookstein, 1982; Klingenberg and Froese, 1991). Principal Component Analysis as traditionally applied to studies of morphology uses the total covariance matrix, which obscures the contribution of within group and between group variability, and assumes that all groups share a common growth pattern and the same eigenvectors. This limits PCA to single species situations (Airoldi and Flury, 1988; Klingenberg, 1996). A common covariance structure

Table 3.2. Characters diagnostic for sexual dimorphism in blennies from the northern Gulf of Mexico.[1] Mature blennies can be sexed externally by examining the anal fin. The urogenital opening forms a papilla in males and is concealed by a hood of tissue in females.

Taxa	Sexual dimorphism		Reference
	Males [2]	Females [3]	
Chasmodes bosquianus [4]	Longer maxillary		Springer (1959); Smith (1974)
Hypsoblennius hentz	Longer, broader supraorbital cirrus		Smith-Vaniz & Acero (1980)
Hypsoblennius invemar [5]	Longer, broader supraorbital cirrus		Smith-Vaniz & Acero (1980)
Hypsoblennius ionthas [5]	Longer, broader supraorbital cirrus		Smith-Vaniz & Acero (1980)
	Weakly or not freckled	Freckled on lower 50% of head	
Lupinoblennius nicholsi	Elongate first dorsal spine	Longer snout at >20 mm SL	Tavolga (1954)
	Thickened, fleshy first dorsal ray		
	Upper and lower canines at maturity	Lower canines only	
Lupinoblennius vinctus	Longer, broader supraorbital cirrus	No basal notch anterior to 1st dorsal fin	Dawson (1970)
	Upper and lower canines	Lower canines only	
Ophioblennius atlanticus [4]			Springer (1962); Smith (1974)
Scartella cristata [4, 5]	1st anal spine obvious	1st anal spine small, barely visible	Smith (1974)

[1] No information for *Hypleurochilus multifilis* and *Parablennius marmoreus*

[2] 1st two-anal spines with flattened, spatulate pads; often becoming fleshy, rugose, glandular knobs during breeding season

[3] 1st anal spine often embedded in urogenital aperature

[4] Fleshy lateral extensions at tips of anal fin rays behind the spatulate pads of 1st two anal spines in breeding males

[5] One of the five major species studied; early-life stages of other taxa were used for comparison

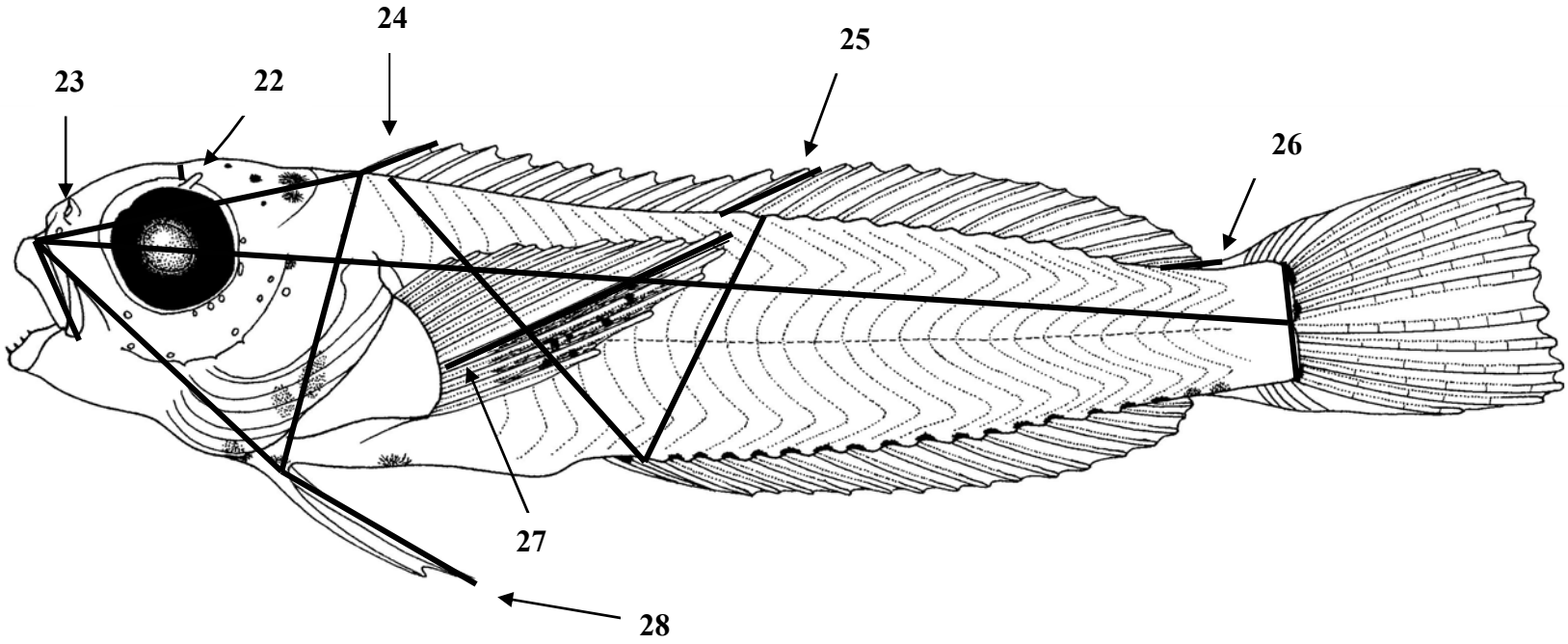

Figure 3.1. Final suite of eight body truss, and seven linear fin and cirrus measurements, used to examine patterns of relative growth in five species of blenny from the northern Gulf of Mexico (see Table 3.1 for codes and explanation of measurements). Numbered lines without arrows are body truss measurements.

model may apply when differences in PC1 eigenvectors within and between groups are small (Klingenberg, 1996). Common Principal Component Analysis (CPCA; Flury, 1988) summarizes the allometric growth patterns of multiple groups into a common set of principal components, but permits flexibility in the variation associated with each group (Flury, 1988; Klingenberg and Zimmermann, 1992). Application of the CPCA model extends PCA to multi-group situations and permits the testing of hypotheses and assumptions that are otherwise difficult to address (Klingenberg and Froese, 1991).

I computed separate PCA's on the reduced data set of 8-body measurements for each species and compared these results with the species-pooled data set examined with a CPCA, to determine whether the five blennies studied share a common pattern of relative growth. Jackknife procedures tested the null hypothesis that the scatter ellipsoids of the principal axes (eigenvectors) share a common directional orientation among all groups. To determine the stability of loadings, I compared first Principal Component (PC1) and first Common Principal Component (CPC1) loadings to means and confidence intervals calculated by resampling methods. I designated the CPC that accounted for the largest proportion of total within group variation as CPC1, and compared PC1 to CPC1 eigenvalues to assess the goodness-of-fit of the CPCA model. Burnaby's (1966) procedure for removing residual size from shape to produce size-free shape was applied to PC2 through PC9, and CPC2 through CPC9 loadings. Since the resultant 'new' CPC1 loadings and factor scores were derived from previously size-adjusted data, CPC's were used only for ordination. Plots of the CPC size-adjusted loadings represent the common shape pattern.

The ratio of PC loadings for different traits characterizes patterns of relative growth (changes in shape). Simple allometric growth occurs when the ratio between two characters

remain isometric with body size and does not significantly differ from the theoretical value of one divided by the square root of 'p', where 'p' represents the number of variables in the analysis (Cheverud, 1982; Shea, 1985). Compound allometric growth occurs when the ratio between characters change with body size (Shea, 1985; Strauss, 1987). Multiplying PC1 or CPC1 loadings by the square root of the number of variables in the analysis translated and rescaled bivariate coefficients into multivariate allometric coefficients (MAC's). A value of one represents multivariate isometry (Shea, 1985). Plots of MAC's represent the underlying 'growth gradient' (Klingenberg, 1996).

Specimens were assigned to the same intervals of development determined by cluster analysis in Chapter 2. I assigned categorical labels ('larvae', 'metamorphs', or 'settlers'; defined in Chapter 2) to intervals of development, but do not imply a hierarchical terminology. I used piecewise linear regression and the quasi-Newtonian method of nonlinear estimation (StatSoft, 1999) to model relative growth trajectories. This identified the location of the 'breakpoint' between intervals where the rate of change in shape was greatest (StatSoft, 1999).

Interspecific comparisons of the timing of shape change require scaling procedures or an index that accounts for non-linear rates of growth (Atchley, 1984; La Barbera, 1989; Fuiman and Higgs, 1997). The ontogenetic index (O_L) of Fuiman (1994) expresses ontogeny (O_L= log L/log L_{juv} x 100) as a proportion of a logarithmic developmental period, where L = standard length (SL) of an individual, and L_{juv} = SL at the beginning of the juvenile period in a given species. Using L_{juv} to formulate O_L corrects for size differences among species and permits comparison of event timing across multiple species.

Results

Comparison of the full (21 original body measurements) and reduced (8 body measurements) data sets (Table 3.1) yielded PC1 eigenvalues that accounted for 91**%** and 88**%** of the variability in these data sets, respectively, suggesting that the reduced suite of truss measurements adequately represented the full data set. Although within group covariance matrices were not equal ($\alpha = 0.05$, $\chi^2 = 0.001$), ANOVA (using a Bonferroni adjustment for five comparisons) did not detect a significant difference ($\alpha \doteq 0.05$) in the direction of PC1 axes among species, consistent with a common first principal component among species. The high percentage and comparable amounts of total variability accounted for by the PC1's and the pooled CPC1 eigenvectors suggested that the pooled data set adequately represented the individual data sets (Table 3.3) and that differences were primarily size-related. The relatively low jackknife-estimated confidence intervals for PC1 in each taxon were consistent with reasonable eigenvector stability for most body truss measurements (Table 3.4). Failure to reject the null hypothesis of a common growth pattern among taxa satisfied the underlying assumptions of PCA and permitted further examination of species-specific differences in relative growth with the PCA model.

Relative growth rates for different body parts varied with body size. The hypothesis of simple allometric growth was rejected for each species because the coefficient for isometry was outside the jackknifed estimated confidence intervals for most allometric coefficients (Tables 3.4 and 3.5). The common growth pattern shared by these blennies revealed positive allometry for most body depth and abdominal measurements, and negative allometry for the upper jaw, interorbital width, and for measurements that involve the lower part of the head and caudal peduncle (Table 3.5). The most obvious differences among species in individual body

Table 3.3. Variability extracted by the first and second eigenvalues of Common Principal Component Analysis (CPC) and one-group Principal Component Analysis (PC) of data for five species of blenny from the northern Gulf of Mexico (N= 114 specimens). Eight body truss measurements and seven linear fin and cirrus measurements were used.

Taxon	Eigenvector	Body truss eigenvalues	% Variability explained	Fin & Cirrus eigenvalues	% Variability explained
Hypsoblennius invemar	CPC1	0.243	92.0	0.135	84.1
	CPC2	0.007	2.6	0.006	4.1
	PC1	0.478	90.2	0.303	92.0
	PC2	0.023	4.4	0.012	3.6
Hypsoblennius ionthas	CPC1	0.251	91.8	0.308	90.3
	CPC2	0.013	4.8	0.022	6.6
	PC1	0.566	87.3	0.309	90.8
	PC2	0.053	8.2	0.023	6.7
Hypleurochilus multifilis	CPC1	0.168	92.3	0.269	89.5
	CPC2	0.005	2.9	0.017	5.8
	PC1	0.363	87.8	0.272	90.5
	PC2	0.033	7.9	0.016	5.4
Parablennius marmoreus	CPC1	0.418	95.8	0.656	87.0
	CPC2	0.006	1.3	0.044	5.9
	PC1	0.784	95.0	0.567	87.8
	PC2	0.017	2.1	0.054	8.4
Scartella cristata	CPC1	0.142	92.3	0.351	88.9
	CPC2	0.001	0.8	0.024	6.2
	PC1	0.314	90.4	0.219	89.4
	PC2	0.010	2.9	0.014	5.7

Table 3.4. Comparison of non-size-adjusted Principal Component (PC) eigenvectors (PC1), adjusted size-free shape (PC2), and multivariate allometric coefficients (MAC's) for five species of blenny from the northern Gulf of Mexico. MAC's were scaled to a value of one for isometry and represent the evolutionary growth gradient. Highest MAC's are in bold. Means and standard errors were estimated by jackknife procedures.

Body truss measurement	Eigenvector		Standard error of	95% C.I. (PC1)		MAC's
	PC1	PC2	PC1	Lower	Upper	
Hypsoblennius invemar						
Standard length	0.324	-0.087	0.016	0.292	0.356	0.978
Premaxillary to first dorsal spine	0.326	-0.081	0.012	0.293	0.358	0.983
First dorsal ray to anal spine	0.424	0.046	0.012	0.392	0.456	**1.270**
Pelvic insertion to premaxillary	0.233	0.043	0.022	0.201	0.266	0.708
First dorsal spine to pelvic insertion	0.380	0.068	0.008	0.348	0.412	**1.144**
First dorsal spine to anal spine	0.431	-0.190	0.015	0.399	0.463	**1.298**
Upper to lower primary caudal ray	0.329	0.012	0.030	0.297	0.361	0.968
Upper jaw length	0.240	-0.498	0.021	0.208	0.272	0.725
Interorbital width	0.243	0.833	0.035	0.211	0.275	0.711
Hypsoblennius ionthas						
Standard length	0.322	-0.080	0.010	0.302	0.342	0.976
Premaxillary to first dorsal spine	0.328	-0.056	0.011	0.306	0.349	0.993
First dorsal ray to anal spine	0.398	0.062	0.030	0.340	0.457	**1.215**
Pelvic insertion to premaxillary	0.236	-0.324	0.031	0.175	0.296	0.725
First dorsal spine to pelvic insertion	0.338	-0.141	0.037	0.265	0.410	1.046
First dorsal spine to anal spine	0.396	-0.098	0.018	0.360	0.431	**1.204**
Upper to lower primary caudal ray	0.448	0.020	0.090	0.272	0.623	**1.277**
Upper jaw length	0.231	-0.058	0.023	0.187	0.276	0.703
Interorbital width	0.225	0.921	0.067	0.095	0.356	0.624
Hypleurochilus multifilis						
Standard length	0.309	-0.028	0.021	0.269	0.349	0.911
Premaxillary to first dorsal spine	0.287	-0.097	0.012	0.263	0.311	0.861
First dorsal ray to anal spine	0.408	-0.051	0.037	0.335	0.481	**1.245**
Pelvic insertion to premaxillary	0.289	-0.009	0.015	0.260	0.319	0.868
First dorsal spine to pelvic insertion	0.360	-0.074	0.012	0.335	0.384	1.084
First dorsal spine to anal spine	0.435	-0.122	0.016	0.403	0.466	**1.313**
Upper to lower primary caudal ray	0.338	-0.185	0.040	0.259	0.417	0.993
Upper jaw length	0.294	-0.065	0.027	0.241	0.347	0.875
Interorbital width	0.230	0.963	0.038	0.157	0.304	0.688

(Table 3.4 continued)

Body truss distance	Eigenvector		Standard error of PC1	Confidence Intervals (PC1)		MAC's
	PC1	PC2		Lower	Upper	
Parablennius marmoreus						
Standard length	0.323	0.164	0.010	0.304	0.341	0.962
Premaxillary to first dorsal spine	0.298	-0.080	0.009	0.280	0.316	0.900
First dorsal ray to anal spine	0.409	0.140	0.013	0.384	0.434	**1.225**
Pelvic insertion to premaxillary	0.312	-0.225	0.011	0.290	0.334	0.939
First dorsal spine to pelvic insertion	0.354	-0.125	0.013	0.328	0.379	1.068
First dorsal spine to anal spine	0.435	-0.111	0.011	0.413	0.456	**1.311**
Upper to lower primary caudal ray	0.282	0.188	0.025	0.233	0.330	0.832
Upper jaw length	0.339	-0.376	0.015	0.310	0.367	1.015
Interorbital width	0.186	0.832	0.024	0.140	0.233	0.549
Scartella cristata						
Standard length	0.321	-0.194	0.028	0.265	0.376	0.960
Premaxillary to first dorsal spine	0.265	-0.101	0.036	0.194	0.336	0.816
First dorsal ray to anal spine	0.397	0.202	0.032	0.335	0.460	**1.195**
Pelvic insertion to premaxillary	0.297	0.309	0.024	0.250	0.344	0.897
First dorsal spine to pelvic insertion	0.342	-0.096	0.014	0.314	0.369	1.023
First dorsal spine to anal spine	0.446	-0.066	0.029	0.388	0.503	**1.371**
Upper to lower primary caudal ray	0.377	-0.611	0.060	0.260	0.495	1.090
Upper jaw length	0.264	0.635	0.059	0.148	0.379	0.779
Interorbital width	0.232	0.160	0.033	0.167	0.297	0.678

Table 3.5. Common Principal Component (CPC1 and CPC2) eigenvector loadings and multivariate allometric coefficients (MAC's) representing the growth gradient for five species of blenny from the northern Gulf of Mexico (N= 114 specimens). MAC's were scaled to a value of one for isometry. Means and standard errors estimated by jackknife procedures. Highest MAC's are in bold.

Body truss measurement	**CPC1 eigen-vector**	**Standard error (CPC1)**	**Confidence intervals (95%)**		**MAC's**
			Lower	**Upper**	
Premaxillary to first dorsal spine	0.329	0.005	0.319	0.339	0.988
First dorsal ray to anal spine	0.388	0.007	0.375	0.401	**1.165**
Pelvic insertion to premaxillary	0.293	0.010	0.274	0.313	0.880
First dorsal spine to pelvic fin insertion	0.366	0.005	0.357	0.375	**1.098**
First dorsal spine to anal spine	0.459	0.006	0.448	0.470	**1.378**
Upper to lower primary caudal ray	0.204	0.007	0.190	0.218	0.613
Upper jaw length	0.193	0.008	0.177	0.208	0.578
Interorbital width	0.135	0.013	0.110	0.160	0.405

measurements involved *P. marmoreus* with nearly isometric upper jaw growth, and *H. ionthas*, with faster allometric growth in the posterior part of the caudal peduncle than displayed by the other species (Table 3.4). The second PC and CPC largely accounted for differences in shape among taxa. Burnaby-adjusted loadings for the species-pooled CPC body truss data set resulted in a new CPC1 that summarized 65% of the variability in size between species. Consequently, common patterns of shape change were revealed. The changing shape of the interorbital region and the lower part of the head in these blennies in preparation for settlement were the largest modifications made to any body dimension (Fig. 3.2a). The greater ordinal distances in overall shape scores for *H. invemar* and *H. ionthas*, and the overlap in scores for *H. multifilis* and *P. marmoreus* suggest that shape has little relationship to phylogenetic distance (Fig. 3.2b).

Shape scores provided nearly complete separation of larvae from metamorphs in the species-pooled data set, at an O_L of 81 (Fig. 3.3a). When analyzed by species, size-free shape scores separated larvae from metamorphs at a mean O_L of 81.5 in *H. invemar*, 80.0 in *H. ionthas*, 84.1 in *H. multifilis*, 80.6 in *P. marmoreus*, and 80.1 in *S. cristata*. When plotted by species, convergence of shape scores at O_L values between 86 and 89 suggested that the common body shape was achieved by the remodeling of form during metamorphosis (Fig. 3.3b). The breakpoint for *H. multifilis* was higher (O_L = 84.1) than in the other species and may reflect the small number of larvae (5 total) available for measurement and the lack of specimens between 9.0 mm and 11.0 mm (O_L = 75.0 and 82.5).

Separate analysis of the fin and cirrus data set provided findings consistent with that for the body truss measurements. The high percentage of within group variability accounted for by the PC1 and CPC1 eigenvectors (Table 3.3), combined with the relatively low standard error for CPC1 (Table 3.6) suggested reasonable eigenvector stability. The common pattern of fin and

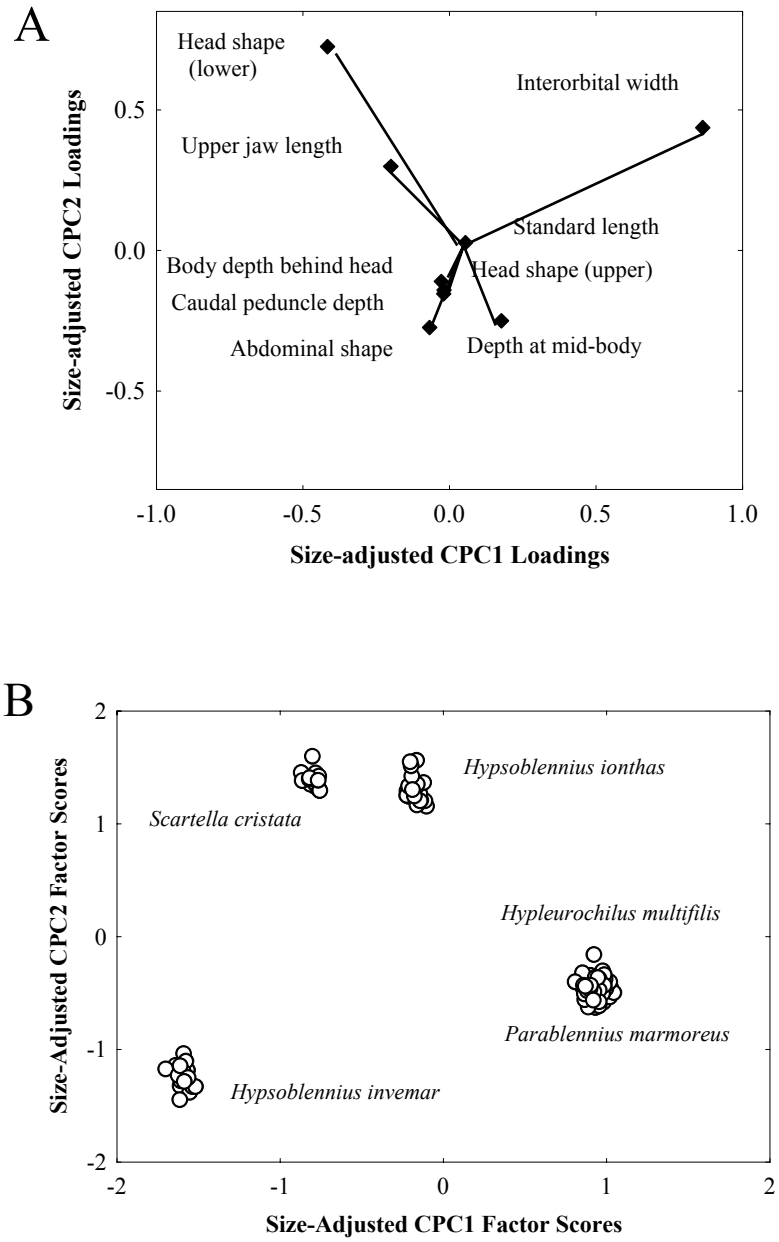

Figure 3.2. Common Principal Component loadings and factor scores for eight body truss measurements for the species-pooled data set of blennies from the northern Gulf of Mexico (N= 114 specimens; 5 species). A. Burnaby-adjusted size-free shape loadings; B. Burnaby-adjusted size-free shape scores.

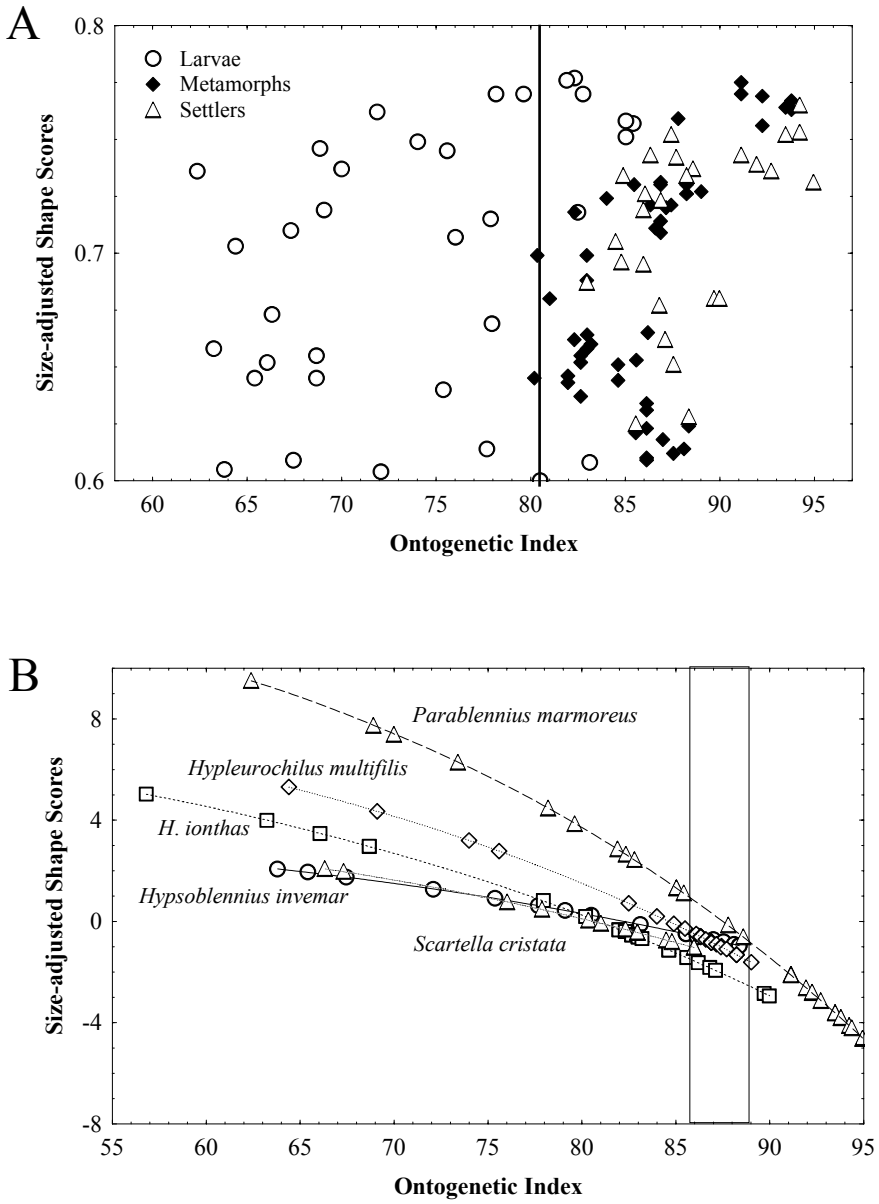

Figure 3.3. Size-free shape factor scores for five species of blenny from the northern Gulf of Mexico. Principal Component Analysis (PCA) was performed on each species separately; factor scores were a composite of eight body truss measurements. A. Burnaby-adjusted size-free shape scores by interval of development. Line denotes O_L at which change in shape occurs; B. Burnaby-adjusted size-free shape scores by species. Rectangle indicates area along index axis where shapes converge.

Table 3.6. First Common Principal Component (CPC1) eigenvector loadings for seven linear fin and cirrus measurements. Data are for five species of blenny from the northern Gulf of Mexico (N= 114 specimens). Multivariate allometric coefficients (MAC's) were scaled to a value of one for isometry. Highest MAC's are in bold.

Character measured	CPC1 eigenvector				CPC1
	Vector	Standard error	Confidence interval		MAC's
			Lower	Upper	
Orbital cirrus	0.252	0.014	0.224	0.280	0.755
Nasal cirrus	0.115	0.011	0.093	0.136	0.344
First dorsal spine	0.442	0.008	0.426	0.458	**1.326**
Last dorsal spine	0.364	0.009	0.345	0.382	1.091
Last dorsal ray	0.316	0.015	0.286	0.346	0.948
Pectoral fin	0.478	0.011	0.456	0.499	**1.433**
Pelvic fin	0.518	0.015	0.489	0.546	**1.553**

cirrus change indicated that traits associated with locomotion (i.e., fins) generally displayed strong positive allometry, whereas orbital and nasal cirri showed negative allometry, probably due to the late development of the cirri (Table 3.6; Fig. 3.4a). Differences in the shape of fins and cirri generally separated larvae from metamorphs, but not metamorphs from recent settlers (Fig. 3.4b). Rates of change in fin and cirrus measurements were both species-specific and trait-specific (Table 3.7). *Scartella cristata* had strong allometric growth for the pectoral fins but displayed weak allometry for the pelvic fins. Pectoral fin allometry was nearly isometric in *H. invemar*, as was the allometry for the last dorsal spine and last dorsal ray in *H. ionthas* (Table 3.7).

Discussion

Potential biases of the data sets analyzed here - uneven distribution of specimens among developmental intervals and species, and relatively small sample sizes were minor. Log-transforming data can generate a nearly normal distribution, eliminate the effect of scale on variances (La Barbera, 1989), and decouple means from variances, ensuring independence of data sets (Underwood, 1997). Further, the multivariate techniques employed have few formal assumptions (James and McCulloch, 1990; Marcus, 1990; Reyment, 1990). Studies with relatively small sample sizes have a higher probability of producing unstable patterns and require estimation of pattern stability by resampling methods (Marcus, 1990). Although the criterion for determining the adequacy of sample size is often arbitrary, Williams and Titus (1988) recommend that the number of observations in PCA exceed variables by about a factor of three. All species met that criterion, except *S. cristata* (N= 14), which suggests that sample sizes were reasonable.

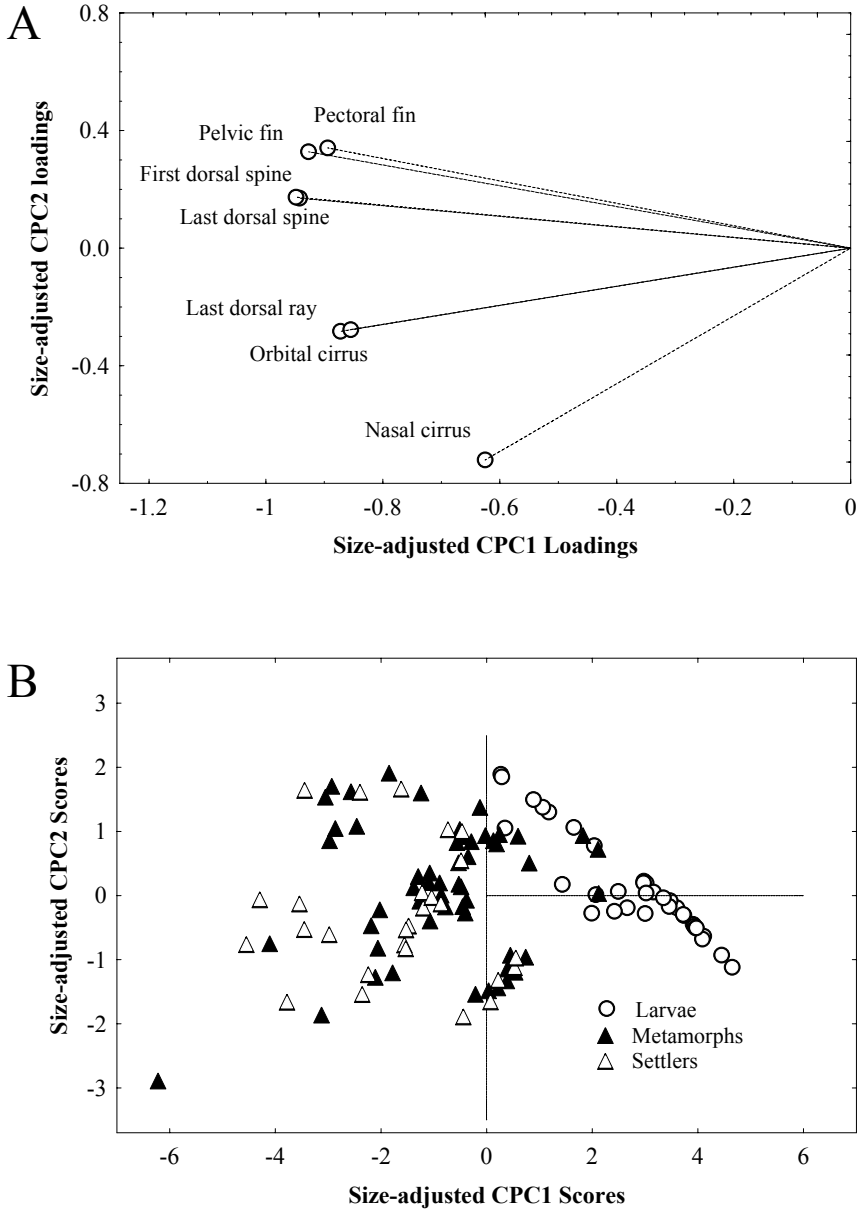

Figure 3.4. Common Principal Component (CPC) shape loadings and scores for five species of blenny from the northern Gulf of Mexico. Data are for the species-pooled fin and cirrus data set (N= 7 linear measurements; 5 species; 114 specimens). A. Burnaby-adjusted CPC size-free loadings; B. Burnaby-adjusted CPC size-free scores by interval of development.

Table 3.7. First Principal Component (PC1) eigenvectors for fin and cirrus measurements. Data are for five species of blenny from the northern Gulf of Mexico. Multivariate allometric coefficients (MAC's) were scaled to a value of one for isometry. Highest MAC's are in bold.

Character measurement	***Hypsoblennius invemar***		***Hypsoblennius ionthas***		***Hypleurochilus multifilis***		***Parablennius marmoreus***		***Scartella cristata***	
	PC1	**MAC**	**PC1**	**MAC**	**PC1**	**MAC**	**PC1**	**MAC**	**PC1**	**MAC**
Orbital cirrus	0.219	0.580	0.244	0.645	0.209	0.554	0.323	0.854	0.242	0.639
Nasal cirrus	0.141	0.373	0.089	0.236	0.105	0.279	0.071	0.188	0.149	0.394
First dorsal spine	0.548	**1.450**	0.430	**1.136**	0.416	1.100	0.457	**1.209**	0.434	**1.149**
Last dorsal spine	0.264	0.699	0.372	0.985	0.337	0.891	0.383	1.015	0.274	0.724
Last dorsal ray	0.298	0.790	0.376	0.996	0.253	0.669	0.287	0.761	0.327	0.865
Pectoral fin	0.372	0.984	0.446	**1.181**	0.522	**1.380**	0.401	1.061	0.558	**1.475**
Pelvic fin	0.579	**1.531**	0.518	**1.371**	0.568	**1.503**	0.540	**1.428**	0.488	**1.291**

Stability of eigenvectors, as evidenced by the concordance between the standard errors of the original and bootstrapped loadings is also consistent with adequate sample sizes, as was found in an earlier study (Fuiman, 1985). While resampling procedures is no remedy for inadequate sample sizes, resampling offers a reasonable alternative for estimation of population parameters (Reyment, 1990; Klingenberg and Froese, 1991) and generally addresses departures from distribution and homogeneity assumptions (Marcus, 1990). Although a small sample size can increase the amount of shared covariance structure accepted, and the size of standard errors in both PCA and CPCA (Marcus, 1990; Steppan, 1997), differential inflation of variability does not invalidate the CPC model when the principal eigenvectors among taxa are parallel (Flury, 1988).

Do Blennies Share a Common Growth Pattern?

Comparable amounts of variability explained by the PC1 and CPC1 eigenvectors (Table 3.3) and the directional similarity of principal axes are consistent with a common pattern of relative growth in the blennies studied. This shared pattern of relative growth involves a general deepening of the head and abdomen, a shortening of the upper jaw (except in *P. marmoreus*), a narrowing of the interorbital region, and an elongation of the pectoral and pelvic fins (Tables 3.4, 3.6, and 3.7). Comparing the findings of this study with others that have employed conventional PCA to simultaneously examine patterns of relative growth in multiple groups requires caution because few studies have verified underlying PCA assumptions with the CPCA model (Klingenberg and Zimmermann, 1992; Steppan, 1997). Further, the assumption of a common covariance matrix among taxa becomes problematic when examining growth patterns over a wide size range of individuals that may also include distinct growth stanzas (Klingenberg and Froese, 1991).

Not all groups or closely related species share a common pattern of growth (Marcus, 1990; Klingenberg and Froese, 1991) because differential growth of body parts can produce morphological differences that are species-specific (Strauss and Fuiman, 1985; Klingenberg and Zimmermann, 1992). The fact that differences in shape show little relationship to phylogenetic distance (Fig. 3.2b) was not surprising given that shape differences, independent of size, are often maintained by adaptive differences in feeding and environmental conditions (Huxley, 1932; Cheverud, 1982; Meyer, 1990). Therefore, growth pattern more closely reflect ecological demands than phylogeny (Kotrschal et al., 1990; Kendall, 1991; Klingenberg and Zimmermann, 1992).

Are Differences in Shape Interval-Specific?

Although these blennies share a common growth pattern, the cumulative effect of differential rates of growth of individual body parts over time produces changes in shape that can be interval-specific and species-specific. These differences in shape permit separation of larvae from metamorphs, but not metamorphs from recent settlers (Fig. 3.3a). The fact that blennies begin to exhibit distinct sexual dimorphism shortly after settlement and at a relatively small size may partly explain this failure to separate metamorphs from recent settlers based on shape alone.

Shape differences produced by sexual dimorphism complicate assessment of growth patterns in fishes (Brooks, 1991; Hastings, 1991). Although sexual dimorphism may not be visually evident until after settlement, failure to eliminate subtle sex-specific differences in growth before analyses can invalidate PCA (Brooks, 1991; Hastings, 1991; Fairbairn, 1997; Crowley, 2000). Hidden sexual dimorphism, though, probably does not account for the ontogenetically later breakpoint (O_L = 84.1) for *H. multifilis*. Inclusion of larvae of another species of *Hypleurochilus* in the data set, or a slower rate of morphological development in

H. multifilis than in the other species examined could provide a similar result. Although not reported from the north-central Gulf of Mexico, *H. caudovittatus* occurs in the northeastern Gulf, where its distribution overlaps with that of *H. multifilis* (Bath, 1994). The young of *H. caudovittatus* are undescribed, but their possible presence in collections could potentially contribute to the higher within-interval variability of *H. multifilis*.

Shifts in patterns of relative growth in these blennies and over discrete size ranges in the windowpane flounder, *Scophthalmus aquosus*, suggest that the timing of shape change may be useful for assigning young to specific intervals of development (Neuman and Able, 2002). Changes in shape often become obvious at profound discontinuities, like metamorphosis (Emerson and Bramble, 1993) or the onset of the juvenile period (Copp and Kovac, 1996; Vilizzi and Walker, 1999), and coincide with shifts in behavior, such as the initiation of schooling in some clupeids (Noakes and Godin, 1988) and carangids (Masuda and Tsukamoto, 1999). Such correspondence between the timing of allometric change and changes in behavior may serve to better predict the timing of important ecological changes in fishes.

Shape characters linked to meaningful ecological and physiological differences make the most useful group discriminators (Bookstein, 1996). Eco-morphological convergence (i.e., ecological similarities often dictate convergent morphologies; Fuiman, 1984) and failing to account for important axes of shape variability can create difficulty in detecting shape differences among species or intervals of development. In fact, several of the variables responsible for discriminating shape in blennies correspond to verticals or diagonals of the truss network, which implies that traditional horizontal measurements along the body axis may be inadequate descriptors of shape change. Unlike organisms with distinct intervals of development such as most arthropods, characterization of allometric growth patterns in organisms with

continuous growth, such as blennies and other fishes, can depend on the methods used to isolate shape. A multivariate approach is best for isolating shape change because multivariate techniques use a composite measure of general body size that reflects the average value of traits for each individual (Strauss, 1993). A general size measure averages out the random variation inherent in individual traits, thereby reducing statistical noise and providing a more comprehensive description of the amount and direction of shape change (Cavalcanti et al., 1993; Strauss, 1993; Cavalcanti et al., 1999).

Do Body and Fin Growth Patterns Reflect the Timing of Ecological and Habitat Changes?

This study is consistent with other studies of relative growth in fishes that support the hypothesis that the timing and priority of morphological changes are related to functional demands (Fuiman, 1983; Osse, 1990; Osse and van der Boogaart, 1995; Osse et al., 1997; Gisbert, 1999). The growth pattern in blennies outlined above - a general deepening of the head and abdomen, rapid elongation of structures associated with swimming and sensory abilities, and a gradual shift in eye position during metamorphosis - is a common developmental pattern in demersal and other species (Fuiman, 1983). A reduction in interorbital width during metamorphosis shifts the field of vision from lateral to dorsal-lateral and permits scrutiny of predators and prey that approach from above (Gatz, 1979; Ninos, 1984; Labelle and Nursall, 1985). Similarly, the state of fin development can influence swimming, schooling, predator avoidance, and prey capture (Blaxter, 1986; Masuda and Tsukamoto, 1996; Salgado and Hoyt, 1996). Rapid elongation of fins prior to settlement provides the added surface area for increased thrust and maneuverability required by transient, ambush swimmers, such as blennies, and other fishes that reside in structurally complex habitats (Gatz, 1979; Felley, 1984; Peters, 1985; Ferry, 1989; Sabates, 1994). The rapid development of cephalic cirri in late metamorphs suggests that

sensory development may be vital to survival after settlement (McCormick, 1993; Fuiman, 1997; Higgs and Fuiman, 1998; Gisbert, 1999).

Changes in body shape experienced by blennies (Fig. 3.3b) and other diverse groups of fishes (Tsukamoto and Okiyama, 1997; McCormick, 1999) during metamorphosis can lead to the common shape and basic adult body form (Penaz, 1983) at settlement. Because mouth gape is approximately twice upper jaw length (Shirota, 1970), the nearly isometric increase between jaw length and SL found in this study would maintain the range of prey options available to organisms, such as *P. marmoreus*, that inhabit less productive offshore waters (Liem, 1993; Vilizzi and Walker, 1999). Changes in feeding morphology during development may help explain the reduced growth rate that accompanies metamorphosis (Vladimirov, 1975; Harmelin-Vivien, 1989; Thorisson, 1994; McCormick, 1999), although changes in jaw and head shape may not always modify diet and feeding habits (Goldschmid and Kotrschal, 1985; Lindquist and Dillaman, 1986; Kotrschal and Thomson, 1989). In fact, blennies and many other fishes have alternate strategies or compensatory prey handling behaviors that permit continued use of similar prey (Motta, 1988; Liem, 1993; McCormick, 1998), such as, using their incisiform teeth to bite off pieces of larger prey, thereby effectively decoupling prey size from mouth size (Kotrschal and Thomson, 1989).

Do Patterns of Relative Growth Contribute to Our Understanding of Developmental Theory?

Differential growth of individual body parts in these blennies conveys a continuous rather than a saltatory progression to ontogeny because changes in shape occur at different times in different parts of the body (Tables 3.4 and 3.7). While differences in shape separate larvae from metamorphs, patterns of relative growth are not consistent with the idea that the timing of shape change can assist in identifying the smaller thresholds that separate ‘steps’. Further, recognizing

shape change can depend on the strength of the environmental effects. If patterns of relative growth are to reveal major thresholds of development, the timing of shape change should co-occur with other changes, such as those in behavior and physiology (Kovac et al., 1999; Simonovic et al., 1999).

The timing, number, and magnitude of ontogenetic events that constitute changes in shape determine the strength of a developmental threshold (Kovac et al., 1999). Changes in shape that occur within a narrow range of O_L values could be interpreted as differential growth rates aligning at a 'threshold' before initiating the next phase of development, as suggested by saltatory theory. These same changes could also reflect the shifting priorities of development because allometric coefficients change progressively along the body in blennies (Table 3.4) and many other fishes (Fuiman, 1983; Strauss, 1993; van Snik et al., 1997).

Comparison of the timing and progression of shape change in blennies with studies used to support saltatory theory is difficult because of different techniques, objectives, and degrees of detail used to assemble and support conclusions, and lack of scaling along the axis of development. Since growth dynamics can be influenced by environmental conditions and are a function of body size (Atchley, 1984; Fuiman and Webb, 1988), differences in size among species at similar developmental milestones can influence morphological comparisons. Without proper scaling, interspecific comparisons of the timing of shape change are impossible or virtually meaningless (Dettlaff and Dettlaff, 1961; Smith-Gill and Berven, 1979; Reiss, 1989; Poling and Fuiman, 1999).

In conclusion, saltatory theory construes ontogeny as a sequence of small, distinguishable steps separated by natural boundaries (thresholds) applicable to all fishes, whether marine or freshwater. Changes in relative shape in different parts of the body as observed here are

inconsistent with the small, distinguishable, incremental steps proposed by saltatory ontogeny over the size range and in the species examined.

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CHAPTER 4: ONTOGENY AND INTERVALS OF DEVELOPMENT IN BLENNIES: A SUMMARY

Summary

Revealing the traits and critical factors that influence the timing of metamorphosis and settlement in fishes requires scrutinizing developmental processes. I examined patterns of development in five species of blennies from the northern Gulf of Mexico and characterized the timing of ontogeny and shape change to determine whether settlement occurs at a common state of ontogeny rather than at a common size. This is the first study to simultaneously evaluate ontogeny in a suite of reef-associated fishes relative to the timing of metamorphosis and settlement; to apply scaling techniques and statistical methods to quantify, differentiate, and select criteria that delimit intervals of development; and to objectively test saltatory theory.

Are There Discrete, Recognizable Intervals of Development in Blennies, and Is There a Common Suite of Interspecific Characters that Identify Them?

Three 'natural' intervals of development were consistently identified in the blennies studied (Figs. 2.7-2.8) based on scoring and summing character states. Larvae had total character state scores ≤13 and an O_L <80; metamorphs had total character state scores from 15 to 25 and an O_L from 80 to 90; and settlers had total character state scores >25 and an O_L >85 (Table 2.6). Scoring individual characters and summing character states provides a standard methodology by which to characterize an individual's ontogenetic state.

Common sets of ontogenetic traits discriminated intervals of development in blennies. Settlers (Discriminant Function Analysis – DFA, canonical root 1) had higher dorsal/anal ray and orbital cirrus scores than metamorphs, and metamorphs (canonical root 2) had higher trunk pigmentation, dorsal/anal ray, orbital cirrus, and tooth scores than blenny larvae (Table 2.9). On the other hand, characters such as the length and timing of resorption of preopercular spines, presence or absence of pectoral fin pigment, and timing of cirrus development must be identified and eliminated from the traits that delineate intervals because of their species-specific nature.

Stability in the timing of ontogeny (Alberch, 1985) makes ontogenetic characters ideal for defining natural intervals of development in blennies and other fishes.

Assigning discrete character state scores to ontogenetic events, when combined with a dimensionless index such as Fuiman's (1994), quantify the timing of ontogeny, identify the events that delimit intervals of development, and permit interspecific comparisons. Establishment of a standardized and objective methodology to characterize intervals of development in the early life of fishes will require a staging system that clearly delimits each interval and considers the diversity in developmental patterns (Kendall et al., 1984; Noakes and Godin, 1988). Extensive examination of internal structures to determine the state of ontogeny, such as was conducted by Balon and others (Balon, 1985; Cunningham and Balon, 1985; Paine and Balon, 1986; Crawford and Balon, 1994) may be unnecessary. Actually, external characters provide information equally as good as internal traits for assessing the timing of ontogeny, at least until all traits characteristic of the larval period are lost. Evaluation of external characters is also less time consuming and labor-intensive. Multiple ontogenetic characters should be employed when characterizing intervals of development and will provide better resolution than individual traits.

The diversity of ontogenetic characters makes selection of a universal suite of traits to develop a standardized staging system in teleosts difficult. The fact that some fishes lack the larval period and go directly to the juvenile, or lack a juvenile period and become sexually mature as larvae (Noakes and Godin, 1988) creates additional problems. I encourage the use of fin ontogeny as a primary source of characters to make interspecific comparisons because all teleosts have fins. Dentition offers another reliable source of characters because most, but not all, teleosts have teeth. Both sets of traits also have obvious growth and survival implications.

While the diversity of teleosts and their life history patterns may prohibit development of a standardized staging system across higher levels of phylogeny, standardization at the family level should be possible.

Does Settlement Occur at a Common State of Ontogeny?

Although size at settlement is species-specific (Table 2.11), study findings and published results (Watson, 1983; Leis, 1987) provide several lines of evidence that settlement takes place at a common state of ontogeny across taxa. In blennies, this evidence includes settlement: 1) over a narrow range of total character state scores; 2) at a comparable state of structural development; and, 3) within a narrow range of O_L (Table 2.4-2.6). In fact, the ontogenetic index is more than an order of magnitude more precise than SL for predicting the timing of settlement in interspecific comparisons, which validates the index (Table 2.12) and permits examination of important early life questions on a common scale (Fuiman et al., 1998). Fuiman (1997) proposed that settlement may occur at a common state of ontogeny because of the possibly unique requirements of a benthic existence. Since ontogeny proceeds on a physiological rather than chronological time scale (Alberch et al., 1979), the fact that some minimum state of ontogeny is required for settlement is not surprising.

The finding that estuarine blennies settle at a common ontogenetic state, but smaller size than shelf species, suggests that natural selection may emphasize rapid ontogeny in species or in areas where competition for available habitat or resources may be high. Rapid ontogeny and settlement at a smaller body size may reduce the length of exposure to constantly fluctuating environmental conditions in the estuary, and partially offset the higher metabolic demands of organisms that occupy warmer estuarine surface waters (Moser, 1981; Beck and Congdon, 1999).

When Does the Juvenile Period Begin and End in Blennies?

Settlement is a behavioral and ecological transition and not an ontogenetic transition (Fuiman, 2002). Whether settlement defines the start of the juvenile period in fishes has been the subject of much speculation because the degree of change at settlement can range from minor pigment changes to extensive morphological remodeling (Leis, 1991). The transition to juvenile morphology does not coincide with patterns of ontogeny and settlement in these blennies, or in a number of other fishes, such as some sciaenids (Poling and Fuiman, 1999), hexagrammids (Matsumoto and Tanaka, 1996), and the dartfish, *Ptereleotris evides* (McCormick and Makey, 1997).

Metamorphosis is, by definition, the end of remodeling and terminates the larval period. Yet, metamorphosis is not complete at settlement in these blennies, per Balon's (1985) definition of a juvenile, because some species have not lost all pectoral fin pigment and others have not completely resorbed the longest preopercular spine. Actually, morphological remodeling may be incomplete until patterns of relative growth stabilize, all characteristics of a larva disappear, fin rays bifurcate, and squamation concludes (Copp and Kovac, 1996; Fuiman and Higgs, 1997; Gozlan et al., 1999). Thus, determining when the juvenile period begins should rely on a suite of morphological, physiological, ecological, or behavioral changes.

Do Blennies Share a Common Growth Pattern?

Blennies share a common pattern of growth that includes a general deepening of the head and abdomen, a shortening of the upper jaw (except in *P. marmoreus*), a narrowing of the interorbital region, and the elongation of the pectoral and pelvic fins during metamorphosis (Tables 3.4, 3.6, and 3.7). These changes produce the common shape and basic adult body form at settlement in blennies (Fig. 3.3b). Not all groups or closely related species of fishes, however,

share a common pattern of growth (Marcus, 1990; Klingenberg and Froese, 1991) because differential growth of body parts can also produce morphological differences that are species-specific (Strauss and Fuiman, 1985; Klingenberg and Zimmermann, 1992).

Although blennies share a common growth pattern, differences in shape show little relationship to phylogenetic distance (Fig. 3.2b) because shape differences, independent of size, are often maintained by adaptive differences in feeding and environmental conditions (Huxley, 1932; Cheverud, 1982; Meyer, 1990). Growth patterns, therefore, more closely reflect ecological demands than phylogeny (Kotrschal et al., 1990; Kendall, 1991; Klingenberg and Zimmermann, 1992).

Are Differences in Shape Interval-Specific?

The cumulative effect of differential rates of growth of individual body parts over time produces changes in shape that can be interval-specific. In blennies, shape differences permit separation of larvae from metamorphs, but not metamorphs from recent settlers (Fig. 3.3a). Changes in shape often become obvious at profound discontinuities, like metamorphosis (Emerson and Bramble, 1993), and can be useful for assigning young to specific intervals of development (Neuman and Able, 2002).

Changes in environmental conditions during growth (e.g., water temperature and salinity) can alter shape (Bookstein, 1996). Consequently, quantification of shape change in organisms that grow continuously (e.g., fishes) can depend on the methods used to isolate shape. Failure to account for important axes of shape variability can create difficulty in detecting shape differences among species or intervals of development. In fact, several of the variables responsible for shape discrimination in blennies correspond to verticals or diagonals of the truss network, which implies that traditional horizontal measurements along the body axis may be

inadequate descriptors of shape change. A multivariate approach is best for isolation of shape change because multivariate techniques use a composite measure of general body size that reflects the average value of traits for each individual (Strauss, 1993). Reducing the random variability of individual traits also provides a more comprehensive description of the amount and direction of shape change (Cavalcanti et al., 1993; Strauss, 1993; Cavalcanti et al., 1999). Shape characters linked to meaningful ecological and physiological differences make the most useful discriminators (Bookstein, 1996).

Do Body and Fin Growth Patterns Reflect the Timing of Ecological and Habitat Changes?

Study findings are consistent with the hypothesis that the timing and priority of morphological changes are linked to functional demands and ecological requirements (Fuiman, 1983; Osse, 1990; Osse and van der Boogaart, 1995; Gisbert, 1999). A general deepening of the head and abdomen, rapid elongation of structures associated with swimming and sensory abilities, and a gradual shift in eye position during metamorphosis is a common developmental pattern in blennies and other demersal species (Fuiman, 1983). A reduction in interorbital width shifts the field of vision from lateral to dorsal-lateral and permits scrutiny of predators and prey that approach from above (Gatz, 1979; Ninos, 1984; Labelle and Nursall, 1985). State of fin development can influence swimming, schooling, predator avoidance, and prey capture (Blaxter, 1986; Masuda and Tsukamoto, 1996; Salgado and Hoyt, 1996). Elongation of fins provides the added surface area for increased thrust and maneuverability required by transient, ambush swimmers, such as blennies. The rapid development in blennies of cephalic cirri just before settlement suggests that sensory development may be vital to survival after settlement (McCormick, 1993; Higgs and Fuiman, 1998; Gisbert, 1999).

Does the Timing of Ontogeny and Shifts in Patterns of Relative Growth Contribute to Our Understanding of Developmental Theory?

Study findings are consistent with ontogeny progressing in a gradual and continuous manner rather than in a saltatory fashion. If saltatory ontogeny were the pattern of development in blennies, plots of individual character state scores should converge at small incremental steps within the larval period (as defined by saltatory theory the larval period terminates at settlement), which they do not. Similarly, differential growth rates of body parts follow a gradual rather than a saltatory progression because allometric coefficients in blennies and other fishes often change at different times in different parts of the body (Strauss, 1995; van Snik et al., 1997).

Subjectivity in identifying developmental thresholds increases with organism complexity and individual variability so that the distinction between a change of structure and a change of function are not always clear (Cunningham and Balon, 1985). Such ambiguity implies that only a certain combination of leaps from quantity to new quality will form a valid threshold, but the number is difficult to determine. The suggestion that thresholds can occur at different times and/or states of development in different species (Balon, 1981) further complicates this issue. Accordingly, recognizing thresholds between proposed steps remains a major obstacle in the acceptance and application of saltatory theory.

The imprecise descriptive terms (e.g., 'most,' 'some,' 'may,' and 'frequently;' Balon, 1981) used to describe saltatory theory, combined with the difficulty of recognizing the thresholds between proposed steps, makes stepwise ontogeny difficult to justify and validate. Evolutionary processes promote diversity and adaptation as fundamental principles. With a virtually limitless variety of developmental patterns and life-history strategies (Kikkawa, 1977), the diversity of ecological habitats, and the fact that metamorphosis has evolved independently in

many lineages, a single ontogenetic theory may not adequately explain developmental processes for such a disparate group of organisms.

Management Implications and Further Research Needs

Blennies possess a life-history strategy that encourages their use as 'indicator species' for monitoring habitat quality. Blennies have demersal, attached eggs, which are continuously exposed to local environmental conditions; adults demonstrate high site fidelity (Stephens et al., 1970) and territoriality; and most species are widely distributed geographically and easily collected (Jacobsson et al., 1986). The use of blennies as indicator species could permit evaluation of habitat quality because ecological disturbances that disrupt physiological processes can affect both the direction and extent of morphological transformations, thereby altering relative growth rates and the timing of ontogeny (Strauss and Fuiman, 1985; Jacobsson et al., 1986; Morey and Reznick, 2000).

Differences in the timing and duration of developmental events among species have important implications for survival because fluctuating environmental conditions can affect development time, stage duration, sensory and morphological development, and an organism's ability to capture prey and avoid predators (Houde, 1987; Pepin, 1991; Frank and Leggett, 1994; Fuiman and Higgs, 1997). Transitions to new environments may be critical periods, since some evidence suggests that density-dependent mortality may be most intense at settlement in demersal fishes (Frank and Leggett, 1994; Schmitt and Holbrook, 1999; Searcy and Sponaugle, 2000). If mortality rates are stage-specific, critical periods of development, such as metamorphosis, may suffer the highest cumulative mortality (Pepin, 1991). Thus, characterization of the differences and constraints of various life-history patterns at the species or

population level may provide insight into the often-criticized stock/recruit relationship (Frank and Leggett, 1994).

Knowledge of developmental patterns could enhance aquaculture production because failure to adjust the feeding regime during critical periods of development often results in high mortality (Bryan and Madraisau, 1977; Winans and Nishioka, 1987; McFarlane et al., 2000). Examination of patterns of development may also discover differences in life-history strategies and habitat use patterns that can facilitate identification of essential fish habitat and important nursery areas for fishery species (Lindeman et al., 1998; Lindeman and Synder, 1999). The state of development at which potential recruits arrive at nursery areas may influence their ability to avoid predation (Keefe and Able, 1993; Higgs and Fuiman, 1998; Poling and Fuiman, 1998). If the number of late metamorphs adequately represents the number of recent settlers in examining abundance patterns (Schmitt and Holbrook, 1999), monitoring the supply of the more easily sampled metamorphs may allow prediction of year-class strength (Bradford, 1992). Although relationships between fisheries recruitment and stock size do not strengthen sufficiently to predict year-class strength until after settlement in demersal fishes (Bradford, 1992), accurate estimation of the number of potential recruits approaching settlement may increase predictive accuracy (Milicich et al., 1992; Thorrold, 1992; Meekan et al., 1993) over traditional ichthyoplankton surveys. Methodology described here could also be used to investigate ways to adjust the interpretation of shifts in otolith daily ring structure and improve information in that historical record.

In conclusion, the complex life cycle of many marine fishes consists of multiple intervals, each interconnected but with different requirements for growth and survival. Accordingly, a better understanding of the factors that influence the early life of fishes will require examination

of the timing of developmental processes and shifts in habitat use because biotic rates (e.g., growth, mortality) can be stage-specific (Richards and Lindeman, 1987; Kingsford, 1988; Bingham, 1992; Cowen and Sponaugle, 1997).

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APPENDIX. COLLECTION INFORMATION FOR RECENT SETTLERS OF THE FIVE PRIMARY SPECIES OF BLENNY STUDIED FROM THE NORTHERN GULF OF MEXICO. N/A MEANS INFORMATION NOT AVAILABLE.

Species	Site/Platform	Date Collected	Size (mm SL/TL)	Location
Hypsoblennius invemar	East Island Block (EI) EI245A	08/27/99	17.9/ N/A 18.3/ N/A	Water depth: 45.7 m Lat. 28°32'19", Long. 91°48'55"
	Matagorda Island, Texas (MI) MI670A	09/27/99	17.5/21.3	Water depth: 34.7 m Lat. 29°59'13", Long. 96°21'14"
	Vermilion Bay Block (VB) VB247A	05/01/00	11.8/14.4 12.0/15.0 12.5/15.1 12.8/15.8 13.0/15.4 13.0/15.7 13.0/16.0 13.0/16.8 13.5/16.4 13.5/16.4 13.5/16.5 13.7/16.5 14.5/17.5	Water depth: 41.1 m Lat. 28°31'13", Long. 92°21'22"
Hypsoblennius ionthas	Barataria Bay, Louisiana Oyster Reef	06/05/98	11.7/14.2 11.7/14.3 12.7/15.6	Water depth: 1 m Lat. 90°00'00", Long. 29°18'30" Boat turn basin at Grand Terre, Louisiana

(Appendix continued)

Species	Site/Platform	Date Collected	Size (mm SL/TL)	Location
Hypsoblennius ionthas	Barataria Bay, Louisiana Oyster Reef (cont'd)	06/05/98	12.8/15.5 13.7/16.9 16.5/20.3 17.0/20.5 17.5/NA	Water depth: 1 m Lat. 90°00'00", Long. 29°18'30" Boat turn basin at Grand Terre, Louisiana
Hypleurochilus multifilis	West Delta Block (WD) WD40	08/28/98	13.8/16.3 14.0/16.3 15.4/18.3 15.5/18.4	Water depth: 51.8 m; 24 km offshore Lat. 29°07'30", Long. 89°48'30"
	Grand Isle Block (GI) GI-9M	08/28/98	11.8/14.0 12.1/14.3 12.5/14.8 12.7/14.7 12.8/15.1 14.5/17.2 16.0/17.6 18.3/20.1	Water depth: 15.2 m; 14.8 km offshore Lat. 29°52'30", Long. 89°12'30"
Parablennius marmoreus	Vermilion Bay Block (VB) VB247A	05/01/00	19.0/22.5 19.5/22.8 20.0/23.5 20.5/23.9	Water depth: 41.1 m Lat. 28°31'13", Long. 92°21'22"

(Appendix continued)

Species	Site/Platform	Date Collected	Size (mm SL/TL)	Location
Parablennius marmoreus	Vermilion Bay Block (VB) VB247A	05/01/00	21.0/24.5 21.5/24.5	Water depth: 41.1 m Lat. 28°31'13", Long. 92°21'22"
Scartella cristata	West Delta Block (WD) WD40	08/28/98	18.0/21.4	Water depth: 51.8 m; 24 km offshore Lat. 29°07'30", Long. 89°48'30"
	Grand Isle Block (GI) GI-9M	08/28/98	16.8/ N/A	Water depth: 15.2 m; 14.8 km offshore Lat. 29°52'30", Long. 89°12'30"
	Galveston Island, Texas	08/20/99 08/30/99 10/11/99	13.5/15.1 13.3/15.2 15.6/18.3 (Live)	Water depth: 1 m Lat. 29° 16'31", Long. 94°48'54"
	Vermilion Bay Block (VB) VB247A	05/01/00	11.0/13.4 11.5/13.7 11.6/13.9 12.0/13.9 12.0/14.5 13.5/16.0 13.5/16.0 14.5/16.4 15.5/18.5	Water depth: 41.1 m Lat.28°31'13", Long. 92°21'22"

VITA

Jim Ditty was born in Wheeling, West Virginia, on January 15, 1955. He attended Brooke County public schools and Marshall University in Huntington, West Virginia, graduating with a Bachelor of Science degree in zoology in 1977. Ditty accepted a graduate research assistantship at Louisiana State University, Baton Rouge, in 1978, graduating with a Master of Science degree in fisheries in 1981. After working for the Louisiana Department of Wildlife and Fisheries in Baton Rouge for six years, he returned to Louisiana State University in 1987, and worked for the Coastal Fisheries Institute in the Center for Coastal, Energy, and Environmental Resources (CCEER) for 12 years. Ditty began working toward his doctoral degree in oceanography and coastal sciences in 1994 and accepted a Research Fishery Biologist position with the National Marine Fisheries Service (NMFS), Galveston Laboratory, in 1999. He manages the Taxonomy and Ecology Laboratory for the Fishery Ecology Branch of NMFS, Galveston, and resides in Houston, Texas. He will receive the degree of Doctor of Philosophy at the December 2002 Commencement.